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FIRE CHARACTERIZATION
AND FOREST RESPONSES TO
FIRE REGIMES ACROSS THE
GRAN CHACO AND PANTANAL
ECOREGIONS A MULTISCALE
APPROACH

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FIRE CHARACTERIZATION AND FOREST RESPONSES TO FIRE REGIMES ACROSS THE GRAN CHACO AND PANTANAL ECOREGIONS A MULTISCALE APPROACH

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DOCTORAL PROGRAMME IN AGRICULTURE AND ENVIRONMENT FOR DEVELOPMENT

LUGO



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This thesis represents my contribution to my country, Paraguay. After 20 years away, I decided to do my part in expanding the limited knowledge in the field of fire science. This has been a hard work, which began in October 2021, requiring immense effort, sacrifice, and countless hours of dedication.

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ABSTRACT

Fire is a natural disturbance agent in many terrestrial ecosystems, with both positive and negative feedback depending on human and climatic influences. Its presence is closely tied to land use and productive systems. Certain ecosystems, such as savannas, oak forests, and pine forests, depend on fire to maintain their stability. However, changes in fire occurrence—regarding location, extent, frequency, intensity, and severity—directly or indirectly driven by human activities can disrupt natural fire regimes. These alterations can result in severe ecological impacts, including biodiversity loss, shifts in structure, composition, and species trajectories, changing landscape patterns.

South America is a global fire hotspot, encompassing fire-prone landscapes such as the Gran Chaco and Pantanal. These regions are also biodiversity hotspots, hosting some of the last remnants of tropical dry forests. However, they face severe threats from land-use changes, deforestation, and increasingly, fire. Understanding fire dynamics in these regions is crucial to mitigating its ecological and socio-economic consequences. Historically, fire has been used in this area since pre-Columbian times for purposes such as pasture management, warfare, and intertribal communication. These practices balanced plant communities and promoted a diversity of native vegetation, including grasslands, savannas, forests, and shrublands. However, ongoing climate and land-use changes threaten the stability of natural fire regimes, endangering these ecosystems. This research aimed to evaluate the responses of forests impacted by fire in the Humid Chaco, focusing on patterns in species assemblages. It was structured around three general objectives: (i) to characterize the spatiotemporal distribution of fire at a regional scale and subsequently define fire regimes in the Paraguayan Chaco, (ii) to evaluate the structure and composition of forest formations along a fire regime gradient, and (iii) to assess response patterns using taxonomic and functional approaches in the Paraguayan Chaco.

To achieve these objectives, spatiotemporal analyses were conducted using remote sensing techniques at two spatial scales: regional (encompassing the Gran Chaco and Pantanal ecoregions) and local (focused on the Paraguayan Chaco). These analyses assessed fire distribution, extent, severity, and frequency. Predictive models (GLM, GAM, and Random Forest) identified key factors driving fire occurrence, while k-means clustering classified standardized fire regimes. A fire regime map guided the selection of field study plots, where stratified sampling evaluated forest structure, composition, and functional traits in response to the identified fire regimes.

The results revealed that 2020 recorded the largest burned area within the study period, with the Humid Chaco being the most affected ecoregion. Predictive models identified maximum temperature, tree cover, and livestock density as key drivers of fire occurrence. Fire regime modeling delineated four distinct fire regimes, each with well-defined characteristics.

At the vegetation level, fire significantly influenced functional traits (e.g., resprouting) and the functional diversity index (functional dispersion), offering insights into forest responses to fire.

However, no significant changes were detected in forest structure or composition, highlighting the resilience of these forests to fire impacts.

This study is the first to assess the impacts of fire regimes on mesoxerophytic forests in the Paraguayan Humid Chaco. The findings enhance understanding of the spatiotemporal distribution of fire and the resilience of mesoxerophytic forests in a region with limited prior research. Moreover, this work provides critical insights into fire regimes at both regional and local scales, elucidating forest ecosystem responses across a fire regime gradient within the complex Gran Chaco-Pantanal ecoregions.

Keywords: *Spatiotemporal analysis, predictive modelling, fire regimes, Gran Chaco, Pantanal, dry forest, climate change, land use changes, livestock density, Paraguayan Chaco vegetation responses, plant traits, functional diversity*

RESUMEN CASTELLANO

El fuego es un agente natural de disturbio en muchos ecosistemas terrestres, con impactos tanto positivos como negativos según las influencias humanas y climáticas. Su presencia está estrechamente ligada al uso del suelo y a los sistemas productivos. Ciertos ecosistemas, como las sabanas, los bosques de robles y los bosques de pinos, dependen del fuego para mantener su estabilidad. Sin embargo, los cambios en la ocurrencia del fuego—en cuanto a ubicación, extensión, frecuencia, intensidad y severidad—impulsados directa o indirectamente por actividades humanas pueden alterar los regímenes naturales de fuego. Estas modificaciones pueden provocar impactos ecológicos severos, incluyendo la pérdida de biodiversidad, cambios en la estructura, composición y trayectoria de las especies, así como modificaciones en los patrones del paisaje.

Sudamérica es un punto crítico de incendios a nivel global, con paisajes propensos al fuego como el Gran Chaco y el Pantanal. Estas regiones también son puntos críticos de biodiversidad, albergando algunos de los últimos remanentes de bosques secos tropicales. Sin embargo, enfrentan amenazas severas debido a los cambios en el uso del suelo, la deforestación y, cada vez más, los incendios. Comprender la dinámica del fuego en estas regiones es crucial para mitigar sus consecuencias ecológicas y socioeconómicas. Históricamente, el fuego ha sido utilizado en esta zona desde tiempos precolombinos para propósitos como el manejo de pastizales, la guerra y la comunicación intertribal. Estas prácticas equilibraban las comunidades vegetales y promovían una diversidad de vegetación nativa, incluyendo pastizales, sabanas, bosques y matorrales. Sin embargo, los cambios actuales en el clima y el uso del suelo amenazan la estabilidad de los regímenes naturales de fuego, poniendo en peligro estos ecosistemas.

Esta investigación tuvo como objetivo evaluar las respuestas de los bosques impactados por el fuego en el Chaco Húmedo, enfocándose en los patrones de ensamblaje de especies. Se estructuró en torno a tres objetivos generales: (i) caracterizar la distribución espacio-temporal del fuego a escala regional y definir los regímenes de fuego en el Chaco Paraguayo, (ii) evaluar la estructura y composición de las formaciones boscosas a lo largo de un gradiente de regímenes de fuego, y (iii) analizar los patrones de respuesta utilizando enfoques taxonómicos y funcionales en el Chaco Paraguayo.

Para lograr estos objetivos, se realizaron análisis espacio-temporales utilizando técnicas de teledetección en dos escalas espaciales: regional (abarcando las ecorregiones del Gran Chaco y el Pantanal) y local (centrada en el Chaco Paraguayo). Estos análisis evaluaron la distribución, extensión, severidad y frecuencia del fuego. Modelos predictivos (GLM, GAM y Random Forest) identificaron los factores clave que impulsan la ocurrencia de incendios, mientras que el clustering k-means clasificó los regímenes de fuego estandarizados. Se utilizó un mapa de regímenes de fuego para seleccionar parcelas de estudio en campo, donde se realizó un muestreo estratificado para evaluar la estructura forestal, la composición y los rasgos funcionales en respuesta a los regímenes de fuego identificados.

Los resultados revelaron que 2020 registró la mayor área quemada dentro del período de estudio, siendo el Chaco Húmedo la ecorregión más afectada. Los modelos predictivos

identificaron la temperatura máxima, la cobertura arbórea y la densidad ganadera como los principales factores que determinan la ocurrencia de incendios. La modelización del régimen de fuego delimitó cuatro regímenes distintos, cada uno con características bien definidas.

A nivel de vegetación, el fuego influyó significativamente en los rasgos funcionales (por ejemplo, la capacidad de rebrote) y en el índice de diversidad funcional (dispersión funcional), proporcionando información sobre las respuestas de los bosques al fuego. Sin embargo, no se detectaron cambios significativos en la estructura o composición del bosque, lo que resalta la resiliencia de estos bosques ante los impactos del fuego.

Este estudio es el primero en evaluar los impactos de los regímenes de fuego en los bosques mesoxerofíticos del Chaco Húmedo Paraguayo. Sus hallazgos mejoran la comprensión sobre la distribución espacio-temporal del fuego y la resiliencia de los bosques mesoxerofíticos en una región con poca investigación previa. Además, este trabajo proporciona información clave sobre los regímenes de fuego tanto a escala regional como local, esclareciendo las respuestas de los ecosistemas forestales a lo largo de un gradiente de regímenes de fuego dentro de las complejas ecorregiones del Gran Chaco-Pantanal.

Palabras clave: Análisis espacio-temporal, modelización predictiva, regímenes de fuego, Gran Chaco, Pantanal, bosque seco, cambio climático, cambios en el uso del suelo, densidad ganadera, respuestas de la vegetación del Chaco Paraguayo, rasgos de las plantas, diversidad funcional.

THESIS SUMMARY (GALICIAN)

ECOSISTEMAS E INCENDIOS

O lume é un axente natural de perturbación en moitos ecosistemas terrestres, con impactos tanto positivos como negativos dependendo das influencias humanas e climáticas. A súa presenza está moi vencellada o uso do solo e aos sistemas de produción tanto agrícola como forestal. Determinados ecosistemas, como as sabanas, piñeirais ou diversos tipos de bosques de caducifolias, amosan certo nivel de dependencia do lume para manter a súa estabilidade. Neste punto, as actividades humanas levan influíndo nos réximes de incendios ao longo de milenios, aumentando as fontes de ignición, a frecuencia dos lumes, as áreas queimadas e a duración das tempadas de incendios. Estes cambios na presenza do lume impulsados directa ou indirectamente polas actividades humanas -en termos de localización, extensión, frecuencia, intensidade ou severidade-, poden conlevar unha alteración nos réximes naturais dos incendios. Estas modificacións poden provocar graves impactos ecolóxicos, incluíndo perda de biodiversidade, cambios na estrutura e composición das especies, así como modificacións nos patróns paisaxísticos.

O comportamento do lume na paisaxe depende da interacción entre a topografía, as características dos combustibles e o clima, factores que ao mesmo tempo determinan a frecuencia, intensidade e distribución dos incendios nos distintos ecosistemas. Porén, o cambio climático está a alterar estas condicións ao reducir a humidade do combustible debido ás temperaturas máis altas e aos cambios estacionais. Estas dinámicas de combustibles representan outro factor clave a considerar na alteración do réxime de incendios. As secas aumentan a inflamabilidade dos bosques ao reducir a humidade e favorecer a acumulación de combustible. A continuidade da biomasa e os ciclos de humidade estacionais determinan a propagación do lume, mentres que a composición da comunidade vexetal e a estrutura do combustible definen os patróns e réximes de lume. Coñecer estes factores é fundamental para a avaliación ambiental, a planificación da restauración e a conservación.

Os incendios tamén teñen certo grao de influencia sobre o clima, por causa da liberación de grandes cantidades de gases de efecto invernadoiro (GEI), que contribúen entre o 19% e o 29% das emisións mundiais de combustibles fósiles. Nembargantes, as ferramentas de vixilancia poden subestimar estas emisións, afectando os compromisos climáticos internacionais. Ademais do cambio climático, o uso da terra e a xestión do combustible están a modificar os réximes de incendios, afectando a composición das especies, contribuíndo ás invasións ecolóxicas, aos ciclos do carbono e da auga, os hábitats da fauna e os diferentes servizos ecosistémicos. De maneira recíproca, estas alteracións aumentaron a magnitude e a severidade dos incendios, afectando aos ecosistemas e ao benestar humano.

Así mesmo, os ecosistemas responden de forma diferente ao lume, xa que algúns dependen del pola súa dinámica natural, mentres que outros poden verse moi afectados, aqueles onde o lume non xogou un papel clave no seu desenvolvemento. Seguindo estes criterios, os ecosistemas pódense clasificar en catro categorías: (i) dependentes do lume, (ii) sensibles ao lume, (iii) influenciados polo lume e (iv) independentes do lume. Os **ecosistemas dependentes do lume** (*fire-prone* ecosystems) requiren incendios para a súa conservación e diversidade, como as sabanas, certas pradeiras, os bosques secos e certos bosques de piñeiros e eucaliptos. Estes

sistemas evolucionaron cunha frecuencia de lumes (de baixa intensidade) elevada ou, tamén, con incendios intensos pero de menor frecuencia. Son sistemas que actualmente atoparíanse ameazados polo cambio climático ou polos cambios no uso do solo. Por outra banda, os **ecosistemas sensibles** son aqueles que non desenvolveron adaptacións para resistir o lume e poden sufrir danos graves mesmo por incendios de baixa intensidade. Atópanse en bosques tropicais e temperado húmidos, onde a fragmentación e a introdución de especies inflamables poden aumentar a súa vulnerabilidade. Os **ecosistemas influenciados polo lume** representan unha transición entre os ecosistemas dependentes e os ecosistemas sensibles, incluíndo, por exemplo, a vexetación de ribeira en sabanas e bosques, así como áreas onde o lume pode desempeñar un papel importante na creación de hábitats. A súa xestión é complexa debido á sutil interacción do lume na súa dinámica. Finalmente, os **ecosistemas independentes do lume** teñen baixa produción de biomasa e non favorecen a combustión, como os desertos e a tundra antártica. Esta clasificación permítenos comprender mellor as ameazas e oportunidades na xestión dos incendios nos diferentes ecosistemas.

A COMPRESIÓN DOS RÉXIMES DE INCENDIOS AO LONGO DO TEMPO

A nivel histórico, a análise do lume e a clasificación do réxime de incendios baseáronse nos datos recollidos no campo. Así e todo, os **recentes avances na teledetección** permitiron explorar e analizar patróns de lume a gran escala cunha precisión e eficiencia sen precedentes. A dispoñibilidade global de produtos satelitais mellorou a medición da actividade do lume en rexións remotas, de difícil acceso ou con condicións desfavorables, onde antes os datos eran escasos, facilitando o estudo da ecoloxía do lume a escala global. Estas tecnoloxías ofrecen vantaxes en **precisión, repetibilidade, velocidade, acceso a datos históricos e integración con outras variables** temáticas. A mellora da resolución espacial e temporal dos satélites permitiu describir con maior detalle a actividade recente do lume, utilizando observacións por satélite de incendios activos ou imaxes anteriores e posteriores ao lume, en combinación con verificacións de campo. Así mesmo, a detección diaria de incendios proporcionou información clave sobre a estacionalidade dos incendios e a relación entre a duración da tempada de incendios e a superficie queimada. Investigacións recentes utilizaron datos MODIS e GFED para clasificar as características globais do lume en función do tamaño, frecuencia, intensidade, estacionalidade e extensión espacial. Ademais, o uso de datos sobre puntos quentes permitiu vincular os patróns de lume coa produtividade dos ecosistemas e a biodiversidade.

Os avances na teledetección facilitaron a integración dos datos de incendios coas variables climáticas, os cambios na cobertura terrestre e diferentes factores antropoxénicos, proporcionando unha mellor comprensión dos motores e retroalimentación dos réximes de incendios. Isto resultou especialmente útil para avaliar o impacto do cambio climático na dinámica dos incendios, xa que o aumento das temperaturas, as secas prolongadas e os cambios nos patróns de precipitación son responsables da frecuencia, a intensidade e a distribución espacial dos incendios. Determinados índices derivados de datos de satélite, como o índice meteorolóxico de incendios (FWI), utilizáronse para avaliar o risco de incendios e prever a actividade futura de incendios en escenarios climáticos cambiantes.

O uso da teledetección para estudar os réximes de incendios non se limita á caracterización dos patróns espaciais e temporais da actividade do lume, senón que ao mesmo tempo proporciona unha base fundamental para comprender a resposta dos ecosistemas a estas perturbacións. A

vexetación, como compoñente central dos ecosistemas, presenta respostas diversas ao lume, dende unha rápida recuperación en sistemas propensos ao lume (*fire-prone ecosystems*) ata unha degradación significativa en ambientes sensibles. Ao caracterizar a frecuencia, intensidade, extensión e severidade dos incendios, é posible predicir como evolucionará a estrutura, composición e funcionalidade da vexetación en diferentes escenarios de incendio. A integración de datos de satélites coa dinámica da vexetación permite avaliar a resistencia dos ecosistemas e a vulnerabilidade ao lume, proporcionando información clave sobre as traxectorias ecolóxicas actuais e futuras.

Porén, e a pesares das súas moitas vantaxes, **a teledetección tamén presenta limitacións** e sesgos na detección de incendios, especialmente no caso de pequenos incendios, como os agrícolas, ou aqueles de baixa intensidade que liberan pouca enerxía. Ademais, os rexistros satelitais cobren só as últimas décadas, a partir dos anos 80. Polo tanto, moitos estudos recomentan complementar os datos de teledetección con observacións de campo para mellorar a precisión das análises.

A **avaliación da composición florística forestal**, incluíndo familias, xéneros e especies, facilita a caracterización das comunidades vexetais e proporciona información crucial sobre a dinámica dos bosques naturais e as súas respostas a diferentes réximes de perturbación. Tradicionalmente, os estudos de composición florística centráronse nas especies arbóreas, polo seu valor representativo en termos de dominancia (biomasa, abundancia, cuberta), que define a estrutura e función do bosque. Porén, é importante considerar os posibles sesgos derivados de factores como o límite do diámetro mínimo á altura do peito (DAP), a área de mostraxe e a fiabilidade da identificación florística.

O estudo da **estratificación vertical** foi relevante pola gran diversidade de especies de diferentes tamaños e o considerable número de individuos nas capas media, alta e emerxente da copa. Aínda que este enfoque segue sendo habitual nos estudos ecolóxicos pola súa sinxeleza e utilidade, non está exento de certa crítica xa que non recolle a dinámica da copa, especialmente despois de perturbacións. A **estrutura horizontal**, entendida como a distribución espacial de diferentes poboacións e individuos, está influenciada por factores ambientais como a altitude, a latitude e, a menor escala, a topografía local e a dispoñibilidade de auga. Algúns estudos demostraron que a composición florística forestal varía segundo a idade de abandono e a frecuencia e intensidade das perturbacións, o que é fundamental para comprender os cambios da vexetación en resposta ao lume.

Nos ecosistemas propensos ao lume, o lume exerce unha importante presión selectiva sobre as especies vexetais, e **as comunidades adaptadas ao lume presentan unha variedade de adaptacións** que lles permiten resistir ou recuperarse despois do lume. Os trazos funcionais, como a capacidade de rebrote, son fundamentais para o crecemento, a reprodución e a supervivencia da vexetación, e a persistencia despois do lume depende da presenza destes trazos funcionais.

A **diversidade funcional**, que fai referencia aos compoñentes da biodiversidade que inflúen directamente no funcionamento dos ecosistemas, avalíase mediante índices que permiten comparar a variabilidade destes trazos dentro e entre especies. Isto facilita a comprensión dos procesos ecolóxicos dentro dun ecosistema, como a produtividade e a resistencia ás perturbacións. Para avaliar a diversidade funcional desenvolvéronse varios índices que permiten captar diferentes aspectos dos trazos funcionais dunha comunidade. Estes índices foron refinando ao longo do tempo para proporcionar unha comprensión máis completa da

diversidade funcional. Neste traballo de investigación recóllense catro dos principais índices de diversidade funcional: índice de riqueza (Fric); índice de equidade (Feve); índice de diverxencia (Fdiv) e índice de dispersión (Fdis). Cada un pondera de forma específica e diferente as respostas da vexetación con respecto a un gradiente ambiental, neste caso, o lume.

A RELEVANCIA GLOBAL DA NOSA ÁREA DE ESTUDIO

América do Sur é un foco global de incendios, con **paisaxes propensas aos incendios como o Gran Chaco e o Pantanal**. Estas rexións acollen **gran biodiversidade**, albergando algúns dos últimos restos de bosques secos tropicais a nivel continental. Porén, estes sistemas enfróntanse a graves ameazas derivadas dos cambios de uso do solo, a deforestación e, cada vez máis, os incendios. Comprender a dinámica do lume nestas rexións é fundamental para mitigar as súas consecuencias ecolóxicas e socioeconómicas.

O Gran Chaco é unha das ecorrexións máis grandes de América do Sur, e a súa historia de incendios está ligada á evolución das sabanas e a herbivoría. Históricamente, **o lume utilizouse nesta zona desde a época precolombina** con fins tan diversos como a xestión de pradeiras, a guerra e a comunicación intertribal. Tras a colonización europea, o uso do lume diminuíu pola sobreexplotación do gando, sen embargo, recentemente aumentou porque a actividade gandeira representa o principal motor económico da rexión. Neste sentido, a gandaría tamén alterou os réximes de lume e a cuberta do solo, favorecendo a expansión da vexetación propensa ao lume. O uso ineficiente dos lumes prescritos pon en risco a rexeneración natural de sabanas e bosques, e as actividades humanas seguen alterando estes réximes de incendios.

O Pantanal é a zona húmida tropical máis grande do mundo, situada nunha extensa chaira de inundación na conca alta do río Paraguai en América do Sur. Cunha superficie de 179.300 km², distribúese entre Brasil (78%), Bolivia (18%) e Paraguai (4%). Aproximadamente o 80% das súas chairas están somerxidas durante a época das chuvias, favorecendo unha rica biodiversidade acuática e anfibia. No ano 2000, a Área de Conservación do Pantanal, que representa o 1,3% do Pantanal brasileiro, foi designada como Patrimonio da Humanidade pola UNESCO, e no mesmo ano, 26,4 millóns de hectáreas foron designadas como Reserva da Biosfera. O Pantanal alberga polo menos 4.700 especies descritas e case dous millóns de persoas.

A nivel de degradación, o agronegocio é considerado como o principal impulsor da deforestación na rexión. Aquí cobra especial relevancia a gandaría, que representa a actividade económica dominante xunto coa expansión dos pastos para alimentar máis de 3,8 millóns de cabezas de gando e o cultivo de grans. Isto supón unha ameaza importante para a vexetación e a biodiversidade autóctonas. Os incendios, xeralmente provocados pola queima de biomasa, son unha parte esencial do ciclo de preparación dos solos e renovación de pastos, converténdose nunha grande ameaza ambiental nesta rexión. A pesares de que o lume ten sido usado dende épocas ancestrais, estas prácticas equilibraron as comunidades vexetais e promoveron gran diversidade de sistemas e de vexetación autóctona, incluíndo pradeiras, sabanas, matogueiras ou diferentes tipos de bosques. Así e todo, **os cambios actuais no clima e no uso do solo ameazan a estabilidade dos réximes naturais de incendios**, poñendo en risco moitos destes ecosistemas.

Dada a complexidade inherente das interaccións espaciais e temporais do lume, especialmente nos ecosistemas onde os réximes de lume están influenciados por factores climáticos,

ecolóxicos e antropoxénicos, é necesario aplicar **un enfoque multiescala para a súa comprensión**. O lume actúa a diferentes escalas, desde patróns rexionais configurados polos gradientes climáticos e os cambios no uso do solo, ata os efectos locais determinados pola estrutura da vexetación e as prácticas de xestión do territorio. Un enfoque multiescala permítenos ademais comprender tanto os factores xerais como os impactos locais do lume. **Esta tese adopta un marco multiescala para examinar a dinámica do lume e os seus efectos sobre os ecosistemas.**

Así, **a nivel rexional**, analízanse as ecorreccións do Gran Chaco e do Pantanal, cruciais pola súa importancia ecolóxica e vulnerabilidade ao lume. **A nivel subrexional**, estúdase o Gran Chaco Paraguayo e, **a nivel local**, o Chaco Húmido Paraguayo, para avaliar as respostas ecolóxicas tras o incendio. Neste plano máis local, considerouse o Gran Chaco Paraguayo, que está situado no corazón de América do Sur e que se caracteriza por ser unha das zonas menos estudadas en canto aos efectos do lume a nivel global. Esta rexión divídese en dúas subrexións: **o Chaco Seco**, con bosques abertos e vexetación resistente á seca, e **o Chaco Húmido**, caracterizado por praderías autóctonas e rica biodiversidade, susceptible de inundacións periódicas. A fauna de ambas as subrexións inclúe especies acuáticas e de sabana, destacando a presenza de especies altamente vulnerables como xaguares, capibaras e lontras. En canto á flora, inclúe ecosistemas de sabanas, praderías, matogueiras e bosques secos tropicais. A rexión enfróntase a altas taxas de deforestación e degradación forestal. Paraguai ocupa un lugar destacado na América Latina en canto ao número de incendios por unidade de superficie, e a expansión da gandería aumentou a demanda de cultivos de pastos, o que provocou unha maior fragmentación da paisaxe. No Chaco paraguaio, os incendios son habituais debido ao uso do lume na gandería e aos cambios climáticos recentes, como as temperaturas récord alcanzadas no ano 2019.

OS NOSOS OBXECTIVOS

Esta investigación tivo como obxectivo principal **avaliar as respostas dos bosques afectados polo lume no Chaco Húmido**, centrándose nos patróns de ensamblaxe de especies. Estruturouse en torno a tres obxectivos xerais: (i) caracterizar a distribución espazo-temporal do lume a escala rexional e definir os réximes de incendios no Chaco paraguaio, (ii) avaliar a estrutura e composición das formacións forestais ao longo dun gradiente de réximes de incendios, e (iii) analizar os patróns de resposta utilizando enfoques taxonómicos e funcionais no Chaco paraguaio.

APROXIMACIÓN E PRINCIPAIS RESULTADOS

Para acadar os obxectivos propostos realizáronse análises espazo-temporais mediante técnicas de teledetección a dúas escalas espaciais: rexional (abranguendo as ecorreccións do Gran Chaco e o Pantanal) e local (centrada no Chaco paraguaio). Estas análises avaliaron a distribución, extensión, severidade e frecuencia do lume. Os diferentes modelos predictivos (GLM, GAM e Random Forest) foron utilizados para identificar os factores clave que impulsan a aparición de incendios, mentres que o k-means usouse para agrupar os réximes de incendios estandarizados clasificados. Utilizouse un mapa de réxime de incendios para seleccionar parcelas de estudo de campo, onde se realizou unha mostraxe estratificada para avaliar a estrutura, a composición e os trazos funcionais do bosque en resposta aos réximes de incendios identificados.

Os resultados revelaron que para o período de estudo (2001-2020), o ano 2020 rexistrou a maior superficie queimada, sendo o Chaco Húmido a ecorrexión máis afectada. Non se observou unha tendencia clara na intensidade dos incendios ao longo da serie temporal, senón unha flutuación constante cun pico extremo e atípico en 2020, mentres que 2014 presentou o valor máis baixo en canto a superficie queimada. Estes resultados mostraron unha certa variabilidade interanual na presenza e intensidade dos incendios, posiblemente influenciados por factores climáticos e antrópicos.

En canto á frecuencia de incendios, o Pantanal foi a ecorrexión con maior repetición de eventos, con máis de cinco eventos de lume durante o período 2001-2020. Seguíronlle o Chaco Húmido, con entre tres e catro eventos, e o Chaco Seco, con entre un e dous eventos de lume. Estes datos suxiren unha menor frecuencia de incendios no Chaco Seco en comparación coas outras ecorrexións, o que podería estar relacionado con diferenzas de dispoñibilidade de combustible, réxime de precipitacións e uso do solo en cada unha destas rexións.

Os modelos predictivos aplicados neste traballo revelaron un patrón espacial de incendios que diminúe de leste a oeste. Entre os principais factores que determinan a aparición de incendios identificáronse a temperatura máxima, a cobertura arbórea e a densidade gandeira. Dos tres modelos avaliados, Random Forest (RF) obtivo a maior precisión (87%), cun índice de concordancia Kappa de 0,74. O mellor modelo aditivo xeneralizado (GAM) acadou unha precisión do 73% e un índice Kappa de 0,43, mentres que o mellor modelo lineal xeneralizado (GLM) obtivo valores de 70% e 0,39, respectivamente. A superioridade do modelo de RF suxire que a relación entre as variables predictoras e a aparición de incendios é complexa e non lineal, o que xustifica o uso de modelos de aprendizaxe automática para abordar este tipo de análise.

A modelización do réxime de incendios permitiu **delimitar catro réximes de lume distintos**, cada un deles cunhas características ben definidas. Observouse que as ecorrexións do Chaco Húmido e do Pantanal presentan lumes frecuentes, de gran extensión pero menor intensidade, principalmente de orixe antrópica e sustentados por combustibles finos continuos. Pola contra, o Chaco Seco experimenta lumes menos frecuentes pero máis intensos, asociados a temperaturas máis altas, estacións secas prolongadas e aumento das fontes de ignición por cambios no uso do solo, o que amplifica a actividade do lume na comarca.

A nivel de vexetación rexistráronse un total de 3.254 individuos representativos dos distintos réximes de lume, entre eles 75 especies leñosas pertencentes a 19 familias botánicas. Entre as especies máis abundantes estaban *Phyllostylon rhamnoides*, *Syagrus romanzoffiana*, *Gymnanthes discolor*, *Trichilia catigua*, *Diplokeleba floribunda*, *Eugenia uniflora*, *Ruprechtia laxiflora* e *Sorocea saxicola*. Non se atoparon diferenzas significativas no índice de diversidade taxonómica entre os réximes de lume, nin na composición e estrutura da vexetación entre eles. Non obstante, describiuse un bosque onde o 49% das especies teñen diámetros entre 10 e 20 cm, mentres que os individuos con diámetros superiores a 45 cm representan só o 1,66% da poboación. En canto á estrutura vertical, a altura máxima rexistrada foi de 30 m, situándose o maior número de individuos (85,08%) no estrato de 1 a 15 m, indicando un bosque de pouca altura.

En relación aos trazos funcionais, a análise CWM revelou algunhas diferenzas entre os réximes de lume nos diferentes trazos funcionais considerados. A capacidade de rebrote das especies seleccionadas difería significativamente entre os réximes de lume identificados, sendo maior nos lugares con maior influencia do lume. En canto aos índices de diversidade funcional, destaca a significación do índice de dispersión, que foi maior nos réximes asociados ao lume.

Este achado pódese atribuír aos trazos avaliados, que están asociados a especies tolerantes ao estrés que están ben adaptadas para prosperar nas primeiras etapas da sucesión.

Este traballo **representa a primeira avaliación dos impactos dos réximes de incendios nos bosques mesoxerofitos do Chaco Húmido Paraguai**. Os seus achados contribúen significativamente á comprensión da distribución espazo-temporal do lume e da resistencia dos bosques mesoxerofitos nunha rexión con pouca investigación previa. Ademais, este traballo proporciona información clave sobre os réximes de incendios a escala tanto rexional como local, dilucidando as respostas dos ecosistemas forestais ao longo dun gradiente de réximes de incendios dentro das complexas ecorrexións do Gran Chaco-Pantanal. Deste xeito, os resultados poden servir de base para o deseño de estratexias de xestión e conservación adaptadas ás condicións específicas de cada rexión, promovendo a mitigación dos impactos negativos do lume sobre os ecosistemas e a biodiversidade.

1. GENERAL INTRODUCTION

1.1 FIRE AS A NATURAL PROCESS IN A CHANGING CLIMATE: ECOLOGICAL ROLES AND IMPACTS

Fire has been a fundamental natural process shaping Earth's systems for millions of years (Archibald et al., 2018; Bowman et al., 2009; Pausas and Keeley, 2009). However, some regions have been recently experiencing changes in climate that have profoundly altered fire patterns, disrupting historical fire regimes and their ecological roles. Rising temperatures, prolonged droughts, and increased frequency of extreme weather events are intensifying fire activity in many regions, with cascading effects on ecosystems (Jones et al., 2022; Feron et al.; 2024). These shifts challenge ecosystems' ability to adapt and alter the balance of fire's ecological roles.

The role of fire as a natural disturbance in many ecosystems is well recognized (Chen et al., 2013). As a multi-scale ecological process, fire acts as a key disturbance that shapes diverse ecosystems, such as Mediterranean landscapes, boreal forests, and certain tropical ecosystems like savannas. Fire's roles in ecosystems are diverse, varying across different temporal and spatial scales, and can range from predictable to stochastic effects (Kobziar et al., 2024).

The use of “good fire”—or fire that benefits ecosystems —provides numerous ecosystem services to humanity and biodiversity alike (Pantoja, 2008). It creates open spaces for pastures, agriculture, and hunting, stimulates the germination of fire-adapted and desirable plant species, and maintains landscapes conducive to grazing and wildlife. Fire also plays a role in pest control, reducing undesirable populations that may harm humans and livestock, helps to mitigate the risk of catastrophic wildfires by reducing fuel loads, accelerates species turnover under changing conditions, and enhances flowering and pollinator activity, supporting biodiversity (Pausas et al., 2019).

However, “bad fire”—or fire outside natural or managed regimes—can have severe negative impacts. It can drastically reduce biodiversity, alter species distribution and abundance (Chia et al., 2016), disrupt trophic networks (Bustamante et al., 2016), and modify habitat availability and land use patterns (Mowat et al., 2015). Such fires can degrade essential ecosystem services, impacting soil fertility, water cycles, and microclimate stability, with long-term repercussions for both ecosystems and human livelihoods (Müller et al., 2013). The “bad side” of fire emerges when natural fire regimes are disrupted—either through excessive fire or by suppressing fire to the extent that it can no longer fulfil its ecological role (Pantoja, 2008). Similarly, this “bad side” of fire also arises when fire—whether naturally occurring or human-caused—poses a threat to people, damaging property and livelihoods (Bowman et al., 2009).

For a fire to occur, a balanced combination of heat, fuel, and oxygen is required and three levels based on the spatial and temporal scale can be considered (**Figure 1**). The finest scale is the “fire triangle,” which focuses on individual combustion events lasting from seconds to a few

days, with monitoring confined to small, defined local areas. In the case of wildfires, the primary fuel may be carbohydrates in the form of cellulose and hemicellulose derived from plant biomass (foliage, wood, humus, etc.). The next scale, the “fire environment,” is the sum of the environment that supports combustion plus individual fire events. At this scale, fire monitoring and modelling are usually evaluated in terms of fuel, heat, and oxygen, which may vary depending on terrain and climate, alongside individual fires with events lasting from hours to months. At the largest scale, the “fire regime” describes the modal type of fire occurring within a community, landscape, or biome over decades or centuries (Cochrane and Ryan, 2009). At this level, descriptors are inferred from dendrological and palaeogeological techniques.

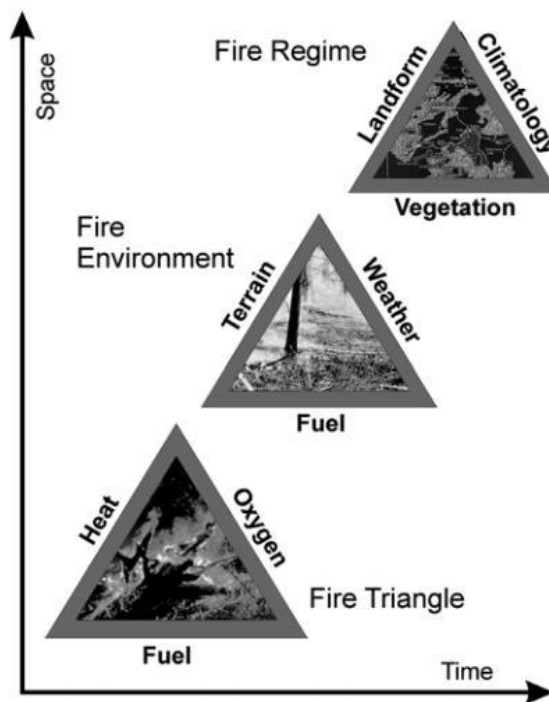


Figure 1. Multiscale approach to understand fire dynamics. Reproduced from Cochrane and Ryan (2009)

Fire regimes are crucial for characterizing and categorizing the diversity of fire behavior and its ecological impacts into a manageable set of classifications (Agee, 1993). The variation in fire patterns and effects across different locations and time periods profoundly influences the structure, composition, and dynamics of biotic communities within many of Earth’s terrestrial ecosystems. Just as grouping diverse plant assemblages into communities is essential in plant ecology, organizing fire activity diversity into fire regimes is foundational to fire ecology (Kobziar et al; 2024).

1.2 DRIVERS OF FIRE REGIME

To understand fire behavior, it’s essential to consider the interplay between topography, fuel characteristics, and climate (Cochrane and Ryan 2009; Manzo-Delgado et al., 2009). These

factors collectively shape the frequency, intensity, and spatial distribution of fires, contributing to the unique fire regimes seen across different ecosystems.

Currently, climate change challenges these stable conditions. It is a significant driver of fire, altering fuel availability through reduced moisture due to higher temperatures and shifts in seasonal patterns (Ellis et al., 2022). Droughts increase forest flammability by exacerbating air dryness and reducing fuel moisture, leading to more fuel accumulation and increased sunlight on the forest floor (Flannigan et al., 2016). As the climate warms or becomes drier, the likelihood of fire conditions in primary forests may rise (Berlinck and Batista, 2020). Reciprocally, climate not only drives fires but is also impacted by it. Wildfires are substantial sources of greenhouse gases (GHGs) and precursors to secondary aerosols and ozone (Randerson et al., 2006; Ward et al., 2012). Cristofanelli et al. (2024) estimated that wildfires contribute between 19% and 29% of global fossil fuel emissions. However, monitoring tools often underestimate these emissions (Datta and Krishnamoorti, 2022), potentially jeopardizing international climate commitments for GHG reduction (da Silva Junior et al., 2020).

Anthropogenic climate change compounds land use and fuel management impacts, leading to shifts in fire regimes that affect species composition, ecological invasions, carbon and water cycling, wildlife habitats, and ecosystem services (Bowman et al., 2009; McLauchlan et al., 2020). Globally, these changes have resulted in larger and more severe fires, which can disrupt ecosystem processes and human wellbeing (Bowman et al., 2017; Halofsky et al., 2020).

Human activities have significantly influenced fire regimes for millennia. Human presence usually leads to an increase in ignition sources, increasing fire frequency, altering burned areas, extending fire seasons, and modifying fire size (Syphard et al., 2009; Andela et al., 2017; Le Page et al., 2010). Human-induced changes in climate, atmospheric properties, and vegetation also modify fire regimes (Bowman et al., 2009; Cochrane and Barber, 2009). For instance, in Mediterranean ecosystems, shifts such as migration from rural to urban areas have influenced wildfire dynamics. Conversely, across different regions of South America, deforestation, agricultural expansion, and inefficient fire use for livestock management have fueled wildfire activity.

Fuel dynamics are another critical driver of fire regime alteration (Bradstock, 2010; Hoffmann et al., 2012). Fires require a continuous biomass to spread, typically involving a seasonal cycle of wet and dry periods to produce and convert potential fuels (Flannigan et al., 2016). Ignition sources, such as lightning, are also necessary in the absence of human activity. Patterns of burning play a vital role in plant adaptations to fire-prone environments, with fuel structure and continuity being crucial for survival (Keeley and Pausas, 2022). Also, plant community composition and fuel structure define fire patterns and regimes, whose detailed knowledge is essential for environmental assessment, restoration, and conservation planning.

1.3 ECOSYSTEM RESPONSES TO FIRES

In ecological terms, ecosystems interact with and respond differently to fire. For some ecosystems, fires are beneficial and part of their natural dynamics and cycle. In contrast, for others, fires can be detrimental, especially in those ecosystems lacking adaptations to withstand fire (Hardesty et al., 2005; Armenteras et al., 2020). Based on this, ecosystems can be classified

as fire-sensitive, fire-dependent, and fire-independent (Hardesty et al., 2005). The Nature Conservancy (2006) included a fourth category: fire-influenced ecosystems. These ecosystems may be hierarchically linked to fire-dependent or fire-sensitive ecosystems, as they are often found as transitions between them.

Not all native ecosystems or vegetation types fit perfectly into one of these categories and, of course, there are gradations and transitional states. However, these groupings provide a way to illustrate and examine the threats, conservation needs, and opportunities associated with fire across different vegetation types and how management actions may vary among them.

- **Fire-dependent Ecosystems.** Some ecosystems rely on fire as a contributing factor to their conservation, functionality, and diversity, such as savannas, grasslands, dry forests, Mediterranean shrublands, Siberian taiga forests, eucalyptus forests in Australia, and certain pine and oak forests (Certini et al., 2021, Bilbao et al., 2020, Hardesty et al., 2005). In pine ecosystems, it has been shown that high-intensity fires promote the regeneration of species like *Pinus oocarpa*, likely due to high temperatures, open spaces for growth, reduced competition, and increased seed availability (Juarez-Martínez and Rodríguez-Trejo 2003).

Fire-dependent ecosystems (46% of global area of major habitat types) have evolved with fire, which maintains a distinct structure and composition. However, not all ecosystems burn the same way. Many forests, grasslands, savannas, and wetlands are associated with frequent, low-intensity surface fires that maintain an open structure of grasses and herbs. Conversely, some types of forests and shrublands experience infrequent but intense fires, displaying high resilience and biotic response capacity within the ecosystem's natural fire regime (Hardesty et al., 2005).

Currently, many fire-dependent ecosystems are threatened mainly by climate change, land-use changes, and human settlements (Hardesty et al., 2005, Bilbao et al., 2020). This has led to alterations in fire regimes, exposing ecosystems to higher fire frequencies, resulting in the loss of forest cover, decreased key fire-dependent species, reduced plant response capacity, loss of soil organic matter, and the rapid release of stored carbon (Hardesty et al. 2005, Bilbao et al. 2020).

- **Fire-sensitive Ecosystems.** Fire-sensitive ecosystems have not developed with fire as a major recurring process. These ecosystems are not highly flammable, and species in these areas lack proper adaptations to respond to fire, with high mortality rates even at very low fire intensity. The structure and composition of vegetation tend to inhibit ignition and fire spread. Under natural, undisturbed conditions, fire may be so rare that these ecosystems can be even considered as fire-independent. Fire becomes a problem only through human-mediated processes including fragmentation, alteration in fuel composition, or increase in ignitions. As fires become frequent and widespread, the ecosystem composition shifts towards a more fire-prone vegetation. In terms of area, fire-sensitive ecosystems dominate 36% of ecoregions (Hardesty et al., 2005).

Examples of fire-sensitive ecosystems include a wide variety of tropical and subtropical broadleaf forests found along altitude and moisture gradients, and broadleaf and conifer forests in temperate zones at the wetter end of the moisture gradient. Tropical forests often turn into

savannas of introduced grasses (Cochrane 2001; Cochrane and Laurance 2002; D'Antonio 1992), and semi-arid grasslands are invaded by non-native grasses that create continuous fuel (McPherson 1997). Some ecosystems, such as the Chilean matorral (a Mediterranean-type shrubland), are uncertain in category. Although it is flammable, it seems to lack the regenerative responses of species found in other Mediterranean-type shrublands worldwide (Armesto and Gutiérrez 1978; Montenegro et al., 2004). In some ecosystems, the ecological role of fire is still uncertain or simply has not been identified.

- **Fire-influenced Ecosystems.** This category includes vegetation types frequently found in the transition zone between fire-dependent and fire-sensitive or fire-independent ecosystems (TNC 2006). Ultimately, it can include broader vegetation types where species responses to fire remain undocumented and where the role of fire in biodiversity maintenance is not clearly recognized. Generally, these are fire-sensitive ecosystems but contain some species that may respond positively to fire disturbances, or ecosystems that could persist without fire, yet fire disturbances play a role in creating certain habitats, favoring the relative abundance of specific species and maintaining biodiversity.

In fire-influenced ecosystems, fires typically originate in adjacent fire-dependent vegetation and spread to fire-influenced vegetation to varying extents and intervals, although low-level traditional slash-and-burn practices for agriculture may have been an important endogenous ignition source (TNC 2006). Here, fire can be an important factor in creating certain habitats, by opening forest or shrub canopies, initiating succession, and maintaining transitional vegetation. Fire-influenced ecosystems pose management challenges due to the subtle role that fire plays within them. Examples include the humid sclerophyll forest transition zone between savanna and rainforest in north eastern Queensland (Russell-Smith and Stanton 2002), riparian vegetation or gallery forests along watercourses within savanna or grassland vegetation (Kellman and Meave 1997). Other examples include fire-sensitive vegetation “islands” often embedded in fire-prone vegetation, such as the “hammocks” in the Florida Everglades (Myers 2000, 2006), or similar vegetation patterns in Brazil’s Pantanal. Also, certain types of tropical and subtropical forests, as identified in Mesoamerica, where fire has maintained the dominance of mahogany (*Swietenia macrophylla*) and associated species (Snook 1993) can be considered as fire-influenced ecosystems.

- **Fire-independent Ecosystems.** These ecosystems are characterized by low biomass production due to water stress, resulting in low combustibility that prevents fire from naturally manifesting. This is typical of ecosystems in arid areas, where there are no intrinsic features that support fire spread. In other words, fire is largely absent due to the lack of ignition sources, as seen in the Namib Desert in Africa, the tundra along the Antarctic coast, Colombia’s Guajira Desert, or the Nazca and Atacama deserts in Peru (Armenteras et al., 2020; Rodríguez et al., 2019). Regarding of area, fire-independent ecosystems occupy 18% of ecoregions (Hardesty et al., 2005).

1.4 CHARACTERIZATION OF FIRE RESPONSES

Historically, the analysis of fires and the classification of different fire regimes relied primarily on ground-based data collection. However, advancements in remote sensing technologies now enable the large-scale exploration and analysis of fire patterns across vast and remote regions with unprecedented accuracy and efficiency. In fact, the global extent of satellite-based products enables measurement of fire activity from remote regions where little data were previously available, advancing the study of fire ecology at global scales (McLauchlan et al., 2020). This technology provides advantages in accuracy, repeatability, speed, historical data, and integration with other thematic data (Daldegan et al., 2014). Advances in the temporal and spatial resolution of imagery from Earth observation satellites have led to unprecedented descriptions of recent fire activity at the global scale. These methods utilize satellite observations of either fire activity or pre- and post-fire imagery, with varying levels of field observations for ground verification. Daily fire detection has provided new insights into the seasonality of burning (Giglio et al., 2006) and the influence of fire-season length on fire size and total burned area (Andela et al., 2019). For instance, Archibald et al. (2013) leveraged MODIS and GFED data (van der Werf et al., 2017) over a decade to classify global fire characteristics based on five key elements: size, frequency, intensity, season, and spatial extent. Additionally, Pausas and Ribeiro (2017) used MODIS hotspot data to link global fire patterns with ecosystem productivity and biodiversity.

Recent advances in remote sensing have also enabled the integration of fire datasets with climatic variables, land cover changes, and anthropogenic factors to better understand the drivers and feedbacks of fire regimes (Archibald et al; 2013, 2018; Chuvieco et al., 2022; Pais et al; 2023). This approach has proven particularly useful for studying the influence of climate change on fire dynamics, as increasing temperatures, prolonged droughts, and shifting precipitation patterns alter the frequency, intensity, and spatial distribution of fires (Bowman et al., 2020). For instance, fire weather indices derived from satellite data, such as the Fire Weather Index (FWI), have been used to assess fire risk and predict future fire activity under changing climatic conditions.

Understanding fire regimes through remote sensing not only sheds light on the spatial and temporal patterns of fire activity but also provides a critical foundation for exploring how ecosystems respond to these disturbances. Vegetation, as a central component of ecosystems, exhibits a wide range of responses to fire, from rapid recovery and adaptation in fire-prone systems to significant degradation in fire-sensitive environments. By characterizing fire regimes—such as fire frequency, burn area, and severity—we can better predict and analyze how vegetation structure, composition, and functionality will evolve under varying fire conditions. The integration of remote sensing data with vegetation dynamics provides a comprehensive approach to assess the resilience and vulnerability of ecosystems to fire disturbances, enabling a deeper understanding of their ecological trajectories under current and future fire regimes (Bowman et al; 2020).

Despite their unquestionable value, remote sensing data and global datasets obtained have detection biases and limitations, particularly in detecting small fires—such as those from agricultural burning—and low-intensity fires, which release low levels of energy. Thus, satellite

records cover only recent decades, beginning in the 1980s. Finally, many studies agree that it is advisable to contrast remotely sensed data with data taken directly in the field (Giglio et al; 2018; Boschetti et al; 2015; Hantson et al; 2016).

1.5 CHARACTERIZING VEGETATION RESPONSES TO FIRE REGIMES

1.5.1 Composition and Structure

The assessment of forest floristic composition—encompassing families, genera, and species—facilitates the characterization of plant communities and provides critical insights into the dynamics of natural forests and their responses to varying disturbance regimes (Delgado et al., 1997). Floristic composition studies traditionally focused on tree species, given their representational value in terms of dominance (e.g., biomass, abundance, coverage), which in turn defines forest structure and function. However, it is essential to acknowledge potential biases arising from factors such as the minimum DBH (diameter at breast height) threshold applied, the sampling area, and the reliability of floristic identification at the site (Berry, 2002). Although these references may not be recent, the methodologies they describe remain widely used and continue to provide valuable frameworks for forest structure assessments.

For a long time, the study of vertical stratification was highly relevant due to the high diversity of species of varying sizes and the substantial number of individuals in the middle, upper, and emergent canopy layers (Bourgeron, 1983). According to their research objectives, authors such as Meave et al., (1992) defined vertical structure as the distribution of individuals within the community based on their heights, a description that involves identifying strata in which trees of similar sizes are grouped. Despite its age, this approach is still commonly employed in ecological studies due to its simplicity and utility in describing forest dynamics.

However, the primary objection to the concept of vertical stratification is that it cannot be constant, and a structural typology fails to capture the dynamics of the canopy (e.g., following disturbances). Furthermore, vertical stratification depends on the methodology employed, the researcher's experience, and other factors (Bourgeron, 1983). Nevertheless, vertical structure based on height provides a practical approach to assessing the physiognomy of vegetation and can even facilitate comparisons of community development following recurrent disturbances such as fire (Bernardino et al; 2021; Dantas et al; 2024; Furquim et al; 2024; Brando et al., 2024).

On the other hand, horizontal structure, understood as the spatial distribution of different populations and individuals, is influenced by environmental factors. At a large scale, it may be shaped by altitude or latitude, while at a smaller scale, local topography and water availability appear to be the primary factors (Clark 2000).

Several studies have demonstrated that forest floristic composition varies with different abandonment ages (Ferreira et al., 2002) as well as with the frequency and intensity of disturbance history (Delgado et al., 1997, Cruz 2000, Spittler 2000). This characteristic is therefore essential for understanding vegetation changes in response to fire.

1.5.2 Functional Diversity

In fire-prone ecosystems, fire exerts significant selective pressure on plant species (Pausas and Keeley, 2014), and so fire-adapted communities exhibit a wide range of adaptations that enable them to resist or recover after fire (Balao et al., 2018; Rundel et al., 2018).

Above the level of the individual, fire severity also has significant effects on plant communities, largely determining their regeneration and recovery (Kimura and Tsuyuzaki, 2011; Vallejo et al., 2012; Crotteau et al., 2013) and strongly influencing their composition and structure (Keeley et al., 2005; Pausas et al., 2008). However, the damage caused by fire to the plant community, as well as its recovery, also depends on the characteristics and condition of the vegetation before the fire (López-Poma et al., 2014). Thus, the post-fire persistence and development of vegetation are largely influenced by the presence of various functional traits (Pausas et al., 2004; Pausas and Verdú, 2005), which support plant community recovery even after highly severe fires (Fernández-García et al., 2020; Huerta et al., 2021).

These functional traits, primarily related to physiological and regenerative characteristics, are essential for the growth, reproduction, and survival of vegetation (Violle et al., 2007). In this regard, resprouting is one of the most recognized adaptations in fire-prone ecosystems (Pausas and Keeley, 2014; Clarke et al., 2015; Lamont et al., 2019), as it is one of the most common survival strategies found in various ecosystems where fire activity is significant. In ecosystems like savannas, thick bark on trees is characteristic as an evolutionary response to fire (Hoffmann et al., 2009; Lawes et al., 2011; Hempson et al., 2014; Pausas, 2015, 2017). There is now extensive literature on fire-related plant traits, covering aspects such as retention of dead branches, flowering (Fidelis and Zironi, 2021; He et al., 2011; Schwilk, 2003), bark thickness, storage structures, and bud placement (Paula et al., 2016; Pausas, 2015; Pausas and Paula, 2019). Other traits that denote resistance to fire include specific plant architecture and branching patterns (Osborne et al., 2018; Schwilk, 2003; Staver et al., 2012). Also, fruits or seeds can also present specific structures or adaptations, such as serotiny, smoke sensitivity, dormancy specific dispersion or storage strategies (Lamont et al., 2019; Pausas et al., 2012).

Based on traits concept, functional diversity, is referred to the components of biodiversity that directly influence how an ecosystem function. It focuses on the values and range of organismal traits within species present in an ecosystem, specifically those traits that affect one or more aspects of ecosystem processes (Tilman 2001). Furthermore, it allows for quantifying and comparing the variation of these traits both within and between species, across different communities. Thus, the analysis of functional traits and functional diversity provides a way to understand ecological processes within an ecosystem, such as productivity and resilience to disturbance or colonization/invasion processes (Villéger et al., 2013), as well as the mechanisms by which species respond to environmental changes (Salgado and Paz, 2015). Functional diversity indices arise from the idea of finding a way to quantify and compare such functional diversity. Two approaches have been developed for this purpose: a categorical approach, which considers the richness of functional plant types in a community, and a continuous and numerical approach, corresponding to the indices (Pla et al., 2010). Indices can be classified in ranges that consider single trait and a single species to multi-trait and multi-species indices (Pla et al., 2010).

Critical points include the selection of functional traits appropriate to the research questions, how to summarise this trait diversity into a measure of functional diversity (statistical analysis), and the validation of these functional diversity measures through quantitative analyses and experimental field tests (Petchey and Gaston 2006). This is particularly important in regions with high taxonomic diversity, such as Neotropical forests (Díaz et al. 2006).

To assess functional diversity, various indices have been developed over time, each designed to capture specific aspects of the functional traits within a community. Early indices, such as FAD1 and FAD2 proposed by Walker et al. (1999), and FD introduced by Petchey and Gaston (2002, 2006), laid the groundwork for further advancements. More recent indices have incorporated multidimensional and abundance-weighted approaches to provide a comprehensive understanding of functional diversity. Table 1 summarizes the most commonly used functional diversity indices, including their acronyms and brief descriptions.

Table 1. Overview of Functional Diversity Indices and their approaches

| Index name | Acronym | Brief Description |
|----------------------------------|---------|---|
| Functional Attribute Diversity 1 | FAD 1 | Index measuring functional diversity based on functional traits, proposed by Walker et al., (1999). |
| Functional Attribute Diversity 2 | FAD 2 | A variation of FAD1, adjusted to better capture differences between species in functional traits (Walker et al., 1999) |
| Functional Diversity Index | FD | Index measuring functional diversity based on functional distances between species (Petchey and Gaston, 2002, 2006). |
| Functional Diversity corrected | FDc | A corrected version of FD that incorporates weights based on the relative abundance of species in the community (Petchey and Gaston, 2002, 2006). |
| Weighted Functional Diversity | wFD | Functional diversity index weighted by the relative abundance of species (Mason et al., 2005). |
| Rao's Quadratic Entropy | Rao's Q | Index measuring functional diversity, considering species abundance and pairwise dissimilarity (Mason et al., 2005). |
| Functional Richness | FRic | Multidimensional index measuring the volume of functional space occupied by species (Villéger et al., 2008). |
| Functional Evenness | FEve | Index assessing how evenly species are distributed within functional space (Villéger et al., 2008). |
| Functional Divergence | FDiv | Index measuring functional divergence, reflecting how species are distributed relative to the functional centroid (Pla et al; 2008). |
| Functional Dispersion | FDis | Index measuring functional dispersion, based on the average |

| | | |
|-------------------------|-----|---|
| | | distance of species to the centroid of functional space(Pla et al; 2008) . |
| Community Weighted Mean | CWM | Single-trait index measuring the weighted mean of a specific functional trait based on species' relative abundance (Pla et al; 2008). |

Representing the distribution of abundance across the volume of the functional space involves visualizing how species occupy different functional niches based on their traits, which can provide valuable information about the structure and functional diversity of a community or ecosystem.

In fire-prone ecosystems, fire explains a significant part of the genotypic and phenotypic variability within species and of the diversity of communities. For example, in savannas, a typical continuous C4 grass layer fuels frequent fires. These fires have been suggested to be important regulators of savanna–forest stability at the local scale, especially in mesic climates (Dantas et al., 2015, Bernardino et al; 2021). However, there are still some fire-prone ecosystems that are not consistently studied, such as the Gran Chaco and Pantanal in Paraguay (Vidal-Riveros et al., 2023). These ecosystems are highly vulnerable not only to fire flames but also to land use change given the rapid deforestation, fragmentation and weak political framework of the country (Milán and González et al; 2022; Da Ponte et al; 2022; Caldas et al; 2015). The situation is further exacerbated by climate change, with recent years witnessing increased heat waves, prolonged droughts, and extended fire seasons. These factors underscore the need for a deeper understanding of fire behavior, its impacts on biodiversity, and the resulting feedback mechanisms.

1.6 DESCRIPTION OF THE STUDY AREA. THE USE OF A MULTISCALE APPROACH

Given the inherent complexity of spatiotemporal fire interactions, particularly in ecosystems where fire regimes are influenced by a combination of climatic, ecological, and anthropogenic factors (Bowman et al., 2020), a multiscale approach becomes essential. Fire operates across scales, from regional patterns shaped by climatic gradients and land-use changes to local effects determined by vegetation structure, soil properties, and specific land management practices (Bowman et al; 2014). Understanding these interactions requires a comprehensive framework capable of integrating these spatial and temporal scales to capture both the overarching drivers and localized impacts of fire.

Following this approach, this thesis adopts such a multiscale framework to examine fire dynamics and their effects on ecosystems:

At the regional scale, the focus encompasses the Dry Chaco, Humid Chaco—together forming the Gran Chaco—and the Pantanal (Figure 2), as defined by Olson and Dinerstein (2003). These ecoregions are critical for their ecological significance and their shared vulnerability to fire-related disturbances.

At the subregional scale, the analysis focuses the Paraguayan Gran Chaco, a landscape that integrates diverse ecological and land-use contexts within the broader Gran Chaco.

Finally, at the local scale, the study zooms in on the Humid Paraguayan Chaco, an area where fire dynamics and ecological responses can be observed at finer spatial resolution, allowing for detailed assessments of forest structure, composition, and functional traits in response to fire. This multiscale approach not only facilitates a holistic understanding of fire regimes but also provides a structured pathway to link broad-scale drivers with specific ecological processes. By examining fire effects at these interconnected levels, the study bridges the gap between macroecological patterns and microecological processes, offering insights that are critical for effective fire management and conservation strategies in fire-prone regions.

1.6.1 Gran Chaco ecoregions

The Gran Chaco ecoregions are located in the heart of South America, being significant biodiversity ecoregions (Olson and Dinerstein, 2003) and key hotspots for soil nature conservation (Guerra et al; 2022) (**Figure 2**). The Gran Chaco, encompassing both the Humid and Dry Chaco, is the continent's largest forested ecoregion after the Amazon and the largest dry forest area in South America (Baumann et al., 2016; De La Sancha et al., 2021). It supports a highly diversity of habitats, species, and cultures, forming a complex biological and social network. These ecoregions span vast areas of Bolivia, Brazil, Argentina, and Paraguay, where intensive grassland management for cattle grazing significantly affects vegetation structure.

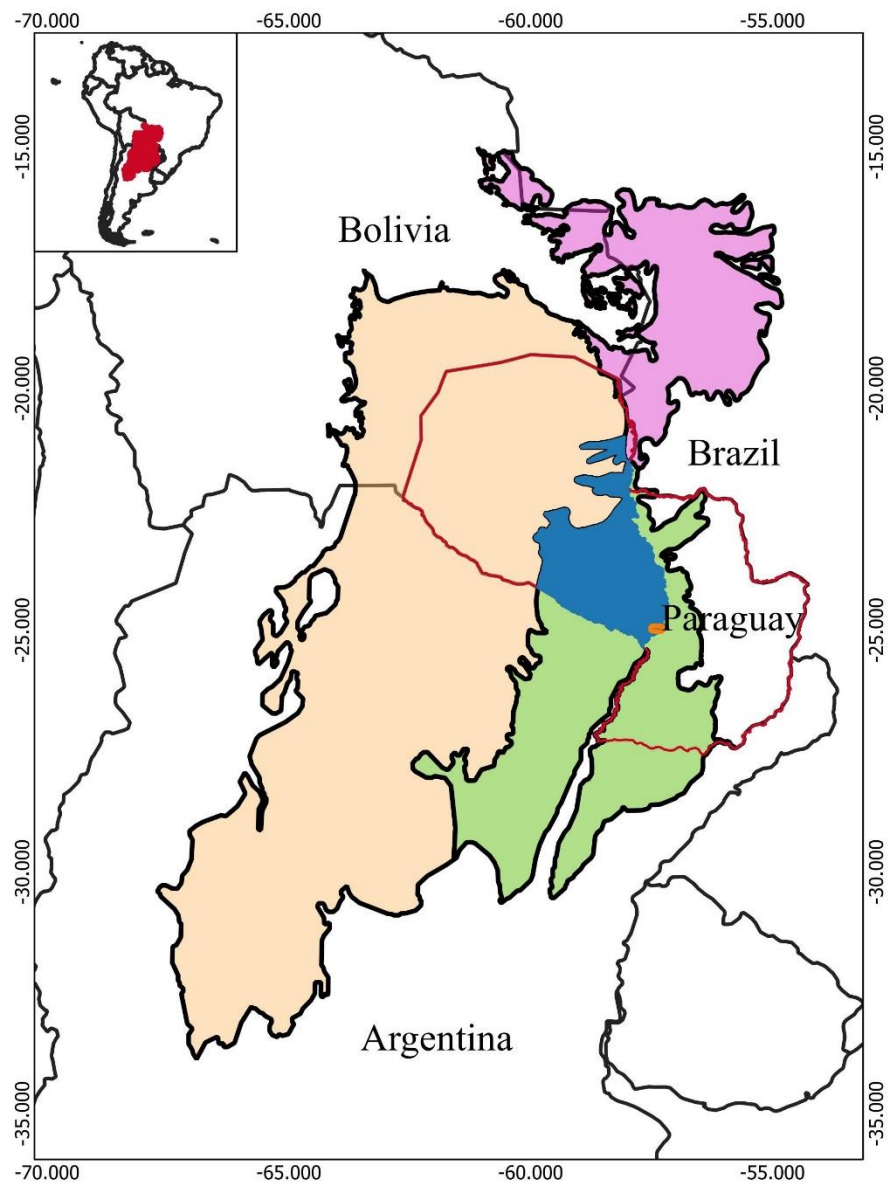


Figure 2. Multiscale approach of the study area. The Dry Chaco is depicted in yellow, the Humid Chaco in green, and the Pantanal in purple (regional scale). The Humid Chaco of Paraguay is highlighted in blue, and the local study area is indicated by an orange dot.

To understand the fire history of this particular and complex ecoregion, we should understand the evolution of the savanna and herbivory legacy. The origin of savanna formations in the Chaco coincides with the global expansion of savannas in the late Miocene/Pliocene (Pennington and Hughes, 2014). At the same time, a rich and diverse megafauna (large herbivores) was present until a large extinction during the transition of the Pleistocene-Holocene (Gallo et al.; 2013). There is significant evidence of coevolution between these large herbivores and the dominant vegetation, e.g., the presence of antiherbivore plant traits (wood density and small leaves) to cope with these large herbivores. After their massive extinction,

fire activity probably increased, also associated with the human presence and the use of fires for several purposes (Dantas and Pausas, 2022). Before the European colonization of the Chaco region, the diversity of large-sized herbivores was already quite restricted. The herbivore assemblage consisted of a few species, including the guanaco (*Lama guanicoe*), two types of deer (*Blastocerus dichotomus* and *Ozotocerus bezoarticus*), and the tapir (*Tapirus terrestris*) (Bucher 1987).

Furthermore, during pre-Columbian times, fire has been used by native populations in the Gran Chaco for hunting and war (Junk and Nunes da Cunha, 2012). In fact, the word “Chaco” comes from the Quechua language meaning “hunting land” (Villalba et al., 2018), describing the main activity of the first inhabitants. Grasslands and savannas were maintained by regular fires (two to five years), caused naturally or by the local population (Bucher, 1998; Bravo et al., 2001, Kunst et al., 2003). After the European colonization, fire intensity probably declined -particularly in the drier Western Chaco- driven by the reduction in fuel availability due to overgrazing caused by introduction of livestock (Adamoli et al., 1990; Mendoza, 2006). At the beginning of the 20th century, the vegetation in the Chaco region comprised a mosaic of forests, woodlands, savannas and shrublands (Bucher, 1998), suitable for livestock raising and/or timber operations. However, the introduction of cattle following the colonization by “Criollos” (Argentina), and the Mennonites (Paraguay and Bolivia) by the end of the 19th century and until the middle of the 20th century accentuated the retreat of grassland and savannas due to overgrazing (Grau et al., 2014, Fernández et al., 2020). These related events led to a change in fire regimes and land cover (increased shrubland areas) throughout the region (Coria et al., 2021).

Currently, cattle ranching is the most important economic activity in the Gran Chaco (Baumann et al., 2016). Livestock activity has expanded greatly during the last century, driving significant land use changes across the region, with different implications for ecosystem stability (Kunst, 2011; Fernández et al., 2020). As stated above, clearing land and promoting rapid growth of pasture using fire has an important function for the expansion and maintenance of agricultural lands and cattle raising purposes. However, the inefficient use of prescribed fires -in addition to natural fires- places the natural persistence of pasture and forest regeneration at risk when fire frequency, severity or intensity overcome the resilience of native species (Landi et al., 2021, Ibañez Moro et al., 2021, Bravo et al., 2022). In grasslands and open savannas, fire regimes altered by dryness and overgrazing promote the encroachment of woody species, thus modifying the natural fire cycle, which is essential for recovering native pasture, maintaining forage potential and ensuring the provision of multiple ecosystem services (Coria et al., 2021).

Currently, anthropogenic activities are influencing and altering fire regimes in the Gran Chaco. Some authors suggest that livestock activity is the main driver of fire occurrence due to the lack of control of some controlled burning responsible for large fires (Kunst, 2011, Argañaraz et al., 2015a; Guyra Paraguay, 2019). Additionally, the forecasted increases in average temperatures and duration of drought periods (Marengo et al., 2021; Feron et al; 2024) will increase the fire risk and the occurrence of extreme events with unpredictable environmental consequences.

1.6.2 Pantanal ecoregion

The Pantanal is the largest tropical wetland in the world, situated within an extensive floodplain at the heart of the upper Paraguay River basin in South America (**Figure 2**). Spanning 179,300 km², it is distributed across Brazil (78%), Bolivia (18%), and Paraguay (4%) (Marengo et al; 2021; Mataveli et al; 2021). The name "Pantanal" comes from the Portuguese word *pântano*, meaning wetland, bog, swamp, quagmire, or marsh. It derives from the fact that roughly 80% of the Pantanal floodplains are submerged during the rainy seasons, nurturing a rich diversity of aquatic and amphibian plant and animal species (Leal Filho et al., 2021). In 2000, part of this ecoregion, the "Pantanal Conservation Area", which represents 1.3% of the Brazilian Pantanal, was designated as a World Heritage Site by the United Nations Education, Scientific, and Cultural Organization (UNESCO). In the same year, 26.4 million hectares were nominated as a UNESCO Biosphere Reserve, making it the third largest biosphere reserve in the world (Pantanal Biosphere Reserve, Brazil | UNESCO s. f.), with a unique diversity of flora and fauna, containing at least 4,700 described species. The World Heritage site and Biosphere Reserve are also home to nearly two million people (Leal Filho et al., 2021).

Agribusiness represents the primary driver of deforestation in the Pantanal, where cattle ranching stands as the region's dominant economic activity (Bergier et al., 2019). Additionally, the expansion of extensive pastures, supporting over 3.8 million heads of cattle, along with grain cultivation, poses significant threats to the native vegetation and biodiversity (Oliveira et al., 2016). Among the environmental challenges faced by the Pantanal, wildfires stand out as a critical issue. Fires, often resulting from biomass burning, lead to substantial biodiversity loss and significant greenhouse gas emissions. These emissions contribute to global warming, intensifying climate change and causing cascading economic, social, and environmental impacts, including desertification and deforestation.

Anthropogenic activities responsible for modifying climate regimes and land use and land cover (LULC) have been altering fire behavior even in fire prone areas, such as the Pantanal. In 2020, the Pantanal experienced the worst fire episode in recorded history, with the record number of fire foci and burned areas registered (Marques et al., 2021), with nearly 900,000 ha burned. Satellite-derived estimates showed that about one-third of the Brazilian section of Pantanal was affected (Libonati et al., 2020), including several indigenous territories and conservation units that burned completely. Consequently, several types of habitats heavily affected, as well as their corresponding ecosystem functions (Libonati et al., 2020). Fire reached regions never burned before, including some conservation areas. Fire activity and climate have been shown to be closely related (Marengo et al., 2021) and the 2020 Pantanal fires were the result of an interaction between extreme heat and drought conditions associated with negligent fire use (Mataveli et al., 2021).

Prior to the 2020 fire season, Pantanal had been under severe drought conditions since 2019 (Marengo et al., 2021), which affected the flammability of vegetation. Soil desiccation conditions coincided with several heat wave episodes, leading to the establishment of strong coupling regimes between soil moisture and temperature (water-limited) that triggered a temperature increase through enhanced sensible heat fluxes from the surface to the atmosphere (Libonati et al., 2020). As a result, the combination of dry and heat conditions observed during

2020 over Pantanal essentially pushed fire danger to levels not seen since 1980 (Libonati et al., 2020).

1.6.3 Gran Chaco of Paraguay

Located in the heart of South America, Paraguay is one of the least studied countries regarding fire effects (Vidal Riveros et al., 2023). It is a small and landlocked country situated in the heart of South America, spans approximately 406,700 square kilometres and consists of two markedly different natural regions, both physically and biologically distinct. These regions, separated by the Paraguay River, are the Eastern region and the Western region, also known as the Chaco. The Eastern region experiences an average temperature of 21-22°C and annual rainfall between 1,400 and 2,000 mm. Paraguay's population currently stands at around 6.1 million, with only 3.5% residing in the Chaco (Instituto Nacional de Estadística. (n.d.)). This population primarily includes indigenous groups from various ethnicities, followed by Mennonite settlers who first arrived in the 1920s and established extensive farming activities, transforming the Chaco into Paraguay's leading dairy production area. The remaining inhabitants are local mestizos, often referred to as "Paraguayans" (Mereles et al., 2020).

The primary economic activity in this region is cattle ranching; the Paraguayan Chaco, managed largely by Mennonite communities, is not only the country's top dairy-producing area but is also well-known for its meat production. In recent years, both sectors have expanded significantly due to the rising of international market prices. This growth has driven an overall increase in cattle ranching, which, in turn, has boosted demand for pasture cultivation. As a result, natural vegetation is gradually being replaced, leading to increased forest fragmentation across the Chaco (Bauman et al; 2018; Milán and González 2022; Da Ponte et al; 2022).

Within this context, Paraguay currently faces severe deforestation rates and forest degradation, and fire plays a pivotal role since it usually starts in pastures. According to Bilbao et al. (2020), Paraguay ranks among the top three countries, following Guatemala, with the highest number of fires per unit of land area in Latin America from 2001 to 2019. The country experienced its hottest year in 2019, with an average annual temperature of 24.3°C, 1.5°C above the 1961-1990 average, and the hottest spring in fifty years (Grassi, 2020). These conditions may lead to changes in fire regimes (Vidal-Riveros et al; 2024a). In addition, the use of fire in livestock activities has been a common practice with significant implications for wildfires in recent years (Vidal-Riveros et al; 2024b).

In the Paraguayan Chaco, two subregions are identified: the Dry Chaco and the Humid Chaco (Maturó et al., 2005). The Dry Chaco is characterized by open forests that vary depending on soil types, with 3 to 4 dominant tree species such as *Ceiba insignis*, *Schinopsis balansae* (Quebracho Colorado), *Aspidosperma quebracho blanco*, and occasionally *Bulnesia sarmientoi*, *Neltuma nigra*, *Ziziphus mistol*, and *Ximenia americana*, among others (Mereles et al; 2013). This subregion reflects a more arid environment with relatively low plant diversity and a landscape dominated by hardy, drought-tolerant vegetation.

In contrast, the Humid Paraguayan Chaco is in a region dedicated to low intensity cattle rearing, with native grasslands as forage within a mosaic of natural plant formations. The region is highly diverse due to the variety of plant formations and the great amount of wild fauna

(Laino et al., 2022). This subregion is prone to periodic flooding from rain and river overflows, showing the typical vegetation mosaic characterized by the forest-palm savanna and aquatic vegetation (**Figure 3**) (Mereles, 2013). In the forest, species such as *Schinopsis balansae* and *Astronium urundeuva* are prominent, referred to as quebrachal de quebracho colorado (Spichiger et al., 1991). Mereles (2005) describes it as a semi-deciduous *mesoxerophytic* forest, adding to the mention by Spichiger et al. (1991) the semi-deciduous nature of several of its woody components.

The fauna in general is not very different compared to other wetland-associated areas. However, it is characterised by the presence of many aquatic species, such as *Hydrochaeris hydrochaeris*, *Lontra longicaudis*, and other savanna species like *Chrysocyon brachyurus* (Mereles, 2013).

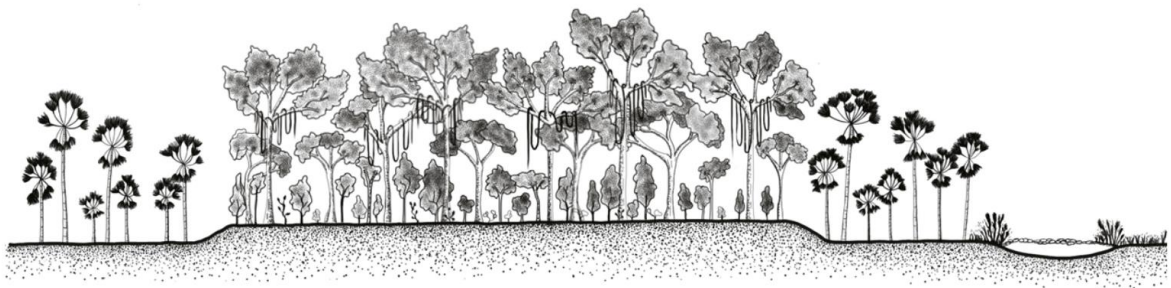


Figure 3. Mosaic vegetation of the Humid Chaco of Paraguay comprised by forest-palm savannas and wetland. Reproduced from Mereles et al., (2020)

Currently, there is little scientific evidence about the impacts of fire within this ecoregion and how the forest is responding to the fire regime. The fire regime itself remains largely unknown, aside from some common characteristics like seasonality. However, other fire attributes and their trends are entirely unexplored. In the context of climate change, it is crucial to understand fire regime and its impact on vegetation responses in order to mitigating the effects of fire and proposing adaptative strategies to face a new fire era.

2. HYPOTHESIS AND OBJECTIVES

Fire activity in the Gran Chaco and Pantanal ecoregions is increasingly influenced by a combination of climatic, environmental, and anthropogenic factors. While global climate studies underscore that warmer, drier conditions contribute to more frequent and intense fires (Flannigan et al., 2008), recent studies indicate that local climate is shifting toward warmer temperatures, extended drought periods, and reduced precipitation, trends that have intensified fire susceptibility across these landscapes (Marengo and Bernasconi 2014; Marengo et al., 2021; Libonati et al., 2022; Calim Costa et al., 2024). Local perception and different studies focused on the Chaco further suggest that fires have become more frequent and severe since the 1970s. This trend was later associated with regional increases in water availability that create conditions conducive to fuel accumulation and, subsequently, fire presence (Bravo et al., 2001). Simultaneously, land-use patterns have evolved over recent decades; agricultural expansion and intensification have introduced fire-dependent practices for land clearing, pasture renewal, and disposal of woody residues, all of which increase fire occurrences (Kunst et al., 2003; Correa et al., 2022; Kumar et al., 2022). Therefore, the simultaneous presence of severe climatic conditions, land use changes and human intervention suggest that fire occurrence in these ecoregions may be trending upward, with potential repercussions for local ecosystems.

Ecosystem responses to different fire regimes vary widely. In fire-affected environments, forest communities frequently adjust by shifting in species composition and structural characteristics, often favoring fire-tolerant species. This shift may show a prevalence of shrubby and grassy vegetation types, with a reduction in overall height and diameter classes, as these species are more resilient to repeated disturbances (Landi et al., 2021). In less fire-affected areas, forests are expected to maintain more developed structural attributes, as fire frequency and intensity are lower, allowing for a greater presence of fire-sensitive species and structural complexity.

Ecosystems change in response to fire, in terms of structure and composition but also in qualitative terms. In fire-prone ecosystems, plant species have developed various adaptive traits that enhance their resilience to recurrent fires. Traits such as resprouting ability, thicker bark, specific life forms, greater height, and defensive structures like spines are prevalent in fire-adapted plants (Torres et al., 2013; Bernardino et al., 2021; Loto and Bravo, 2020). As fire regimes intensify, ecosystems tend to support a higher abundance of species with these traits, contributing to greater functional diversity in terms of fire tolerance. This functional diversity reflects an ecosystem's adaptive capacity to fire disturbance, maintaining resilience and ecological balance despite the increasing frequency of fire events.

Considering all this information, this thesis establishes several working hypotheses:

1. We hypothesized that fire occurrence has increased, driven primarily by climatic, environmental, and anthropogenic factors in the Gran Chaco and Pantanal ecoregions.

2. We expected that a low fire regime predominates in the Dry Chaco of Paraguay, while high fire regimes are more prevalent in the Humid Chaco and Pantanal ecoregions of Paraguay. This hypothesis is based on the limited fuel availability in the western region of Paraguay, where arid conditions constrain fire occurrence. In contrast, we expect higher fire regimes in the Humid Chaco and Pantanal due to greater precipitation, which increases fuel accumulation, and the widespread use of fire in livestock management practices.
3. We hypothesized that the structure and composition of mesoxerophytic forest communities would shift toward a dominance of fire-tolerant species, with the magnitude and direction of these changes varying across different fire regimes. The resilience of this ecosystem to fire is primarily supported by its canopy closure and the high moisture content of the forest formation, which mitigate fire intensity and spread. However, we assume that under conditions of higher fire frequency and severity, this resilience may be exceeded.
4. We assumed that fire-adaptive traits and functional diversity indices related to fire tolerance would vary across fire regimes, reflecting the interplay between fire behaviour and forest responses. Specifically, we expected higher fire regimes to exhibit a greater abundance of fire-adaptive traits and distinct patterns in functional diversity, driven by the coexistence of species with contrasting strategies for fire tolerance. Functional richness (FRic) was hypothesized to increase under moderate fire regimes, as fire creates opportunities for niche differentiation and the incorporation of species with diverse trait combinations. Functional dispersion (FDis) was also expected to increase under moderate fire regimes, indicating the coexistence of species with contrasting fire-adaptive traits. In contrast, functional evenness (FEve) was expected to decrease under intense fire regimes, where dominance by certain highly fire-adapted traits may reduce trait uniformity. Finally, functional divergence (FDiv) was hypothesized to increase in fire-prone environments, as extreme trait values confer advantages under the selective pressures imposed by fire.

To address these hypotheses, our **general objective is to characterize fire dynamics over the last two decades and assess the forest's response to fire across the Gran Chaco and Pantanal ecoregions.**

Consequently, we established a set of specific objectives to solve each of the proposed hypotheses:

- **Objective I:** To assess fire patterns in order to explore fire behavior and its drivers across the three studied ecoregions, and to model the relationships between fire activity and climatic, environmental, and anthropogenic factors (hypothesis 1).
- **Objective II:** To characterize the frequency, extent, and severity of fires over the past two decades to delineate the fire regime gradient in the Gran Chaco of Paraguay (hypothesis 2).
- **Objective III:** To evaluate the structure and composition of the mesoxerophytic forest in the Humid Chaco of Paraguay according to the fire regime gradient identified in objective 2 (hypothesis 3).

- **Objective IV:** To characterize functional traits and functional diversity indices related to fire tolerance within the mesoxerophytic forest along the identified fire regime gradient (hypothesis 4).

2.1 DISTRIBUTION OF CHAPTERS

The development and justification of working hypotheses and objectives are distributed in this thesis in different chapters ordered as follows:

- **Chapter 1** provides a literature review on the study area concerning the effects of fire in the Gran Chaco, which served as the basis for developing the previously stated objectives and hypotheses.
- **Chapter 2** deal with objective I and hypothesis 1: the analysis of fire patterns and modelling at regional scale (Gran Chaco and Pantanal ecoregions).
- **Chapter 3** addresses objective II: the fire regime analysis of the Paraguayan Chaco. This analysis and fire regime classification served as the basis to evaluate the vegetation responses to fire regime.
- **Chapter 4** includes objectives III and IV, and hypotheses 3 and 4. This chapter comprises the results of the field work based on the objective II.

3. METHODOLOGY

3.1 MULTISCALE APPROACH

As previously mentioned, this study examines fire regime changes across three distinct spatial scales: regional, sub regional, and local. The regional and sub regional analyses were conducted using remote sensing techniques, while the local scale incorporated field-based assessments:

- At the **regional scale**, encompassing an area of approximately 1,340,000 km², the analysis included three ecoregions as defined by Olson and Dinerstein (2003): the Humid Chaco, Dry Chaco, and Pantanal (**Figure 2**). As indicated above, these ecoregions were selected for their ecological significance and their shared exposure to fire-related disturbances, providing a broad context for understanding fire dynamics in South America. The **sub regional scale** focused specifically on the Paraguayan Chaco, situated in western Paraguay. This region spans three departments and 14 districts, covering approximately 250,000 km², which accounts for more than 60% of Paraguay's total land area (**Figure 2**). This scale allowed for a more detailed exploration of fire regimes within a nationally relevant portion of the Gran Chaco, where diverse land-use practices and ecological conditions intersect. Finally, the **local scale** focused on assessing the impacts of fire on the structural and functional characteristics of forest ecosystems within the Paraguayan Humid Chaco. Fieldwork was conducted in semi-deciduous mesoxerophytic forests, which naturally occur in islets interspersed with palm groves and seasonally flooded savannas along the Paraguay River floodplain (Pérez de Molas, 2016). This scale encompassed approximately 14,000 hectares distributed across eight cattle ranches of extensive or semi-extensive ecosystem-based livestock production (Laino et al; 2022). Forest harvesting is limited to building infrastructure for internal use (e.g., corrals and bridges) (Laino et al., 2018). These forests hold significant ecological importance, as they represent a unique blend of species from both the Humid and Dry Chaco. They are distinguished by their high diversity of woody and herbaceous plants and the large extensions that remain relatively intact in the region (Mereles et al., 2020). Their distinctive structural and functional characteristics make them a critical focus for understanding the localized effects of fire on ecosystem dynamics.

3.2 SPATIO-TEMPORAL ANALYSIS OF FIRES

3.2.1 Selection of attributes characterizing the fire regime

An extensive literature review of fire regime attributes was conducted to gain a general understanding of the most important variables in defining fire regimes. An initial reconnaissance was also carried out to better understand the study area and organize logistics.

Based on the literature review, three study variables were selected: frequency, severity, and burned area. To characterize fire frequency and burned area, the MODIS product MCD64A1

version 6 was selected. This is a global monthly gridded 500 m product containing pixel-level information on burn area and quality. It uses 500 m MODIS surface reflectance imagery along with 1 km active fire observations (Giglio et al., 2018). All necessary data were obtained from NASA's Land Processes Distributed Active Archive Center (LP DAAC) (<https://lpdaac.usgs.gov>, last accessed 11/18/2022). To measure severity, the MOSEV product was used, derived from MODIS and presenting the most widely used severity indices for the 2000-2020 period. This product is based on combining Terra MOD09A1 and Aqua MYD09A1 surface reflectance products to obtain dense time series of the normalized burn ratio (NBR), and the MCD64A1 product was used to identify burn area and date (Alonso-González and Fernández-García, 2021). Beyond NBR, this product also offers other indices such as the differenced normalized burn ratio (dNBR) or the relative differenced normalized burn ratio (RdNBR), both of which are considered highly suitable for characterizing fire impacts. This product was retrieved from <https://zenodo.org/record/4265209#.Y3dbG3bMK3A> (last accessed 11/10/2022).

3.2.2 Predictive models

To model fire occurrence, three types of predictive models were run, which are well-known and widely used in the literature. The Generalized Linear Model (GLM) is one method that has been widely applied in fire prediction, as well as in other fields (Nurdiati et al., 2022). The Generalized Additive Model (GAM) provides smoothed functions that make the interpretation of relationships more intuitive (Lindenmayer et al., 2023). The Random Forest (RF) model is frequently applied to solve binary classification problems and to study fire prediction (Coughlan et al., 2021). Our dependent variable was the presence/absence of fires, while the predictor variables selected were elevation, vapor pressure deficit, precipitation (mean monthly precipitation), maximum temperature, net primary production, tree cover, land use, and livestock presence. These predictor variables were selected based on regional-scale literature and expert consultation and were obtained through the GEE platform with various algorithms developed for the study area, averaging each variable for the period of interest (2000-2020). For the livestock variable, the global product from Gibert et al. (2018), which refers to livestock density for the year 2010, was used. The predictive model analysis was performed using the R software.

3.3 FIRE REGIME MODELING

To identify fire incidence gradients at the scale of the Paraguayan Chaco, a cluster analysis was performed using MODIS and MOSEV products. Prior to the analysis, frequency and burned area were calculated based on MODIS data. Frequency was calculated as the total number of times a pixel burned during a year. The burned area was calculated using a 7x7 pixel circular window, with a maximum of 49 pixels per window. Additionally, the average severity for the studied time series was calculated. For this, applicable MOSEV data mosaics were obtained and adjusted to the local scope.

Subsequently, the dNBR index was chosen as it reflects the change caused by fire in relation to pre-fire conditions (Veraverbeke et al., 2010). To perform the cluster analysis, the variables

were scaled using Z-scores with a mean of zero and unit variance. The clustering strategy was K-means, and the number of clusters was defined using the 'elbow' method. To categorize by fire incidence gradient and describe each cluster, we visualized the distribution of each variable per cluster using packages from the ggplot and patchwork libraries in R Studio Version 4.2.2.

3.4. CHARACTERIZATION OF FOREST COMPOSITION, STRUCTURE, AND FUNCTIONAL TRAITS BASED ON THE FIRE GRADIENTS.

3.4.1. Field experimental design and sampling

For field sampling purposes, different categories were established based on the observed fire regimes: No Fire (NF) (no fire event), low fire (L), and medium fire (M). Given the limited number of forest areas affected by high fire incidence, the resulting categories from the cluster analysis were reduced by merging the "moderate-high" and "moderate-low" categories into a single "medium" category.

Fieldwork was conducted in 31 plots (NF=12; L=11; M=8) distributed across 8 cattle ranches in the Paraguayan Humid Chaco, covering an extensive area of approximately 14,000 ha. The design of each individual plot was 20 x 50 m, divided at the 25 m mark, arranged with a North-South orientation within each of the selected forest patches. Within the plot, the diameter (DBH) and total height of all individuals in the southwestern quadrant ($DBH \geq 5$ cm) were measured, and for the entire plot ($DBH \geq 10$ cm). Subsequently, 80% of the basal area abundance in each plot was calculated, providing a list of the most abundant species. Using this list, the plots where these species were present were selected, and an analysis of key functional traits was carried out to evaluate fire responses (Pérez-Harguindeguy et al., 2013). Field data were collected between April and June 2023.

3.4.2. Selection of Functional traits

A set of functional traits was selected for our purposes:

- **Bark thickness:** Measurements were taken on the main stem near the base, between 10 and 40 cm from the ground, as this is primarily the height associated with the occurrence of surface fires. For each species, three random measurements of bark thickness were taken from different individuals using a caliper. The average of the measurements per sample was then estimated. Thus, bark thickness (mm) was calculated as the mean of the averages for all samples.
- **Spinosity:** Two categories were established based on the presence (category 1) or absence (category 0) of spines.
- **Resprouting intensity:** no resprouting = 0, low resprouting = 1 (<10 shoots per plant), high resprouting = 2 (>10 shoots per plant).
- **Life Form:** Four categories were defined based on the life forms observed in these forest stands: mainly lianas (category 1), shrubs (cat. 2), trees (cat. 3), and palms (cat. 4).

3.4.3. Functional Diversity Indices

This study used single-trait, multi-trait, and multi-species indices, which also account for the relative abundance of species. The relative basal area of dominant species was used as a measure of relative abundance to calculate the indices. Additionally, the indices were calculated for each of the fire regimes evaluated. The indices calculated in this study were:

Single-trait indices: Community Weighted Mean (CWM). Multi-trait indices: Functional richness (FRic), functional evenness (Feve), functional divergence (FDiv), and functional dispersion (FDis).

An ANOVA was subsequently performed to compare the indices across the studied fire regimes, followed by Fisher's test to observe differences between the means of each regime (R Studio Version 4.2.2)

4.RESULTS

4.1 CHAPTER 1. A REVIEW OF WILDFIRES EFFECTS ACROSS THE GRAN CHACO REGION

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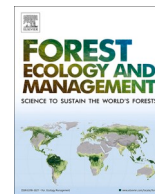
b.- Quality indexes: The journal in which this article is published corresponds to level 1 (quartile Q1 of the SCImago Journal Rank). In this case, this journal is indexed in the SCOPUS in the category of Forestry. It has an impact factor of 3.7 in the 2023 ranking (latest available year), and Cite score (2023) of 7.5.

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d.- Author's contribution: In this article, the author of the Thesis has participated in the conceptualization of the subject of study, the data extraction, the writing, the project administration, and the incorporation of the changes suggested in the review process. The author of the Thesis contributed significantly to overall sections of this article.

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f.- Names and affiliations of all the co-authors: The first author (Cristina Vidal-Riveros) is a PhD. student in at the University of Santiago de Compostela. The co-author Pablo Souza-Alonso is a Professor at the University of Santiago de Compostela and the thesis supervisor/tutor; the co-author Sandra Bravo is a professor at the National University of Cordoba, Argentina. The co-author Rafaela Laino is a researcher at the Chaco Americano Research Center, Paraguay and the co author Marie Ange Ngo Bieng is the thesis supervisor, she is affiliated at Center for International Cooperation in Agricultural Research (CIRAD) and the Tropical Agricultural Research & Higher Education Center-CATIE.



A review of wildfires effects across the Gran Chaco region

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1. Introduction

Fire is an ecological disturbance across several regions of the world, representing a factor of change in landscapes and having a fundamental influence on terrestrial and atmospheric systems (Bowman et al., 2009). Throughout geological history, fire has played an important role in regulating atmospheric conditions, e.g. O₂ levels (Belcher et al., 2010), influencing the evolution of plants (Pausas & Keeley, 2009) and determining the distribution of biomes and plant communities (Bond & Keeley, 2005). Many ecosystems depend on fire activity for their maintenance; e.g. in savannas and grasslands (Bowman et al., 2009) fire stimulates plant resprouting and seed bank expression. In forested ecosystems, the role of fire varies according to the historical evolution of flora, individual adaptations and gradually acquired specific traits. Thus, fire is recognized as a selective pressure, favouring the evolution of species with morphological adaptations to survive both fire and fluctuations in environmental conditions (Dantas et al., 2013).

However, in the last few decades, there has been an increase in forest fires worldwide, which has further increased the vulnerability of sensitive ecosystems to the effects of fire. The increase in fire dynamics is related to global warming derived from human activities, with an increase in the average temperatures and changes in natural precipitation patterns in diverse regions of the world during the last century (Prudhomme et al., 2014; NOAA, 2022). In the last few decades, South America has been particularly severely affected by climate change. Temperature anomalies in the form of heatwaves have increased significantly in recent years, especially in northern cities such as Santiago (Chile), Caracas (Venezuela), Bogotá (Colombia) and Lima (Perú) (Feron et al., 2019). Forecasts of the warming climate indicate that conditions will become even more severe. Risks and projected adverse impacts (including fires) related to climate change also include an increase in weather conditions that exacerbate the effects of fire (IPCC,

2023). This is particularly relevant for South America, already known as one of the world's top fire hotspots (Andela et al., 2017). Fire is now a major cause of natural ecosystem vulnerability, degrading megadiverse tropical American ecosystems that play a vital role in climate and vegetation cover. Another dramatic consequence is the increasing threat to the wellbeing of rural people -including local communities and indigenous cultures- whose livelihoods depend on natural resources and agriculture (IPCC, 2023).

The Chaco represents an example of a key endangered forest ecosystem in tropical America. The Gran Chaco encompasses a large number of ecosystems of high ecological value, serving as a corridor of wildlife and plant diversity between the tropical (Amazon) and the temperate belt (Atlantic forest) (Mereles et al., 2020). This region is home to several endemic and near endemic species in a unique transitional landscape (TNC, 2005). The Chaco comprises exceptional socio-environmental diversity (FAO, 2018), making the ecoregion a key global area in terms of ecosystem services and biodiversity conservation (TNC, 2005). Despite the vast area occupied and its great ecological importance, very little is known about fire dynamics within this biome, specifically in countries such as Paraguay, Bolivia and Brazil (Baumann et al., 2016). Worryingly, land use changes are increasingly promoted by increased agricultural and livestock production and the associated high deforestation rates at regional level (Hansen et al., 2013; De Marzo et al., 2022), threatening to fragment the largest block of tropical dry forest in South America.

The main objective of this review paper is to synthesize studies related to fire occurrence, the effects of fire on native vegetation at the Gran Chaco scale and changes in fire regimes, in order to identify current knowledge gaps and limitations. The information collected may contribute to facilitating capacity building and the generation of alliances between national stakeholders, thus enabling a more efficient response to the changing environmental conditions in the following

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decades. We based our work on indexed and non-indexed (grey literature) literature published in the last two decades. We used information from different databases, including Web of Science and Scopus, and used different search engines such as Google Scholar and science repositories such as ResearchGate. This review consisted of the analysis of 157 papers, out of which 86.62% were peer-reviewed. We limited the number of papers/articles considered as “grey literature”, and only exceptional cases were included in the analysis. Of this total, 91 studies (57.96%) were related to fire regime and its regional effects (Table 1). We classified the different papers by topics, countries, and the type of literature to assess the gaps and identify the challenges across the region.

The paper is organized in three separate sections: (i) the first section describes the study region, including its historical, biotic and socio-economic characteristics and also the fire history and fire regimes, (ii) the second section provides insights into post-fire effects within the landscape, and (iii) the final section discusses these findings in detail and proposes future research lines that would address the knowledge gaps identified.

2. The Gran Chaco americano region

2.1. Location and general characteristics

The Gran Chaco is a vast region that occupies an area of approximately 1,141,000 km² (Fig. 1), representing the second largest forested region in South America -after the Amazon rainforest- and the third largest ecoregion (Rodríguez & Morello, 2009; Assine et al., 2016). It comprises regions of Argentina (61%), Paraguay (28%), Bolivia (11%) and Brazil (0.12%) (Olson et al., 2001).

A tropical monsoon climate dominates throughout the Chaco ecoregion, with hot and wet summers followed by dry and cold winters (Boletta et al., 2006). The minimum temperature reaches -10° to -15° °C and the maximum temperature increases from south to north, reaching up to 40 °C during summer, with extreme temperatures (50 °C) occurring in some locations in the Paraguayan Chaco (Grassi et al., 2005). Precipitation is quite variable within and between seasons and tends to decrease from east (1200 mm) to west (400 mm). The Gran Chaco is predominantly flat and the elevation varies little; generally speaking, is between 0 and 200 m above sea level (m.a.s.l), except in the west and southwest of the ecoregion where more hilly terrain prevails (Baumann et al., 2016). Here, elevations oscillate between 500 and 2900 m.a.s.l with the Champaquí hill as the highest peak (Naumann et al., 2006). The climatic gradient, edaphic conditions, flood pulse and fire dynamics together make a heterogeneous mosaic of xerophilous and sub-xerophilous forests, savannas and grasslands (TNC, 2005; Oyarzabal et al., 2018; Zeballos et al., 2020). These vegetation types are associated with different soils and also with differences in drainage, which are related to geomorphological processes associated with water run-off (Bucher, 1982).

Table 1

Number of studies analysed by main topic and geographical scope.

| Main Topic | Argentina | Bolivia | Paraguay | Regional* | Total |
|-------------------------|-----------|---------|----------|-----------|--------|
| Fire regime and drivers | 17 (2) | 2 | – | 6 | 25 (2) |
| Social aspects | 3 (2) | 3 | 2 (1) | 1 | 9 (3) |
| Effects on soil | 5 | – | – | 3 | 8 |
| Livestock and herbivory | 5 | – | – | 2(1) | 7 (1) |
| Vegetation Responses | 21 (1) | – | – | – | 21 (1) |
| Invasive Species | 11 | – | – | 4 | 15 |
| Fauna | 1 | 4 (3) | 1 (1) | – | 6 (4) |

*Regional: study cases that comprise two or three countries including other S.A that are not within the boundaries of the Gran Chaco.

**The number of grey literatures is given in parenthesis.

The xerophytic character of the Chaco forests is represented by various adaptations of the trees and shrubs to dry conditions (small leaves and presence of thorns). Within these forests, species composition is mainly driven by a climatic gradient related to the water availability (Bucher, 1982), creating two clear and distinct subregions in the Chaco: the humid Chaco and the dry Chaco. On the one hand, the humid Chaco corresponds to areas with high average rainfall (1400 mm year⁻¹), located at the confluence of the Paraguay and Paraná rivers. Soils in this subregion have a high clay content, and the native vegetation is composed of a forest-palmar savanna-wetlands mosaic. Forests in this subregion are mainly associated with elevated areas with deep soils. These forests are mainly dominated by *Schinopsis balansae* and *Astronium urundeuva* (Spichiger et al., 1991). Savannas of *Copernicia alba* palm (Fig. 2) appear in the floodplain dominated by herbaceous vegetation, while wetlands dominated by aquatic-marshy vegetation appear in lowlands and depressed areas with permanent water and/or water-courses that cross the plain (Mereles et al., 2020). Extreme weather conditions and the influence of seasonal fluctuations in the level of Paraguay river create an aquatic-terrestrial transition zone which concentrates a large number of endemisms in an area where water is scarce (Mereles et al., 2019). On the other hand, *Aspidosperma quebracho-blanco*, *Schinopsis lorentzii* and *Bulnesia sarmientoi* are the most representative species of the dry and semi-arid Chaco forest. These species create open canopy formations, with large trees reaching up to 18 m. The intermediate forest layer includes other dominant species, such as *Neltuma alba*, *Neltuma nigra*, *Acacia praecox* and *Sarcomphalus mistol*, reaching 6–12 m in height. The shrub stratum (2–4 m in height) is dominated by species of the genera *Celtis*, *Atamisquea*, *Larrea* and *Schinus* (Loto & Bravo, 2020).

Besides the dry forests, other ecosystems are distributed to a different extent throughout the Chaco. Savannas and natural grasslands occupying interfluvial homogeneous soils are highly diverse and dominated by different grass species such as *Elionurus muticus* Spreng. (“aibe”, “espartillo” or “paja amarga”), *Heteropogon contortus*, *Schyzachirium* spp., *Trichloris crinita*, *T. pluriflora*, *Gouinia paraguariensis*, *G. latifolia*, *Setaria argentina*, *S. gracilis*, *Digitaria sanguinalis*, *Pappophorum pappiferum* and *P. mucronulatum* (Herrera et al., 2003). These extensive pasture areas are typical of arid and semi-arid climates, and the systems are often the origin of fires that propagate further and reach dry forests and shrublands. In addition, fires are also driven by slash and burn agriculture, locally known as “chaqueo”, to maintain and promote the regrowth of pastures for livestock purposes (Devisscher et al., 2018).

2.2. Fires in the Chaco region: Political and social aspects

South America has one of the highest incidences of fires worldwide (Andela et al., 2017). At a broad scale, fire effects can vary across regions with different climates (Lehmann et al., 2014) and different social contexts. The countries across which the Gran Chaco extends are considered developing countries and, not surprisingly, the regions most affected by changes produced in the fire regimes are those with high levels of poverty, rurality and poor governance of natural resource management (Pivello et al., 2021). Fire is a frequent disturbance across the Gran Chaco, affecting different ecosystems including grasslands, savannas and forests (Bucher 1982; Bravo et al., 2001, 2010; Landi et al., 2021; De Marzo et al; 2022). However, considering the complex interactions with environmental factors, human land transformations and dominant vegetation, fire may have variable effects within the same ecosystem (Nogueira et al., 2017; Giorgis et al., 2021).

As fire ignitions across the Chaco are generally caused by anthropogenic factors, human populations and socioeconomic activities are also very important for understanding fire behaviour. Across the Gran Chaco, the density of human populations is generally low or very low, particularly in Bolivia and Paraguay e.g. the population density in the Paraguayan Chaco is on average 0.9 inhabitants/km² (DGEEC, 2020). The late colonization of both of these countries by Mennonite

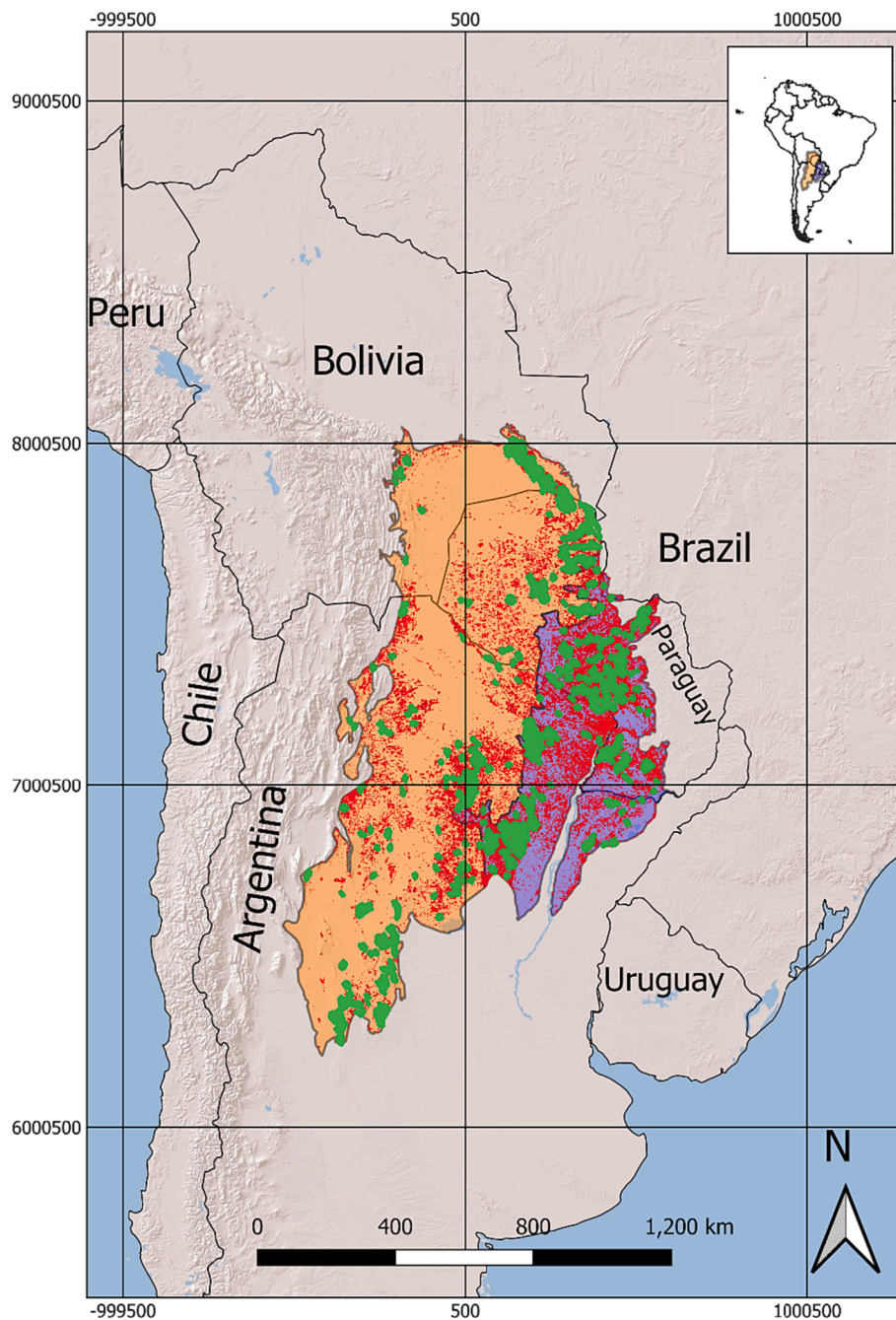


Fig. 1. Simplified map of the Gran Chaco (in colour) on a map of South America. The Gran Chaco consists of two large ecoregions: the Dry Chaco (orange area) and the Humid Chaco (purple area). Red dots represent burnt area during the last two decades detected by MODIS Version 6.1. Characterization of individual fires based on MODIS Version 6.1: prescribed burning (0–100 ha) in red colour and wildfires (>100 ha) in green colour.

communities (late 19th century and early decades of the 20th century) led to differences in land use relative to that in Argentina, where the population is mainly formed by native peoples. Indeed, the population density in Argentina is much higher (11.97 inhabitants/km², 2019) due to a longer history of occupation (Instituto Nacional de Estadística y Censos de la República Argentina, 2022). To understand fire occurrence, it is important to consider local fire use, as landowners apply different management practices and approaches in the use of fire. The type and extend of farming, both crop and livestock, are relevant. Thus, while farmers in indigenous communities practice local, subsistence cultivation (1–2 ha per household), recently settled farmers (mixed population from other Bolivian regions) produce primarily for commerce (1–5 ha per household), and private cattle ranchers may use manual or

mechanized land clearing in larger extensions (>20 ha) (Devisscher et al., 2018). Fire is used to maintain pastures, facilitate grass regeneration, remove invasive species and to eliminate pests, with a fire frequency that varies from one to five years.

In the Gran Chaco, as in other natural regions in the world, the geographical limits do not coincide with the administrative limits of the different countries-regions across which it extends (Naumann et al., 2006). This geographical context may hamper fire management strategies, as different countries have distinct policies and budgets for the purpose. Countries with fewer resources and weak governance structures may fail to monitor plant fuel accumulation that promotes fires or they may not implement systems for recording fire events. In addition, fire and its impacts have been studied rather unevenly across different



Fig 2. Representative formations of the Humid Chaco ecosystem (left), with the palm *Copernicia alba* dominating the tree stratum, and the dry Chaco (right) with *Schinopsis lorentzii* (large tree in the centre of the photograph).

systems and countries. Therefore, there is a knowledge gap that should be identified for a complete overview of the regional context.

2.3. Fire history in the Gran Chaco

To understand the fire history of this particular region, we should understand the evolution of the savanna and herbivory legacy. The origin of savanna formations in the Chaco coincides with the global expansion of savannas in the late Miocene/Pliocene (Pennington & Hughes, 2014). At the same time, a rich and diverse megafauna (large herbivores) was present until a large extinction during the transition of the Pleistocene-Holocene (Gallo et al.; 2013). There is significant evidence of coevolution between these large herbivores and the dominant vegetation, e.g., the presence of antiherbivore plant traits (wood density and small leaves) to cope with these large herbivores. After their massive extinction, fire activity probably increased, also associated with the human presence and the use of fires for several purposes (Dantas & Pausas, 2022). Before the European colonization of the Chaco region, the diversity of large-sized herbivores was already quite restricted. The herbivore assemblage consisted of a few species, including the guanaco (*Lama guanicoe*), two types of deer (*Blastocercus dichotomus* and *Ozotocercus bezoarticus*), and the tapir (*Tapirus terrestris*) (Bucher 1987).

Furthermore, during pre-Columbian times, fire has been used by native populations in the Gran Chaco for hunting and war (Junk and Nunes da Cunha, 2012). In fact, the word “Chaco” comes from the Quechua language meaning “hunting land” (Villalba et al., 2018), describing the main activity of the first inhabitants. Grasslands and savannas were maintained by regular fires (two to five years), caused naturally or by the local population (Bucher, 1998; Bravo et al. 2001; Kunst et al. 2003). After the European colonization, fire intensity probably declined -particularly in the drier Western Chaco- driven by the reduction in fuel availability due to overgrazing caused by introduction of livestock (Adamoli et al., 1990; Mendoza, 2006). At the beginning of the 20th century, the vegetation in the Chaco region comprised a mosaic of forests, woodlands, savannas and shrublands (Bucher, 1982), suitable for livestock raising and/or timber operations. However, the introduction of cattle following the colonization by “Criollos” (Argentina), and the Mennonites (Paraguay and Bolivia) by the end of the 19th century and until the middle of the 20th century accentuated the retreat of grassland and savannas due to overgrazing (Grau et al. 2014; Fernández et al., 2020). These related events led to a change in fire regimes and land cover (increased shrubland areas) throughout the region (Coria et al., 2021).

Currently, cattle ranching is the most important economic activity in the Gran Chaco (Baumann et al., 2016). Livestock activity has expanded greatly during the last century, driving significant land use changes

across the region, with different implications for ecosystem stability (Kunst, 2011; Fernández et al., 2020). As stated above, prescribed fire has an important agricultural and livestock function, mainly for clearing land and promoting rapid growth of pasture. However, the inefficient use of prescribed fires -in addition to natural fires- places the natural persistence of pasture and forest regeneration at risk when fire frequency, severity or intensity overcome the resilience of native species (Landi et al., 2021; Ibañez Moro et al., 2021; Bravo et al., 2022). In grasslands and open savannas, fire regimes altered by dryness and overgrazing promote the encroachment of woody species, thus modifying the natural fire cycle, which is essential for recovering native pasture, maintaining forage potential and ensuring the provision of multiple ecosystem services (Coria et al., 2021).

Currently, anthropogenic activities are influencing and altering fire regimes in the Gran Chaco. Some authors suggest that livestock activity is the main driver of fire occurrence due to the lack of control of some controlled burning responsible for large fires (Kunst, 2011; Argañaraz et al., 2015; Guyra Paraguay, 2019). Additionally, the forecasted increases in average temperatures and duration of drought periods (Marengo et al., 2021) will increase the fire risk and the occurrence of extreme events with unpredictable environmental consequences.

2.4. Fire regimes in the Chaco

The fire regime is defined by the by the extent, patchiness frequency, seasonality, intensity and severity of the fires that affect a given area (Morgan et al., 2001; Keeley, 2009; Jones and Tingley, 2021). Fire regimes are complex and depend on the current vegetation and climate, and the intricate interactions between fire, climate, vegetation and human activities make the identification of specific fire regimes a complicated task (Archibald et al., 2018).

The assessment of natural fire regimes is dependent on temporal and spatial scales. In this respect, different fire regime parameters for the semi-arid Chaco region of Argentina have been described using paleoecological (Lindskoug, 2016) and dendroecological analyses (Bravo et al., 2001). Paleo-environmental studies provide a wide temporal framework for certain types of ecological analysis and data interpretation. There is clear evidence for the occurrence of natural fire events during at least the last 4500 years in the Argentine Chaco region. This evidence is based on information provided by paleoecological studies, which have detected fluctuations in fire frequency and intensity related to climatic changes (Lindskoug, 2016).

Dendroecology and dendrochronology use similar ecological approaches that serve to investigate fire patterns across a longer time span, and both are essential for understanding fire ecology in specific environments. Dendrochronology is mainly based on two principles: the

formation of annual rings and accurate cross-dating to associate each tree ring with an annual calendar year. Dendroecology comprises the analysis of ecological aspects such as fire, insect outbreaks, pathogen attacks and stand structure, along with growth rings (Speer, 2010), providing information that enables estimation of the intensity and extent of past fires and the survival potential of native woody species. In this regard, both dendroecological and dendrochronological approaches have served to describe the frequency and severity of past fire regimes in the savannas of the Argentinean Semiarid Chaco (Bravo et al., 2001). The fire season in the Argentinean Chaco is prolonged, extending from April to October (Kunst et al., 2003; Bravo et al., 2010; Argañaraz et al., 2015, 2016; Landi et al., 2021), and is characterized by cold weather conditions and a high level of dryness that decreases the moisture content of vegetation and thus generates changes in fuel conditions and ignition probability. Fires often start in grasslands and savannas during the late winter (August–September), and under extreme climate conditions they can extend into adjacent forests and shrublands (Bravo et al. 2010).

Moreover, some native woody species in the Argentine Chaco region are particularly appropriate for dendroecological studies as they survive fires but are affected by different types of fire injuries or scars that remain identifiable for a long time (Bravo et al., 2008). Some common native trees in the Chaco forests, such as *Schinopsis lorentzii* and *Aspidosperma quebracho-blanco*, several of the medium-size species, such as *Neltuma alba*, *Neltuma nigra* and *Neltuma pugionata*, and some understorey species, such as *Vachellia aroma* and *Senegalia gilliessi*, are suitable for such studies as they usually exhibit characteristic post-fire effects. In this respect, Bravo et al. (2001, 2021) identified different fire intensities based on the typology (mainly size) of bark wounds. The height of fire scars represents a useful indicator of the intensity of past fires due to its positive relationship with flame length (Kunst et al. 2003). In the semi-arid savanna ecotone in the Chaco forest (average annual precipitation, 600 mm), the height of fire wounds increased between 1970 and 2000, suggesting a change in fire intensity that is probably related to greater availability of fine fuel (Bravo et al. 2001; 2010). Rainfall (water availability in general) is the main factor affecting biomass accumulation in arid and semi-arid savannas globally (Allen et al. 2018). In this regard, a period of increased water availability at regional level coincided with an increase in the fire frequency and extension for the period 1970–2000, resulting in a mean fire interval (MFI) of 2.2 years (Bravo et al., 2010). In arid Chaco savannas (400 mm average annual precipitation) fire frequency was similar to that in the semi-arid Chaco savannas, but the fire scars were much smaller, suggesting lower fire intensity (Bravo et al., 2021). These findings may be related to lower fine fuel availability, but further studies are necessary to corroborate this.

In the last few decades, remote sensing (RS) has been the approach most commonly used to assess fire regimes in the Gran Chaco. RS enables exploration of past and current land conditions and monitoring of vegetation changes over large geographic areas. In fact, the use of RS has important applications in fire ecology, including fire risk assessment and mapping, fuel mapping, active fire detection, burned area estimation, burn severity assessment and post-fire vegetation recovery monitoring (Szpakowski and Jensen, 2019). The use of RS is particularly important when physical field data are not generally available. The different data obtained from satellite sources represent valuable tools for analyzing the extent, periodicity and severity of fire, providing a consistent approach to fire regime studies (Morgan et al., 2001). In the absence of local information, frequency and burnt area are generally used to define fire regimes according to the availability of satellite products. Fire regimes have traditionally been studied by examination of their main components. Thus, some studies of fire regimes in woody and grassland communities have been carried out to understand the implication of the spatio-temporal patterns of fires in the landscape (Fischer et al., 2007), the effects of climatic variables (Argañaraz et al. 2015) and the post-fire recovery potential of forests (Landi et al., 2021). The variables most commonly used to study fire regimes are fire frequency (Kowaljow

et al., 2019; Carbone & Aguilar, 2021), fire intensity (Maillard et al., 2022), and fire seasonality (Landi et al., 2021). However, few studies have combined different variables to assess fire patterns at regional and local scales (Silva et al., 2021).

Different authors have also investigated how fire regime is related to climate, vegetation and anthropogenic activities. Navarro (2016) characterized the fire regime in the Chaco province (Argentina) using information provided by the Fire Information for Resource Management System (FIRMS). Navarro indicated that 10% of the fires occurred in the Chaco region, mainly in forests and grasslands during late winter (August–September). Argañaraz et al. (2015, 2016) showed that burning of large areas occurred after years with higher precipitation and was attributed to the increased biomass production. With lower temperatures and drought, the accumulated fuel also dries out and generates suitable conditions for fire ignition.

Fire regimes are also associated with forest fragmentation, but the relationship varies within different areas of the Gran Chaco (Torrella et al. 2015). In some of the countries across which the Gran Chaco extends, such as Bolivia, the effect of the size of the vegetation patches is of crucial importance. In this regard, 61.9% of the fires occur in larger vegetation patches, serving as a starting point for forest fragmentation and subsequent degradation due to reduced connectivity between key components (Maillard et al., 2020). In addition to this fragmentation, we must consider fire recurrence another important factor. Analysis of community resilience and of the effect of fire on biodiversity indicates that recurrence is also a determining factor in the restoration of forest cover and the initial composition of species (Maillard et al., 2022; Hartung et al., 2021).

RS studies are extremely helpful to characterize fire regime in a cost-efficient way, especially in remote and difficult access zones like the Gran Chaco. However, most studies have not yet been validated with field data, relying only on sensor data, GIS and machine learning techniques to make predictions (Lentile et al., 2006). However, the combination of field observations and RS data may be useful for calibrating remote data (Cardil et al., 2019) in post-fire ecosystem management and restoration scenarios, e.g. to understand land cover or species composition change in post-fire scenarios (Barker et al., 2019; Smith-Ramírez et al., 2022).

Although not essential, data validation is highly recommended as the use of sensors and derived products has certain limitations. These limitations may include the already mentioned poor integration between RS and field assessment, studies that compile the entire fire process, the complex understanding of the ecological effects of fires at the landscape level (Lentile et al., 2006) and challenges involved in estimating many forest fuel attributes (Gale et al., 2021). In addition, remote data acquisition does not consider social aspects such as the *in situ* perception of fire or the local perspective regarding fire activity as a key tool for socioeconomic activities (Devisscher et al., 2016). Therefore, RS techniques should be complemented with local information to improve the understanding of fire dynamics in fragmented and diverse cultural landscapes such as the Gran Chaco.

3. Post fire research and efforts to understand ecosystem recovery

3.1. Fire effects across the Chaco region

The Chaco region has received little international attention, despite its enormous extent, great diversity and variety of ecosystem services, uniqueness in South America, strategic location and function as a biological corridor. Regarding research studies, most of the published papers report post-fire studies, many of which are focused on ecological aspects e.g. plant taxonomy and post-fire traits (90.11%). Considering the origin and amount of available information, the imbalance in efforts to characterize fire behaviour at the geographic level is also clear. Thus, many published papers concern the Argentinean Chaco (78.75% of the

reviewed papers), while the Paraguayan Chaco region has been much less studied (1.25%).

3.2. Effect of fire on soil

Despite the undoubted importance of soils for CO₂ storage, water conservation, erosion control and pasture production, the effect of fire on soils remain largely unexplored in the Chaco region. Fire produces alterations in the physical structure of soil, changes in the chemical composition of nutrients, altered infiltration potential, increased water repellency and decreased water conservation (Neary et al., 1999; Certini, 2005). Fire effects are particularly notable in soil organic matter (SOM), a highly vulnerable fraction that greatly determines soil health and productivity (González-Pérez et al., 2004), which is especially important in land mainly dedicated to pasture for livestock. These changes are derived from (soil) burn severity, a parameter which is directly related to fire intensity and which should preferably be used to study the energy released during various phases of a fire (Keeley, 2009). It is therefore important to make a clear distinction between these two concepts, which are traditionally -and erroneously- used interchangeably (Keeley, 2009).

Although soil properties are of key importance for evaluating fire severity, erosion potential, soil stability and the need for urgent or future interventions, post-fire studies regarding physical, chemical and biological soil properties are very scarce. Nevertheless, studying soil is one of the most neglected aspects of the evaluation of post-fire impacts, not only in the Chaco but across South America and the Caribbean (Souza-Alonso et al., 2022). All of the above factors become even more relevant in relation to recognition of the Chaco as a soil biodiversity hotspot (Guerra et al., 2022). The Chaco region is an extensive plain that borders sub-Andean mountains to the northwest and Sierras Pampeanas to the southwest (Naumann et al., 2006). The absence of steep slopes across the region means that the risk of post-fire erosion is relatively low, unlike in other neighbouring mountainous countries such as Chile (Ubeda & Sarricolea 2016). Fires produce short-term increases in soil nutrients. However, the sharp increases are due to the release of compounds that would otherwise be retained in SOM and are therefore irretrievably lost. In general, fire induces mineralization of SOM; thus, organic C and N are partly volatilized, while phosphorus (P) can either be recycled by plants or lost by leaching. High fire frequency also has a significant impact on soil erosion, depleting soil C and N (Certini, 2005; Pellegrini et al., 2014). Quantification of C, N and SOM in burned and unburned areas of the Chaco region has revealed decreases in microbial activity and nutrient mineralization in soils subjected to high frequency burning for prolonged periods (Gonzalez et al., 2001). The combination of fire and overgrazing by livestock can lead to even large C losses (Abril et al., 2005).

Although the Chaco comprises diverse ecosystems, a large part of the area is occupied by grasslands, scattered shrublands and savannas. In these systems, fine and medium fuel loads are closely associated with climatic (rainfall gradient), edaphic and land management factors. The increased fire frequency is due to changes in land use or recurrent burning conducted in order to increase soil fertility through the rapid release of nutrients. A large number of the fires affecting the Chaco are related to the land clearance by massive pasture burning and slash-and-burn practices for agricultural and livestock production (Hansen et al., 2013). It is essential to consider the fertility of soils under livestock pressure, since the potential to produce abundant and high-quality pastures depends largely on soil nutrient content. As well as significantly affecting non-adapted ecosystems, recurrent fires can also cause long-term alteration in adapted ecosystems by depleting available soil nutrient resources.

Although fire is considered a negative force, it can be used to provide benefits, as long as fire of low intensity is used, with appropriate interval between fire events. This is the case of the disturbance caused by land use change using fire in the Argentine Chaco; in some areas land is left

fallow for periods of 14–20 years after fire in order to increase nutrient content and favour weed control, promoting local plant diversity by creating opportunities for species that otherwise would only regenerate after natural disturbances (Grau & Brown, 2000). By contrast, in some areas of the Bolivian sector where population pressure has shortened the burning cycle to 4 years, this length of time is not enough to allow forest and soil regeneration (Grau & Brown, 2000). The critical fire interval will vary according to multiple factors such as fire severity, fire intensity, time since last fire, vegetation and soil resilience, land use history, among others.

3.3. Livestock pressure and grazing by herbivores

In many areas, soils and vegetation are impacted by the combined pressure of different factors mainly attributed to the land use change. Thus, the effects of fire and grazing -two types of disturbance that play a fundamental role in the rapid and intense desertification affecting the Chaco- have dramatic consequences for soil and biodiversity conservation. As in many livestock-dominated landscapes, the relationship between grazing and fire is essential in the Chaco. Grazing is indirectly responsible for fire presence, since many land-use changes (brought about using fire) are caused by the transformation of natural or already transformed ecosystems to pasture land and cattle ranching areas (Fig. 3). Fire is traditionally used in livestock activity, and several functional grass species are associated with historical grazing intensity and fire frequency (Coria et al., 2021). Burning releases soil and plant nutrients, increasing the volume and palatability of the pasture (Kunst, 2011). However, considering that livestock activity is of the utmost importance the Chaco, studies exploring this fire-animal-plant interaction are clearly underrepresented (7.69% of the reviewed studies).

There is a broad general debate about the positive and negative aspects of livestock production for the long-term provision of ecosystem services. In general, fire and grazing shape the structure in many Chaco ecosystems, contributing to maintaining the typical open structure of grasslands/savannas. Moreover, woody formations (with some exceptions such as *Eucalyptus* forests) are generally more susceptible to fire than grasslands, which are considered flammable ecosystems with better post-fire responses (Bond and Keeley, 2005; Jaureguiberry et al., 2011), creating positive feedbacks that maintain low tree presence and generally favour fire-adapted species (Hoffmann et al., 2012). In addition, livestock grazing can interfere in this fire-grass feedback, indirectly shaping vegetation structure and leading to large-scale effects on vegetation distribution and structure (Bernardi et al., 2019). The presence of herbivores also contributes to reducing the frequency and intensity of fires via the consumption of vegetation, which reduces fuel loads, although it also delays post-fire regeneration of tree species due to browsing (Alinari et al., 2015; Alessio et al., 2008).

Nonetheless, the fire-grazing relationship does not always favour fire prevention. Thus, controlled burning of pasture for livestock activity leads to unexpected (accidental) fires due to strong winds and high temperatures that hamper fire control. The presence of cattle can also act as a selective pressure favouring the occurrence of some shrub species that increase the fuel load. On the other hand, shrub encroachment represents a significant problem in some Chaco ecosystems, as it conflicts with some types of silvopastoral uses (Rejzék et al., 2017). Silvo-pastoral systems have been adopted in some Chaco forests as a way of maintaining the native tree layer and ecosystem functions, while at the same time obtaining new areas for livestock grazing (Rejzék et al., 2017). However, in some areas of the Chaco, herbivores transport seeds to areas with reduced competition. The seeds are scarified by passage through the digestive tract of herbivores and are deposited in areas with less grass (due to grazing), ultimately favouring shrub encroachment (Adamoli et al., 1990). Moreover, overgrazing can also reduce grassland fires leading to woody encroachment, by increasing shrub and tree cover layers and decreasing the herbaceous biomass (Coria et al., 2021).

It is important to note that the recommendations will also vary

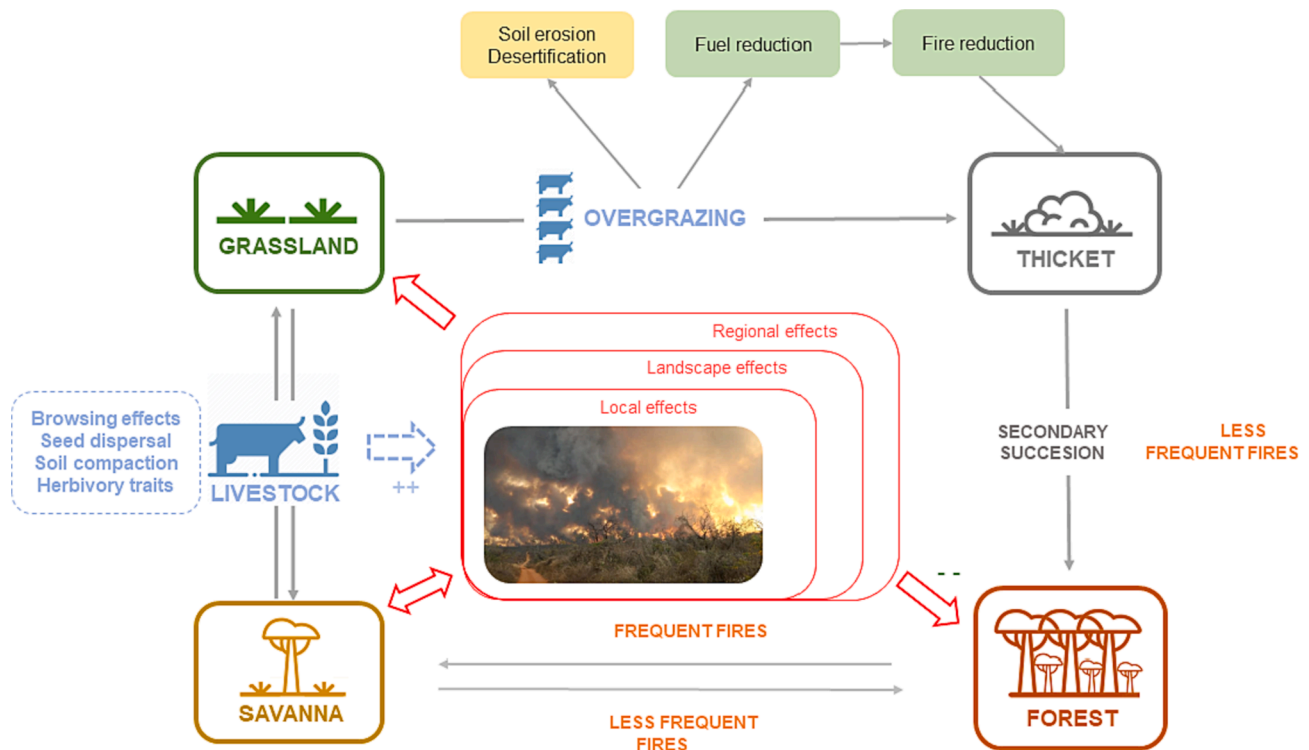


Fig. 3. Conceptual model showing the potential interactions between fire, livestock and vegetation that can theoretically result in stable mosaics of forest, savanna, grassland and thicket. Frequent fires are fires recurring at intervals of 2–5 yr. Less frequent fires are fires recurring once within a 10 yr. period.

depending on different aspects such as livestock pressure. Regarding animal pressure, livestock activity in the Gran Chaco is carried out extensively, and thus, the usual stocking rate does not always play a critical role since cattle stocks can be less than one head per hectare. The ratio of animal per hectare is even lower in Bolivia, reaching 0.18 heads per hectare (FAOSTAT 2022). Nevertheless, appropriate recommendations will depend on the geographical conditions of the specific area. Thus, livestock density can be adapted according to different site types e. g. in rockier or more sensitive areas, it may even be advisable to avoid the presence of livestock and to restrict the presence of fire for soil conservation (Cingolani et al., 2013).

Although constituting the most visible part of herbivore systems, the effect of fire -alone or in combination with livestock pressure- is not restricted to livestock but extends to different levels of the food chain. The partial loss of herbivorous mammals, such as the South American tapir *Tapirus terrestris*, has been verified by the decrease in plant diversity due to overgrazing by cattle (Mereles & Rodas, 2014). On the other hand, increased fire frequency can have greater negative effects on specialist insects (seed predators) than on general feeding insects such as herbivores and pollinators (Carbone et al., 2021), which in turn may have direct consequences on plant sexual reproduction.

3.4. Fire effects on the Chaco vegetation. Resistance, adaptation and plant functional traits

The effects of fire on vegetation are directly related to the evolutionary adaptations and traits that allow plants to resist and survive heat shock (Jaureguiberry & Díaz, 2015) and changes in environmental factors (temperature, precipitation, biotic exchanges) and land use (Bravo et al. 2001; Arganaraz et al., 2016). Functional traits (FTs) represent individual plant responses and adaptations (morphological, physiological or phenological) to environmental change that potentially affect plant fitness (Lavorel et al., 2007; Violle et al., 2007) or plant environments (Lavorel & Garnier, 2002). FTs have been used in ecology to quantify differences between communities after disturbance (Cadotte

et al., 2015).

Considering the different post-fire responses and regeneration, woody plants can generally be grouped into *obligatory seeders* (seed-dependent regeneration: recruiting species) or *regrowth species* (resprouting strategies) (Keeley et al., 2011). In this regard, Torres et al. (2013) reported for the Chaco Serrano, Central Argentina, that the ratio of crown recovery given resprouts and seedlings was 1562:1, concluding that for this ecosystem, resprouting is the main mechanism to recover from fire perturbations. Therefore, studies were mainly focus on resprouting strategy.

3.4.1. Post fire recruitment

Obligate seeders often need the fire occurrence to establish new individuals. They do not resprout and rely on seeding to regenerate their population after fire. Seeds may be stored in the soil or in the canopy (Pausas and Keeley 2009). There is no data on native Chaco species with canopy seed banks which are usually considered obligate seeders, and more studies about reproductive biology are desirable to establish most post-fire regeneration strategies. Some species from the Argentine Chaco region have demonstrated a relative tolerance to heat shock under controlled conditions, but the thermal thresholds are lower than those observed during fires. Jaureguiberry and Díaz (2015) determined that only four out of the 26 native species from the Chaco region were able to germinate after the 180 °C heat shock treatment, and only seven species showed stimulated germination with temperature ranges between 70 and 120 °C. On the other hand, Ibañez Moro et al. (2021) communicated that only one out of 6 native woody species from the Western Argentine Chaco region has heat shock-stimulated germination in the mentioned temperature range. It is probable that those fire-stimulated germination species, such as *Vachellia aroma*, *Senegalia gilliessi*, *Cercidium praecox*, *Celtis ehrenbergiana*, *Moya spinosa*, and *Neltuma flexuosa*, become dominant in areas with high fire frequency replacing other native woody species of the native forest canopy.

In burnt areas recruitment from soil seed banks (SSB) is essential to maintain the genetic diversity of plant species. Recruitment efficiency

varies according to fire intensity, the tolerance of seeds to heat shock and the capacity of the seeds to germinate and become established in the post-fire environment (Ocampo-Zuleta and Bravo, 2019). Seed banks can be altered or depleted by physical disturbances such as fire and grazing, which consume biomass during combustion or vegetation removal (Bravo et al. 2022). In different ecosystems across the Chaco, different seeds exhibit inter and intraspecific variability in their ability to resist fire events (Jaureguiberry and Díaz, 2015; Ibañez Moro et al., 2021). Moreover, the floristic composition of the SSB can differ markedly from that of standing vegetation, both in burned and unburned sites, suggesting that some species do not form SSB, and that opportunistic species may have the potential to colonize fire-affected areas. Depending on the predominant fire regime, more or less fire-adapted SSBs can be identified in those environments where fire is present on a regular basis. The SSB of some species may be more susceptible to fire than others, leading to changes in the dominance of plant communities in burnt areas (Jaureguiberry and Díaz, 2015; Lipoma et al., 2020). For instance, a highly intense bush fire in the semi-arid Chaco had a negative effect on the abundance of native seeds and low similarity of floristic composition between the established post fire vegetation and the SSB (Lipoma et al., 2018). Therefore, the SSB is far from being the main source of genetic material; other mechanisms like seed rain from neighbouring vegetated patches or resprouting capacities may play more important roles in vegetation recovery.

Woody plants in the Chaco region have SSB with short persistence, and almost 50 % of woody species are not present in the SSB, thus hampering their recruitment (Abella et al., 2013; Jaureguiberry et al., 2015; Lipoma et al., 2016; Bravo et al., 2022). This may be related to a high recurrence of disturbance, which could limit seed regeneration due to environmental factors e.g. water limitation or predation. Recruitment studies are also scarce and mainly focus on the influence of biomass removal in seed production and the capacity of seeds to become incorporate in the soil and germinate in disturbed environments (Lipoma et al., 2020; Bravo et al., 2022).

3.4.2. Fire tolerance, resistance and resprouting

Fire adaptations benefit the ecological fitness of some forest species in the Chaco Serrano (Torres and Renison, 2017). It has also been suggested that adaptations to dryness and grazing could provide woody Chaco species with a high level of fitness enabling them to overcome defoliation and the loss of aerial structures (leaves, branches) produced by fire (Santacruz-García et al., 2021). Post-fire changes in species composition and vegetation structure in burnt areas in the Central Chaco have been found to favour those species with traits better adapted to post-fire environmental conditions (Carbone and Aguilar, 2016). These changes include lifeform substitution based on the dominance of graminoid/herbaceous species that regenerate faster after fire than woody species.

Fire tolerance studies indicate that the persistence of woody species relies on the presence of structures (traits) that protect growing tissues; bark thickness and density protect cambial tissues (essential to maintain plant aerial structures alive) and epicormic buds allow post-fire sprouting responses (Bravo et al., 2014, 2019; Herrero et al. 2016). Physiologically, resprouting from protected meristems allows plants to reduce mortality and rapidly recover biomass (Lawes & Clarke, 2011). Nevertheless, different resprouting mechanisms may occur in post-fire scenarios; in the Argentinean Chaco, basal resprouting has been identified as the main type of resprouting occurring after severe and frequent disturbance (Herrero et al., 2016; Torres et al., 2013), whereas resprouting from aerial stems should be more abundant in relatively undisturbed areas. In the Chaco, even herbaceous species showed a high resprouting capacity -especially graminoids- displaying lower interspecific variability than woody species (Jaureguiberry, 2012). However, the influence of morphological and structural characteristics on fuel flammability in other subregions of the Chaco forests remains poorly studied.

In the Argentine Chaco region, plant survival is due to a combination of the protection of sensitive tissues and the resprouting ability. Some woody species in this region, such as *A. quebracho blanco*, *S. lorentzii*, *Neltuma alba* and *Neltuma nigra*, can diminish the negative effects of fire on the cambium through the combination of bark thickness and density and thus maintain the tree growth habit (Bravo et al., 2001, 2008, 2010, 2019; Bravo et al., 2021), whereas shrubby species, such as *Vachellia aroma*, *Senegalia gilliesii* and *Schinus fasciculatus*, accentuate their shrubby growth habit and thus intensify their resprouting capacity (Bravo et al. 2019). Although bark density and thickness contribute to fire resistance and tolerance (Bravo et al. 2014), plant species can also increase fire resistance by relocation of buds. Thus, *Aspidosperma quebracho-blanco*, a species with thick bark, can resist high severity fires due to greater isolation of cambial tissues and buds. Other species with thinner bark can resist fire of low-to-medium severity, but the protection may be insufficient in the face of more intense fires (Bravo et al., 2014). In addition to epicormic resprouting, some species have the capacity to resprout from belowground organs (plant collar, roots, xilopods or lignotubers (Bravo et al., 2014, 2019). Basal resprouting is representative of the tolerance in pole-sized individuals, since bark thickness cannot efficiently protect aerial buds.

3.4.3. Plant flammability

The study of species or ecosystem flammability is of key importance for forest management and planning and firefighting strategies. In the dry Argentine Chaco, plant flammability has been studied at the individual species level (Jaureguiberry et al., 2012; Santacruz-García et al., 2019, 2021). At the ecosystem level, flammability largely depends on the type, quantity and quality of vegetation formations, and vegetation patterns therefore play a key role in defining the risk of fire occurrence. Different secondary metabolites such as resins, oils and terpenoids are also commonly associated with plant flammability (Ormeño et al., 2009). Other secondary metabolites such as tannins, terpenes and phenols have also been considered to be involved in the biochemical response to fire and related to post-fire resprouting in different Chaco species. In this regard, Santacruz-García et al. (2021) identified the biochemical response to fire is better in shrubby species than in tree species. These authors observed a significant correlation between the biochemical response (increase of secondary metabolites) to fire and resprouting capacity years after experimental burning.

Considering the plant community level, flammability will depend on the vegetation cover (%) (Hargrove et al., 2000), the quantity and continuity of the biomass fuel (Palma et al., 2007; Ghermandi et al., 2016) and the fuel moisture content (Arganaraz et al., 2016). Biomass fuel is also related to plant type, volume and drying rate, and as mentioned above, herbaceous plants (broadleaf fuel, grasses) are generally considered more flammable than woody species (Jaureguiberry et al., 2011). However, fuel accumulation also depends on other environmental factors such as temperature and relative humidity; warmer and drier climates may decrease the fuel moisture content and increase the risk of fire ignition, especially in humid ecosystems like the Humid Chaco. Plant flammability may be related to particular regeneration strategies such as seed bank (soil or aerial) recruitment, since post-fire conditions reduce the interspecific competition promoting new individual establishment.

3.5. Effects of fire on wildlife

In general, it can be said that the representation of studies that include animal species is relatively low (6.59%), and within them, only 16.66% of these studies relate the impact on wildlife with fire severity metrics. We found evidence of a negative effect in response to fires in different bird groups in the mountain Serrano forest in central Argentina (Albanesi et al., 2014). Fire also produced moderate to high impacts in bird biodiversity in the Chiquitano forests of Bolivia (Aponte et al., 2021).

On the contrary, invertebrates tended to increase in burned areas (Giorgis, 2021); this is in agreement with Pinto-Viveros et al. (2021), who reported for the Chiquitano Forest that the abundance of amphibians was higher in burned areas than in areas without burning, one year and a half after the fire event. This issue could be attributed to its capacity for mobilization.

Likewise, Aponte et al. (2021) revealed that larger mammals, such as lowland tapirs (*Tapirus terrestris*), jaguars (*Panthera onca*), pumas (*Puma concolor*), and brocket deer (*Mazama americana*), as well as those of smaller size (felids and foxes), have been observed in burned environments in several studied sites across the Chiquitano Forest, even in areas with higher levels of fire impact. These findings suggest that mobility and size are key attributes for fire resilience in this group. Additionally, a technical report (Guyra Paraguay, 2019), highlighted that the fauna of the Paraguayan Chaco could be mostly adapted to fire events, and it is expected that populations will recover fast after this perturbation. However, this country has no study of species population after fires.

3.6. Invasive alien species

The presence of invasive alien species (IAS) has been gaining importance in recent decades, becoming a major threat to diversity. Thus, IAS affect a wide range of ecosystem properties, ranging from physico-chemical factors such as soil nutrient composition and hydrology, to ecological factors such as plant community composition and ecological networks; in addition, ecosystem processes such as nutrient cycling and fire regimes are also affected (Pyšek et al., 2020). Invasive species, and more appropriately here invasive alien plants (IAPs), are usually opportunistic species that take advantage of environmental disturbances. One of the major disturbances at ecosystem level is caused by fire, especially in non-adapted ecosystems. Fire directly and selectively excludes sensitive plant species (Hoffmann and Moreira, 2002; Brooks et al., 2004); indirectly, fire transforms the ecosystem making it less habitable for non-adapted species. This is particularly notable when the frequency, intensity or severity of fire modifies local regimes, creating conditions that allow the entry of pioneer or fast-growing species (Zouhar and Smith, 2008) or the occurrence of new fires that will feed back into the cycle (Brooks et al., 2004), even increasing the spread and intensity of fire events relative to naturally occurring fires (Paritsis et al., 2018).

Despite the corresponding debate and the importance on a global scale, the presence of IAPs in the Chaco has not been considered in detail, in line with other topics mentioned above. The entry and impact of IAPs has scarcely been studied in the region, with the likely exception of the Chaco Serrano, where some information is available regarding the reproductive capacity or regenerative strategies of some IAPs such as *Ligustrum lucidum* and *Gleditsia triacanthos*. *Ligustrum lucidum* is responsible for changes in the dynamic of native forest stands, where suppression regeneration and dead canopy in trees appear to be the most relevant changes (Hoyos et al., 2010). In addition, this type of forest simplifies the bird assemblage structure by reducing bird richness with prevalence of species that feed on *L. lucidum*, which in turn promotes the spread of such species (Bellis et al., 2021). Some authors suggest that IAPs have specific traits that favour the invasion process, e.g. *Gleditsia* produces more seeds per plant and has a higher percentage of scarified seed germination and density of seedlings around the focal individuals than the native species *Vachellia aroma*, making the former more competitive (Ferrerías and Galetto, 2010). Moreover, other authors studied the fruiting phenology as a trigger attribute for IAPs, as in the case of *Pyracantha* species (Gurvich et al., 2005). By contrast, Vergara-Tabares et al., (2016) did not find a direct relationship between fruiting phenology and dispersal, suggesting that other plant traits are important in invasiveness, including colour of the fruit, fruit display and fruit grouping on the plant.

As may be expected, the type of invaders that become prevalent in these ecosystems are, precisely, those species that adapted to or that

have characteristics that allow them to thrive in fire-adapted systems. If exotic species have adaptations to fire (regrowth, thick bark, stimulation of germination by temperature, seeds with dormancy, serotiny) they will have the potential to compete more efficiently and outperform local species within non-adapted native communities. However, the results of using prescribed fire to control woody IAPs on different communities in the Argentinean Chaco Serrano did not show significant differences between IAP and native species related to post fire survival and resprouting traits, suggesting a strong similarity at the group level (Herrero et al., 2016).

Several IAPs (*Pinus*, *Cytisus*, *Ulex*, *Bromus*) and plant forms (trees, shrubs and grasses) are considered dangerous invaders. These genera include flammable species capable of promoting fire spread (Speziale et al., 2013; García et al., 2015; Cobar et al., 2014; Paritsis et al., 2018), thereby increasing the probability of frequent wildfires (Davis et al., 2016; Paritsis et al., 2018). Beyond species-species substitution, when IAPs belong to different plant forms, the change introduced in the system may lead to rapid and permanent modification of ecosystems (Brooks et al., 2004), as in the case of savannization (the transformation from tropical forest to savannah) observed at the edges of the Amazon (Silvério et al., 2013).

In addition to having different forms, reproductive capacities and post-fire responses, IAPs can also have different physiological attributes that enable them to outcompete native plants. In the Chaco Serrano Forest, IAPs have demonstrated a more efficient hydric strategy than native plants. In a regional comparison including 20 species (8 IAPs, 12 native species), Zeballos et al. (2014) found that water transport efficiency was higher (i.e. higher minimum leaf water potential and lower wood density values) and resource acquisition and use was faster (higher SLA values) in IAPs than in native species. These findings indicate that the use of more resources and at a higher rate than native species could confer IAPs a higher competitive ability in semi-arid ecosystems of the Gran Chaco.

It is important to consider that invasions are highly context-dependent processes. In this respect, a system exposed to continuous disturbances, regardless of the intensity and the available resources and niches that eventually appear, will become highly susceptible to invasion. Traits promoting invasiveness are also strongly linked to the ecological and historical context (Palma et al., 2021), and local environmental conditions and species characteristics may therefore vary across sites. In addition, in regard to this type of variability, it is also important to note that some species considered IAPs may provide certain benefits and their presence may also lead to positive interactions (Tecco et al., 2006). For example, these authors found that the richness of both native and exotic species increased significantly under *Pyracantha angustifolia* due to the shade and mechanical protection provided.

4. Current needs and future prospects in the Chaco region

Fire regime studies across the Chaco have developed unevenly both at the regional level and in terms of the topics considered. Several gaps related to different fields must be addressed in order to improve understanding of fire patterns and the impact across the landscape. There is also a clear imbalance in terms of available information between the different regions and ecosystems of the Chaco; thus, while there is abundant information about some regions (although not studied in detail) as in the Argentinean Chaco (69.23% of the reviewed studies), information about other regions is scarce, as in the Bolivian (9.89%) or the Paraguayan Chaco (3.30%). However, local information is specific and cannot be extrapolated to the Chaco as a whole. To some extent, this review has allowed us to detect some gaps (Table 2) that deserve attention in future studies.

Most of the studies reviewed (96%) have not completely characterized the fire regime, and most (68%) have focused on fire frequency using remote sensing data. Fire severity has seldomly (8%) been considered and mainly assessed on the basis of a single event, which

Table 2
Key challenges identified in the framework of this review.

| Research priority topics | Challenges |
|--------------------------------------|---|
| Fire regime | Modelling fire regime using a combination of area burned, severity, fire frequency and other fire metrics to understand its behaviour Including social variables such as land tenure, land use pattern, socioeconomic activities in fire regime characterization Documenting individual fire events in a dataset to identify the causes and type of fires Integrating fuel availability to understand its contribution to fire regime Including fire severity in fire regime models Implementing field validation of fire regime models at local and regional scales |
| Soil effects | Studying the fertility of soils Analysing effects of recurrent fires on soil nutrients Studying the relationships of fire issues (severity, recurrence) on soil physical, chemical, and biological characteristics |
| Herbivory and livestock | Investigating the potential synergy cause-effect of fire and livestock to soil, vegetation, and food chain |
| Vegetation responses | Assessing aerial seed bank, seed dispersal and colonization |
| Invasion | Assessing the presence invasive alien plants (IAPs) at different scales to understand plant interaction with changes in fire regimes |
| Wildlife | Investigating the impact of fire severity, intensity, and fire regime on wildlife |
| Social and cultural knowledge | Including local and traditional knowledge (LK, TK), and other social issues as land use tenure into fire governance |
| Increasing research and transference | Increasing the effort of research and publication regarding fire regime and its effects, especially in Paraguay and Bolivia Linking social issues with ecological knowledge. |

contributes little to characterizing these attributes in a particular time-frame. Fire severity has generally been poorly studied. A few (2.20%) *in situ* studies have also fulfilled a double function by i) studying the immediate impact of fire on soil nutrients and degradation and further consequences on fertility and future recovery of the system, especially considering productive livestock systems and extensive crop systems, and ii) serving as validation of the data obtained by remote sensing data. In this respect, the effects of fire on soil pH, soil burn severity (SBS) and the relationships between fire intensity-duration and soil humidity are interesting aspects that should be addressed in the future. Further studies of fuel load in relation to fire occurrence are necessary to understand the current fire regime and for proposing fire management strategies at the regional scale.

The role of local communities in fire management, traditional fire use and the perception and knowledge held on the ground are discussed in the grey literature, mainly in national newspapers (La Voz 2021; La Nueva Mañana 2023; La Nación 2022), but are scarcely considered in peer-reviewed scientific literature (McDaniel et al., 2005; Devisscher et al. 2016; 2018; Coronel et al. 2021). Likewise, conflicts over land use changes and their relationship with dominant fire regimes, another relevant topic, are also seldomly (2.20%) considered in the specialized literature. Land use patterns and socioeconomic activities are other relevant aspects that should be taken into account in proposing a comprehensive fire management system.

To the best of our knowledge, there is no available study describing the obligate seeders of the Gran Chaco in detail. In addition to the already mentioned above, studies about aerial seed banks and dispersal are also required to further understand this regeneration strategy across the different ecosystems of this ecoregion. The presence of IAPs is often a consequence of ecosystem disturbance caused by fire. The presence of IAPs can be assessed at different spatial scales at which invasion is obviously driven by different processes. At the regional scale, invasion

studies often quantify the frequency of occurrence, or the area occupied across the landscape, while at the local level, studies are more focused on ecosystem impacts, comparison of performance of different species and the different acquisition or preservation of strategies for a given habitat and fire regime. In the case of the Chaco, local studies are more common, although the literature regarding IAPs remains scarce. In the coming years it will be interesting to elucidate the magnitude and importance of the presence of IAPs across other regions of the Chaco, as well as to scale up individual studies to the study of invasion at regional or landscape scale. Finally, few efforts to assess wildlife and biodiversity impacts after fire were identified in the published studies.

5. Conclusion

Fire regimes and their effects are key to understanding fire behaviour across the Gran Chaco region. The fire research community has made progress in the last decades to understand several aspects of fire regimes and their effects across this diverse and multicultural landscape. However, the imbalance in terms of research between the different countries of the study area seems evident. Therefore, a large effort should be made to address different aspects of fire research at a multiscale level to cover these gaps. Here, we shed some light on key progress, highlighting some of the main gaps (including geographical), issues, and priority topics to solve. Finally, it is also important to highlight the importance of increasing collaboration and alliances facing a common problem in a territory with different socioeconomic and governance contexts.

Web references & other Gray literature.

Aponte, M.A., Peñaranda, E. M. & Gutierrez, S. (2021). Impacto de incendios forestales mamíferos del Bosque Seco Chiquitano. Informe Técnico. Proyecto Bases del conocimiento para la restauración. Fundación para la conservación del Bosque Chiquitano. Museo de Historia Natural Noel Kempff Mercado. Santa Cruz, Bolivia, retrieved on Aug. 30, 2023 from <https://www.fcbc.org.bo/project/impacto-de-incendios-forestales-en-mamiferos-del-bosque-seco-chiquitano/>.

Aponte, M.A. (2021). Impacto de incendios forestales en aves del Bosque Seco Chiquitano. Informe Técnico. Proyecto Bases del conocimiento para la restauración. Fundación para la Conservación del Bosque Chiquitano. Museo de Historia Natural Noel Kempff Mercado. Santa Cruz, Bolivia, retrieved on Aug. 30, 2023 from <https://www.fcbc.org.bo/project/impacto-de-incendios-forestales-en-aves-del-bosque-seco-chiquitano/>.

Dirección General de Estadísticas y Censos (DGEEC) Paraguay. Población Paraguay, retrieved on Aug. 15, 2022, from <https://www.ine.gov.py/vt/Poblacion-Paraguay-2020-por-departamento-y-sexo-segun-proyeccion.php>.

FAOSTAT_data_en_11-1-2022, retrieved on Nov. 1st, 2022, from <https://www.fao.org/faostat/en/#data/QCL>.

Guyra Paraguay. (2019). Informe de Incendios en el área del Pantanal Paraguay 2019. 32p.

Instituto Nacional de Estadística y Censos de la República Argentina (2022), retrieved on Nov.3, 2022, from: <https://censo.gob.ar/>.

IPCC. SYNTHESIS REPORT OF THE IPCC SIXTH ASSESSMENT REPORT (AR6) Summary for Policymakers. Preliminary report 2023, retrieved on Mar. 28, 2023, from <https://www.ipcc.ch/report/sixth-assessment-report-cycle/>.

Navarro, L. M. (2016). Caracterización espacio temporal de los incendios en la provincia de Chaco y su relación con las actividades antrópicas. Facultad de Agronomía. Universidad de Buenos Aires. Retrieved on Feb.10, 2022, from <https://ri.agro.uba.ar/files/download/tesis/especializacion/2020navarroluismiguel.pdf>.

NOAA National Centers for Environmental Information, State of the Climate: Global Climate Report for 2021, retrieved on Jul. 12, 2022, from <https://www.ncdc.noaa.gov/sotc/global/202113>.

La Nación newspaper. Incendios forestales: Infona detectó 14.418 focos de calor entre julio y agosto, retrieved on Aug. 25, 2023, from: <https://www.lanacion.com.py/pais/2022/08/29/incendios-forestales-in>

fo-na-detecto-14418-focos-de-calor-entre-julio-y-agosto/.

La Voz newspaper. Crecen las brigadas comunitarias para ayudar en incendios en Cordoba, retrieved on Aug. 25,2023, from: <https://www.lavoz.com.ar/ciudadanos/crecen-las-brigadas-forestales-comunitarias-para-ayudar-en-incendios-en-cordoba/>.

La Nueva Mañana newspaper. Alto al fuego, retrieved on Aug. 25,2023, from: <https://lmdiarario.com.ar/contenido/389565/alto-al-fuego-las-brigadas-forestales-que-guardian-el-monte-cordobes>.

Pinto-Viveros, M.A. & Gonzales, L. (2021). Impacto de incendios forestales en anfibios y reptiles del Bosque Seco Chiquitano. Informe Técnico. Proyecto Bases del conocimiento para la restauración. Fundación para la Conservación del Bosque Chiquitano. Museo de Historia Natural Noel Kempff Mercado. Santa Cruz, Bolivia, retrieved on Aug. 30, 2023 from <https://www.fcbo.org.bo/project/impacto-de-incendios-forestales-en-anfibios-y-reptiles-del-bosque-seco-chiquitano/>.

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Data availability

No data was used for the research described in the article.

References

- Abella, S.R., Chiquoine, L.P., Vanier, C.H., 2013. Characterizing soil seed banks and relationships to plant communities. *Plant Ecology* 214, 703–715. <https://doi.org/10.1007/s11258-013-0200-3>.
- Abril, A., Bartfeld, P., Bucher, E., 2005. The effect of fire and overgrazing disturbs soil carbon balance in the dry chaco forest. *Forest Ecology and Management* 206, 399–405. <https://doi.org/10.1016/j.foreco.2004.11.014>.
- Adamoli, J., Sennhauser, E.B., Steel, J.M., Rescia, A., 1990. Stress and disturbance: vegetation dynamics in the dry chaco region of Argentina. *Journal of Biogeography* 17, 491–500.
- Albanesi, S., Dardanelli, S., Bellis, L.M., 2014. Effects of fire disturbance on bird communities and species of mountain serrano forest in central Argentina. *Journal of Forest Research* 19 (1), 105–114.
- Alessio, G., Penuelas, J., Llusia, J., Ogaya, R., Estiarte, M., De, M., 2008. Influence of water and terpenes on flammability in some dominant Mediterranean species. *International Journal of Wildland Fire* 17, 274–286. <https://doi.org/10.1071/WF07038>.
- Alinari, J., von Müller, A., Renison, D., 2015. The contribution of fire damage to restricting high mountain polylepis australis forests to ravines: Insights from an unreplicated comparison. *Ecologia Austral* 25, 11–18.
- Allen, E.B., Williams, K., Beyers, J.L., Phillips, M., Ma, S., D'Antonio, C.M., 2018. Chaparral restoration. In: Underwood, E.C., Safford, H.D., Molinari, N.A., Keeley, J. E. (Eds.), *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives*. Springer International Publishing, pp. 347–384. https://doi.org/10.1007/978-3-319-68303-4_13.
- Andela, N., Morton, D., Giglio, L., Chen, Y., Werf, G., Kasibhatla, P., Defries, R., Collatz, G., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F., Mangan, S., Melton, J., Yue, C., Randerson, J., 2017. A human-driven decline in global burned area. *Science* 356, 1356–1362. <https://doi.org/10.1126/science.aal4108>.
- Archibald, S., Lehmann, C.E.R., Belcher, C.M., Bond, W.J., Bradstock, R.A., Daniu, A.-L., Dexter, K.G., Forrester, E.J., Greve, M., He, T., Higgins, S.I., Hoffmann, W.A., Lamont, B.B., McGlenn, D.J., Moncrieff, G.R., Osborne, C.P., Pausas, J.G., Price, O., Ripley, B.S., Rogers, B.M., Schilck, D.W., Simon, M.F., Turetsky, M.R., Van der Werf, G.R., Zanne, A.E., 2018. Biological and geophysical feedbacks with fire in the earth system. *Environmental Research Letters* 13 (3), 033003.
- Argañaraz, J.P., Gavier, P.G., Zak, M., Landi, M.A., Bellis, L.M., 2015. Human and biophysical drivers of fires in semiarid chaco mountains of central Argentina. *Science of The Total Environment* 520, 1–12. <https://doi.org/10.1016/j.scitotenv.2015.02.081>.
- Argañaraz, J., Landi, M., Bravo, S., Gavier-Pizarro, G., Scavuzzo, C., Bellis, L., 2016. Estimation of live fuel moisture content from MODIS images for fire danger assessment in southern gran chaco. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 9, 5339–5349. <https://doi.org/10.1109/JSTARS.2016.2575366>.
- Assine, M., Merino, E., Pupim, F., Warren, L., Guerreiro, R., & McGlue, M. (2016). Geology and Geomorphology of the Pantanal Basin. In *Handbook of Environmental Chemistry* (pp. 23–50). 10.1007/698_2015_349.
- Barker, B.S., Pilliod, D.S., Rigge, M., Homer, C.G., 2019. Pre-fire vegetation drives post-fire outcomes in sagebrush ecosystems: evidence from field and remote sensing data. *Ecosphere* 10, 1–29. <https://doi.org/10.1002/ecs2.2929>.
- Baumann, M., Piquer-Rodríguez, M., Fehlenberg, V., Gavier Pizarro, G., Kuemmerle, T. (2016). Land-Use Competition in the South American Chaco. In *Land Use Competition. Human-Environment Interactions* (pp. 215–229). 10.1007/978-3-319-33628-2_13.
- Belcher, C., Yearsley, J., Hadden, R., Mclwain, J., Rein, G., 2010. Baseline intrinsic flammability of earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. *Proceedings of the National Academy of Sciences of the United States of America* 107, 22448–22453. <https://doi.org/10.1073/pnas.1011974107>.
- Bellis, L.M., Astudillo, A., Gavier-Pizarro, G., Dardanelli, S., Landi, M., Hoyos, L., 2021. Glossy privet (*Ligustrum lucidum*) invasion decreases chaco serrano forest bird diversity but favors its seed dispersers. *Biological Invasions* 23 (3), 723–739.
- Bernardi, R., Staal, A., Xu, C., Scheffer, M., Holmgren, M., 2019. Livestock herbivory shapes fire regimes and vegetation structure across the global tropics. *Ecosystems* 22, 1457–1465. <https://doi.org/10.1007/s10021-019-00349-x>.
- Boletta, P., Ravelo, A., Planchuelo, A., Grilli, M., 2006. Assessing deforestation in the Argentine chaco. *Forest Ecology and Management* 228, 108–114. <https://doi.org/10.1016/j.foreco.2006.02.045>.
- Bond, W., Keeley, J., 2005. Fire as a global 'Herbivore': the ecology and evolution of flammable ecosystems. *Trends in ecology & evolution* 20, 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J. E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., Pyne, S.J., 2009. Fire in the earth system. *Science* 324 (5926), 481–484.
- Bravo, S., Kunst, C., Gimenez, A., Moglia, G., 2001. Fire regime of an elionorus muticus spreg. Savanna, western chaco region. Argentina. *International Journal of Wildland Fire* 10, 65–72. <https://doi.org/10.1071/WF01014>.
- Bravo, S., Kunst, C., Grau, R., 2008. Suitability of the native woody species of the chaco region, Argentina, for use in dendroecological studies of fire regimes. *Dendrochronologia* 26, 43–52. <https://doi.org/10.1016/j.dendro.2007.05.004>.
- Bravo, S., Kunst, C., Grau, R., Araújo, E., 2010. Fire-Rainfall relationships in Argentine chaco savannas. *Journal of Arid Environments* 74, 1319–1323. <https://doi.org/10.1016/j.jaridenv.2010.04.010>.
- Bravo, S., Kunst, C., Leiva, M., Ledesma, R., 2014. Response of hardwood tree regeneration to surface fires, western chaco region, Argentina. *Forest Ecology and Management* 326, 36–45. <https://doi.org/10.1016/j.foreco.2014.04.009>.
- Bravo, S., Basualdo, M., Kunst, C., del Corro, F., 2019. Aerial bud bank and structural changes of woody species from Argentine chaco in response to disturbances. *Journal of environmental science and health - part A: environmental science and Engineering* 8, 58–69. <https://doi.org/10.17265/2162-5298/2019.02.002>.
- Bravo, S., Abdala, N., Ibañez Moro, A., 2022. Soil seed banks of dry tropical forests under different land management. *Forests* 14, 1–11. <https://doi.org/10.3390/f14010003>.
- Bravo, S., Bogino, S., Leiva, M., Lepiscopo, M., Cendoya, M., Kunst, C., & Biurrun, F. (2021). Wood anatomy, fire wounds and dendrochronological potential of *Prosopis pugiata* Burkart (Fabaceae) in arid Argentine Chaco. *IAWA Journal / International Association of Wood Anatomists*, 42, 1–10. 10.1163/22941932-bja10056.
- Brooks, M., D'Antonio, C., Richardson, D., Grace, J., Keeley, J., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688. [https://doi.org/10.1641/0006-3568\(2004\)054\[0677:EOIAP0\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAP0]2.0.CO;2).
- Bucher, E., 1987. Herbivory in arid and semi-arid regions of Argentina. *Revista Chilena de Historia Natural* 60, 265–273.
- Bucher, E., 1998. Sustainable land use management in the south American chaco. *Advances in GeoEcology* 31, 905–910.
- Bucher, E. H. (1982). Chaco and Caatinga—South American Arid Savannas, Woodlands and Thickets. In B. J. Huntley & B. H. Walker (Eds.), *Ecology of Tropical Savannas* (pp. 48–79). Springer. 10.1007/978-3-642-68786-0_4.
- Cadotte, M.W., Arnillas, C.A., Livingstone, S.W., Yasui, S.-L.-E., 2015. Predicting communities from functional traits. *Trends in Ecology & Evolution* 30, 510–511. <https://doi.org/10.1016/j.tree.2015.07.001>.
- Carbone, L.M., Aguilar, R., 2016. Contrasting effects of fire frequency on plant traits of three dominant perennial herbs from chaco serrano. *Austral Ecology* 41, 778–790. <https://doi.org/10.1111/aec.12364>.
- Carbone, L.M., Aguilar, R., 2021. Abiotic and biotic interactions as drivers of plant reproduction in response to fire frequency. *Arthropod-Plant Interactions* 15, 83–94. <https://doi.org/10.1007/s11829-020-09792-3>.
- Cardil, A., Mola-Yudego, B., Blázquez-Casado, Á., González-Olabarria, J.R., 2019. Fire and burn severity assessment: Calibration of relative differenced normalized Burn Ratio (RdNBR) with field data. *Journal of Environmental Management* 235, 342–349.
- Certini, G., 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143, 1–10. <https://doi.org/10.1007/s00442-004-1788-8>.
- Cingolani, A.M., Vaieretti, M.V., Giorgis, M.A., La Torre, N., Whitworth-Hulse, J.L., Renison, D., 2013. Can livestock and fires convert the sub-tropical mountain rangelands of central Argentina into a rocky desert? *The Rangeland Journal* 35 (3), 285.
- Cóbar, A., Pauchard, A., García, R., Peña, E., 2014. Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria*

- araucana and *Nothofagus Antarctica* forests. *Biological Invasions* 16, 2273–2291. <https://doi.org/10.1007/s10530-014-0663-8>.
- Coria, R.D., Bravo, S., Kunst, C., 2021. Un aporte al entendimiento de la lignificación de los pastizales/sabanas del Chaco Semiárido sudamericano. *Ecología Austral*, 31, 390–574. <https://doi.org/10.25260/EA.21.31.3.0.1615>.
- Coronel, G., et al., 2021. Wildfires in Paraguay: Environmental and human impacts. In: Leal Filho, W., Azeiteiro, U.M., Setti, A.F.F. (Eds.), *Sustainability in Natural Resources Management and Land Planning*. World Sustainability Series. Springer, Cham. https://doi.org/10.1007/978-3-030-76624-5_25.
- Dantas, V., Batalha, M., Pausas, J., 2013. Fire drives functional threshold on the savanna-forest transition. *Ecology* 94, 2454–2463. <https://doi.org/10.1890/12-1629.1>.
- Dantas, V., Pausas, J., 2022. The legacy of the extinct neotropical megafauna on plants and biomes. *Nature Communications* 13. <https://doi.org/10.1038/s41467-021-27749-9>.
- Davis, K., Maxwell, B., McWethy, D., Pauchard, A., Nuñez, M., Whitlock, C., 2016. *Pinus contorta* invasions increase wildfire fuel loads and may create a positive feedback with fire. *Ecology* 98, 678–687. <https://doi.org/10.1002/ecy.1673>.
- De Marzo, T., Gasparri, N., Lambin, E., Kuemmerle, T., 2022. Agents of forest disturbance in the Argentine dry chaco. *Remote Sensing* 14, 1–19. <https://doi.org/10.3390/rs14071758>.
- Devisscher, T., Boyd, E., Malhi, Y., 2016. Anticipating future risk in social-ecological systems using fuzzy cognitive mapping: the case of wildfire in the Chiquitania, Bolivia. *Ecology and Society* 21, 1–28. <https://doi.org/10.5751/ES-08599-210418>.
- Devisscher, T., Malhi, Y., Boyd, E., 2018. Deliberation for wildfire risk management: Addressing conflicting views in the Chiquitania, Bolivia. *The Geographical Journal* 185, 1–16. <https://doi.org/10.1111/geoj.12261>.
- FAO - Food and Agriculture Organization of the United Nations, 2018. *el estado de los bosques del mundo: las vías forestales hacia el desarrollo sostenible*. Roma, Editorial ONU.
- Fernández, P.D., Matthias, B., Germán, B., Natalia, B.R., Sandra, B., Ignacio, G.N., Mauro, L., Sofía, M., Sofía, N.A., Nasca, J.A., Torcuato, T., Ricardo, G.H., 2020. In: *Encyclopedia of the World's Biomes*. Elsevier, pp. 562–576.
- Feron, S., Cordero, R., Damiani, A., Llanillo, P., Jorquera, J., Sepulveda, E., Ascencio, V., Laroze, D., Labbe, F., Carrasco, J., Torres, G., 2019. Observations and projections of heat waves in South America. *Scientific Reports* 9, 1–15. <https://doi.org/10.1038/s41598-019-44614-4>.
- Ferreras, A.E., Galetto, L., 2010. From seed production to seedling establishment: important steps in an invasive process. *Acta Oecologica* 36 (2), 211–218.
- Fischer, M.D.L.A., Di Bella, C.M., Jobbágy, E.G., 2007. Factores que controlan la distribución espacio-temporal de los incendios en la región semiárida argentina. In XII Congreso de la Asociación Española de teledetección.
- Gale, M.G., Cary, G.J., Van Dijk, A.I.J.M., Yebra, M., 2021. Forest fire fuel through the lens of remote sensing: Review of approaches, challenges and future directions in the remote sensing of biotic determinants of fire behaviour. *Remote Sensing of Environment* 255, 112282.
- Gallo, VALERIA, AVILLA, L.S., PEREIRA, R.C.L., ABSOLON, B.A., 2013. Distributional patterns of herbivore megamammals during the late pleistocene of South America. *An. Acad. Bras. Cienc.* 85 (2), 533–546.
- García, R., Engler, M., Peñ, E., Pollnac, F., Pauchard, A., 2015. Fuel characteristics of the invasive shrub *telina monspessulana* (L.) K. Koch. *International Journal of Wildland Fire* 24, 372–379. <https://doi.org/10.1071/WF13078>.
- Ghermandi, L., Beletsky, N.A., de Torres Curth, M.L., Oddi, F.J., 2016. From leaves to landscape: A multiscale approach to assess fire hazard in wildland-urban interface areas. *Journal of Environmental Management* 183, 925–937. <https://doi.org/10.1016/j.jenvman.2016.09.051>.
- Giorgis, M., Zeballos, S., Carbone, L., Zimmermann, H., Von Wehrden, H., Aguilar, R., Ferreras, A., Tecco, P., Kowaljow, E., Barri, F., Gurvich, D., Villagra, P., Jaureguiberry, P., 2021. A review of fire effects across South American ecosystems: the role of climate and time since fire. *Fire Ecology* 17, 1–20. <https://doi.org/10.1186/s42408-021-00100-9>.
- González, C.C., Studdert, G., Kunst, C., Albanesi, A., 2001. Behavior of some soil properties in a savanna of the “Chaco semiárido occidental” under different fire histories. *Ciencia Del Suelo* 19, 92–100.
- González-Pérez, J., González-Vila, F.J., Almendros, G., Knicker, H., 2004. The effect of fire on soil organic matter—A review. *Environment International* 30, 855–870. <https://doi.org/10.1016/j.envint.2004.02.003>.
- Grassi, B., Pastén, A.M., Armoa, J., 2005. Un análisis del comportamiento de la precipitación en el Paraguay: Informe final. Facultad Politécnica, Universidad Nacional de Asunción, Asunción.
- Grau, A., Brown, A.D., 2000. Development threats to biodiversity and opportunities for conservation in the mountain ranges of the upper Bermejo river basin, NW Argentina and SW Bolivia. *AMBIO: A Journal of the Human Environment* 29, 445–450. <https://doi.org/10.1579/0044-7447-29.7.445>.
- Grau, H., Torres, R., Gasparri, N., Blendinger, P., Marinero, S., Macchi, L., 2014. Natural grasslands in the Chaco. A neglected ecosystem under threat by agriculture expansion and forest-oriented conservation policies. *Journal of Arid Environments* 123, 40–46.
- Guerra, C.A., Berdugo, M., Eldridge, D.J., Eisenhauer, N., Singh, B.K., Cui, H., Abades, S., Alfaro, F.D., Bamigboye, A.R., Bastida, F., Blanco-Pastor, J.L., de los Ríos, A., Durán, J., Grebenc, T., Illán, J.G., Liu, Y.-R., Makhalyane, T.P., Mamet, S., Molina-Montenegro, M.A., Moreno, J.L., Mukherjee, A., Nahberger, T.U., Peñaloza-Bojacá, G.F., Plaza, C., Picó, S., Verma, J.P., Rey, A., Rodríguez, A., Tedersoo, L., Teixido, A.L., Torres-Díaz, C., Trivedi, P., Wang, J., Wang, L., Wang, J., Zaady, E., Zhou, X., Zhou, X.-Q., Delgado-Baquerizo, M., 2022. Global hotspots for soil nature conservation. *Nature* 610 (7933), 693–698.
- Gurvich, D.E., Enrico, L., Cingolani, A.M., 2005. Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. *Austral Ecology* 30, 868–875. <https://doi.org/10.1111/j.1442-9993.2005.01529.x>.
- Hansen, M.C., Potapov, P., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J., 2013. High-Resolution global maps of 21st-Century forest cover change. *Science* 342, 850–853. <https://doi.org/10.1126/science.1244693>.
- Hargrove, W., Gardner, R.H., Turner, M., Romme, W., Despain, D.G., 2000. Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* 135, 243–263. [https://doi.org/10.1016/S0304-3800\(00\)00368-9](https://doi.org/10.1016/S0304-3800(00)00368-9).
- Hartung, M., van der Sande, M., Peña-Claros, M., Carreño-Rocabado, G., 2021. Tropical dry forest resilience to fire depends on fire frequency and climate. *Frontiers in Forests and Global Change* 4, 1–18. <https://doi.org/10.3389/ffgc.2021.755104>.
- Herrera, P., Torella, S., Adámoli, J., 2003. Los incendios forestales como modeladores del paisaje en la región chaqueña. In: Kunst, C., Bravo, S., Panigatti, J. (Eds.), *Fuego en los Ecosistemas Argentinos*. Ediciones INTA, Argentina, pp. 145–156.
- Herrero, M.L., Torres, R., Renison, D., 2016. Do wildfires promote woody species invasion in a Fire-Adapted ecosystem? post-fire resprouting of native and non-native woody plants in central Argentina. *Environmental Management* 57, 308–317. <https://doi.org/10.1007/s00267-015-0616-8>.
- Hoffmann, W.A., Moreira, A.G., 2002. The role of fire in population dynamics of woody plants. In: OLIVEIRA, O.S., MARQUIS, R.J., (Ed.), *Cerrados of Brazil*. Columbia University Press, New York, USA, pp. 159–177.
- Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C., Lloret, F., 2012. Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15 (7), 759–768.
- Hoyos, L., Gavier-Pizarro, G., Kuemmerle, T., Bucher, E., Radeloff, V., Tecco, P., 2010. Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the sierras chicas of Córdoba, Argentina. *Biological Invasions* 12, 3261–3275. <https://doi.org/10.1007/s10530-010-9720-0>.
- Ibañez Moro, A.V., Bravo, S.J., Abdala, N.R., Borghetti, F., Chaib, A.M., Galetto, L., 2021. Heat shock effects on germination and seed survival of five woody species from the Chaco region. *Flora* 275, 151751. <https://doi.org/10.1016/j.flora.2020.151751>.
- Jaureguiberry, P., 2012. Caracteres funcionales, flammabilidad y respuesta al fuego de especies vegetales dominantes en distintas situaciones de uso de la tierra en el centro-oeste de Argentina (Tesis doctoral). Universidad Nacional de Córdoba, Argentina.
- Jaureguiberry, P., Bertone, G., Díaz, S., 2011. Device for the standard measurement of shoot flammability in the field. *Austral Ecology* 36, 821–829. <https://doi.org/10.1111/j.1442-9993.2010.02222.x>.
- Jaureguiberry, P., Díaz, S., 2015. Post-burning regeneration of the Chaco seasonally dry forest: Germination response of dominant species to experimental heat shock. *Oecologia* 177, 689–699. <https://doi.org/10.1007/s00442-014-3161-x>.
- Jones, G., Tingley, M., 2021. Pyrodiversity and biodiversity: A history, synthesis, and outlook. *Diversity and Distributions* 28, 1–18. <https://doi.org/10.1111/ddi.13280>.
- Junk, W.J., Nunes da Cunha, C., 2012. Pasture clearing from invasive woody plants in the pantanal: A tool for sustainable management or environmental destruction? *Wetlands Ecology and Management* 20, 111–122. <https://doi.org/10.1007/s11273-011-9246-y>.
- Keeley, J., 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire* 18, 116–126. <https://doi.org/10.1071/WF07049>.
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16 (8), 406–411.
- Kowaljow, E., Morales, M.S., Whitworth-Hulse, J.I., Zeballos, S.R., Giorgis, M.A., Rodríguez Catón, M., Gurvich, D.E., 2019. A 55-year-old natural experiment gives evidence of the effects of changes in fire frequency on ecosystem properties in a seasonal subtropical dry forest. *Land Degradation & Development* 30, 266–277. <https://doi.org/10.1002/ldr.3219>.
- Kunst, C., 2011. Ecología y uso del fuego en la región chaqueña Argentina: Una revisión. *CIDEU* 10, 81–105.
- Kunst, C., Bravo, S., Monti, Cornacchione, M., & Godoy. (2003). El fuego y el manejo de pasturas naturales y cultivadas en la región chaqueña. In C. Kunst, S. Bravo y J. Panigatti Editors (Ed.), *Fuego en los ecosistemas argentinos* (pp. 1–12).
- Landi, M.A., Di Bella, C.M., Bravo, S.J., Bellis, L.M., 2021. Structural resistance and functional resilience of the Chaco forest to wildland fires: An approach with MODIS time series. *Austral Ecology* 46, 277–289. <https://doi.org/10.1111/aec.12977>.
- Lavorel, S., Flannigan, M.D., Lambin, E.F., Scholes, M.C., 2007. Vulnerability of land systems to fire: Interactions among humans, climate, the atmosphere, and ecosystems. *Mitigation and Adaptation Strategies for Global Change* 12, 33–53. <https://doi.org/10.1007/s11027-006-9046-5>.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* 16, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Lawes, M.J., Clarke, P.J., 2011. Ecology of plant resprouting: Populations to community responses in fire-prone ecosystems. *Plant Ecology* 212, 1937–1943. <https://doi.org/10.1007/s11258-011-9994-z>.
- Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.S., Bond, W.J., 2014. Savanna Vegetation-Fire-Climate relationships differ among continents. *Science* 343 (6170), 548–552.

- Lentile, L., Holden, Z., Smith, A., Falkowski, M., Hudak, A., Morgan, P., Lewis, S., Gessler, P., Benson, N., 2006. Remote sensing techniques to assess active fire characteristics and post-fire effects. *International Journal of Wildland Fire* 15, 319–345. <https://doi.org/10.1071/WF05097>.
- Lindskoug, H.B., 2016. Fire events, violence and abandonment scenarios in the ancient andes: the final stage of the aguada culture in the ambato valley, northwest argentina. *Journal of World Prehistory* 29, 155–214. <https://doi.org/10.1007/s10963-016-9095-y>.
- Lipoma, M.L., Funes, G., Díaz, S., 2018. Fire effects on the soil seed bank and post-fire resilience of a semi-arid shrubland in central argentina. *Austral Ecology* 43, 46–55. <https://doi.org/10.1111/aec.12533>.
- Lipoma, M.L., Fortunato, V., Enrico, L., Díaz, S., Bullock, J.M., 2020. Where does the forest come back from? soil and litter seed banks and the juvenile bank as sources of vegetation resilience in a semiarid neotropical forest. *Journal of Vegetation Science* 31 (6), 1017–1027.
- Lipoma, M., Gurvich, D., Urcelay, C., Díaz, S., 2016. Plant community resilience in the face of fire: Experimental evidence from a semi-arid shrubland. *Austral Ecology* 41, 501–511. <https://doi.org/10.1111/aec.12336>.
- Loto, D., Bravo, S., 2020. Species composition, structure, and functional traits in argentine chaco forests under two different disturbance histories. *Ecological indicators* 113, 106232. <https://doi.org/10.1016/j.ecolind.2020.106232>.
- Maillard, O., Vides-Almonacid, R., Flores-Valencia, M., Coronado, R., Vogt, P., Vicente-Serrano, S.M., Azurduy, H., Anívarro, R., Cuellar, R.L., 2020. Relationship of forest cover fragmentation and drought with the occurrence of forest fires in the department of santa cruz, bolivia. *Forests* 11, 1–16. <https://doi.org/10.3390/f11090910>.
- Maillard, O., Herzog, S.K., Soria-Auza, R.W., Vides-Almonacid, R., 2022. Impact of fires on key biodiversity areas (KBAs) and priority bird species for conservation in bolivia. *Fire* 5, 1–20. <https://doi.org/10.3390/fire5010004>.
- Marengo, J., Cunha, A.P., Cuatras, L., Deusdará-Leal, K., Broedel, E., Seluchi, M., Michelin, C., Baiaó, C., Chuchón Angulo, E., Almeida, E., Kazmierczak, M., Mateus, N., Silva, R., Bender, F., 2021. Extreme drought in the brazilian pantanal in 2019–2020: Characterization, causes, and impacts. *Frontiers in Water* 3, 639204. <https://doi.org/10.3389/frwa.2021.639204>.
- McDaniel, J., Kennard, D., Fuentes, A., 2005. Smokey the tapir: Traditional fire knowledge and fire prevention campaigns in lowland bolivia. *Society & Natural Resources - SOC NATUR RESOUR* 18, 921–931. <https://doi.org/10.1080/08941920500248921>.
- Mendoza, M. (2006). *Skulls Collected for Scalping in the Gran Chaco* (pp. 113–118).
- Mereles, M., Céspedes, G., De Egea, J., Spichiger, R., 2020. Estudios fitosociológicos en el gran chaco: Estructura, composición florística y variabilidad del bosque de *Schinopsis balansae* en el Chaco húmedo boreal, Paraguay. *Bonplandia* 29, 39–55. <https://doi.org/10.30972/bon.2914108>.
- Mereles, M., Céspedes, G., Cartes, J., Goerzen, R., De Egea, J., Rodríguez, L., Yanosky, A., Villalba, L., Gustafson, A., Cacciali, P., 2019. Biological Corridors as a Connectivity Tool in the Region of the Great American Chaco: Identification of Biodiversity Hotspots in the Ecoregions of the Paraguayan Chaco. *Research in Ecology*, 2, 27–36. <https://doi.org/10.30564/re.v2i1.1324>.
- Mereles, M., Rodas, O., 2014. Assessment of rates of deforestation classes in the paraguayan chaco (Great south american chaco) with comments on the vulnerability of forests fragments to climate change. *Climatic Change* 127, 55–71. <https://doi.org/10.1007/s10584-014-1256-3>.
- Morgan, P., Hardy, C., Swetnam, T., Rollins, M., Long, D., 2001. Mapping fire regimes across time and space: Understanding coarse and fine-scale fire patterns. *International Journal of Wildland Fire* 10, 329–342. <https://doi.org/10.1071/WF01032>.
- Naumann, C.M., Maldonado, P., Höhne, E., 2006. Atlas del gran chaco sudamericano. In: *Sociedad Alemana de Cooperación Técnica (GTZ). Buenos Aires. ErreGé & Asoc, Argentina*, p. 92 p..
- Neary, D.G., Klopatek, C.C., DeBano, L.F., Folliott, P.F., 1999. Fire effects on belowground sustainability: A review and synthesis. *Forest Ecology and Management* 122, 51–71. [https://doi.org/10.1016/S0378-1127\(99\)00032-8](https://doi.org/10.1016/S0378-1127(99)00032-8).
- Nogueira, J., Rambal, S., Barbosa, J.P., Mouillot, F., 2017. Spatial pattern of the seasonal drought/Burned area relationship across brazilian biomes: Sensitivity to Drought metrics and global Remote-Sensing fire products. *Climate* 5, 1–21. <https://doi.org/10.3390/cli5020042>.
- Ocampo-Zuleta, K., Bravo, S.J., 2019. Recruitment of woody species in tropical forests exposed to wildlandfires: an over-view. *Ecosistemas: Revista Científica y Tecnica de Ecología y Medio Ambiente* 28 (1), 106–117.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. terrestrial ecoregions of the world: A new map of life on earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2).
- Ormeño, E., Céspedes, B., Sánchez, I.A., Velasco-García, A., Moreno, J.M., Fernandez, C., Baldy, V., 2009. The relationship between terpenes and flammability of leaf litter. *Forest Ecology and Management* 257, 471–482. <https://doi.org/10.1016/j.foreco.2008.09.019>.
- Oyarzabal, M., Clavijo, J., Oakley, L., Biganzoli, F., Tognetti, P., Barberis, I., Maturó, H. M., Aragón, R., Campanello, P.I., Prado, D., Oesterheld, M., León, R.J.C., 2018. Unidades de vegetación de la argentina. *Ecología Austral* 28, 040–063. <https://doi.org/10.25260/EA.18.28.1.0.399>.
- Palma, C.D., Cui, W., Martell, D.L., Robak, D., Weintraub, A., Palma, C.D., Cui, W., Martell, D.L., Robak, D., Weintraub, A., 2007. Assessing the impact of stand-level harvests on the flammability of forest landscapes. *International Journal of Wildland Fire* 16, 584–592. <https://doi.org/10.1071/WF06116>.
- Palma, E., Mabey, A.L., Veski, P.A., Catford, J.A., 2021. Characterising Invasive Species. In: *Routledge Handbook of Biosecurity and Invasive Species*, pp. 15–39. Routledge.
- Paritsis, J., Landesmann, J., Kitzberger, T., Tiribelli, F., Sasal, Y., Quintero, C., Dimarco, R., Barrios-García, M.N., Iglesias, A., Diez, J., Sarasola, M., Nuñez, M., 2018. Pine plantations and invasion alter fuel structure and potential fire behavior in a patagonian Forest-Steppe ecotone. *Forests* 9, 1–16. <https://doi.org/10.3390/f9030117>.
- Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. *Bioscience* 59, 593–601. <https://doi.org/10.1525/bio.2009.59.7.10>.
- Pellegrini, A., Hedin, L., Staver, A., Govender, N., 2014. Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna. *Ecology* 96, 1275–1285. <https://doi.org/10.1890/14-1158.1>.
- Pennington, R.T., Hughes, C.E., 2014. The remarkable congruence of new and old world savanna origins. *new Phytologist* 204 (1), 4–6. <https://doi.org/10.1111/nph.12996>.
- Pivello, V., Guimarães Vieira, I., Christianini, A., Ribeiro, D., Menezes, L., Berlinck, C., Melo, F., Marengo, J., Tornquist, C., Tomas, W., Overbeck, G., 2021. Understanding brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation* 19, 233–255. <https://doi.org/10.1016/j.pecon.2021.06.005>.
- Prudhomme, C., Giuntoli, I., Robinson, E.L., Clark, D.B., Arnell, N.W., Dankers, R., Fekete, B.M., Franssen, W., Gerten, D., Gosling, S.N., Hagemann, S., Hannah, D.M., Kim, H., Masaki, Y., Satoh, Y., Stacke, T., Wada, Y., Wisser, D., 2014. Hydrological droughts in the 21st century, hotspots and uncertainties from a global multimodel ensemble experiment. *Proceedings of the National Academy of Sciences* 111, 3262–3267. <https://doi.org/10.1073/pnas.1222473110>.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, L., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. *Biological Reviews* 95 (6), 1511–1534.
- Rejzék, M., Coria, R.D., Kunst, C., Svátek, M., Kvasnica, J., Navall, M., Ledesma, R., Gómez, A., Matula, R., 2017. to chop or not to chop? tackling shrub encroachment by roller-chopping preserves woody plant diversity and composition in a dry subtropical forest. *Forest Ecology and Management* 402, 29–36. <https://doi.org/10.1016/j.foreco.2017.07.032>.
- Rodríguez, A., & Morello, J. (2009). *El Chaco sin bosques: La Pampa o el Desierto del Futuro*. ISBN 978-987-9260-73-9.
- Santacruz-García, A.C., Bravo, S., del Corro, F., Ojeda, F., 2019. A comparative assessment of plant flammability through a functional approach: the case of woody species from argentine chaco region. *Austral Ecology* 44, 1416–1429. <https://doi.org/10.1111/aec.12815>.
- Santacruz-García, A.C., Bravo, S., del Corro, F., García, E.M., Molina-Terrén, D.M., Nazareno, M.A., 2021. How do plants respond biochemically to fire? the role of photosynthetic pigments and secondary metabolites in the Post-Fire resprouting response. *Forests* 12, 1–20. <https://doi.org/10.3390/f12010056>.
- Silva, P., Nogueira, J., Rodrigues, J., Lemos, F., Pereira, J., Dacamara, C., Daldegan, G., Pereira, A., Peres, L., Schmidt, I., Libonati, R., 2021. Putting fire on the map of brazilian savanna ecoregions. *Journal of Environmental Management* 296, 1–14. <https://doi.org/10.1016/j.jenvman.2021.113098>.
- Silvério, D., Brando, P., Balch, J., Putz, F.E., Nepstad, D., Oliveira-Santos, C., Bustamante, M., 2013. Testing the amazon savannization hypothesis: Fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 368, 20120427. <https://doi.org/10.1098/rstb.2012.0427>.
- Smith-Ramírez, C., Castillo-Mandujano, J., Becerra, P., Sandoval, N., Fuentes, R., Allende, R., Paz Acuña, M., 2022. Combining remote sensing and field data to assess recovery of the chilean mediterranean vegetation after fire: Effect of time elapsed and burn severity. *Forest Ecology and Management* 503, 119800.
- Souza-Alonso, P., Saiz, G., García, R., Pauchard, A., Ferreira, A., Merino, A., 2022. Post-fire ecological restoration in latin american forest ecosystems: Insights and lessons from the last two decades. *Forest Ecology and Management* 509, 1–20. <https://doi.org/10.1016/j.foreco.2022.120083>.
- Speer, J.H., 2010. *Fundamentals of tree-ring research*. University of Arizona Press, Flagstaff, AZ.
- Speziale, K., Lambertucci, S., Ezcurra, C., 2013. *Bromus tectorum* invasion in south america: Patagonia under threat? *Weed Research* 54, 1–8. <https://doi.org/10.1111/wre.12047>.
- Spichiger, R., Ramella, L., Palese, R., Mereles, F., 1991. Proposición de leyenda para la cartografía de las formaciones vegetales del chaco paraguayo. III. *Candollea* 46, 541–564.
- Szpakowski, D.M., Jensen, J.L., 2019. A review of the applications of remote sensing in fire ecology. *Remote Sensing* 11, 1–31.
- Tecco, P.A., Gurvich, D.E., Díaz, S., Pérez-Harguindeguy, N., Cabido, M., 2006. Positive interaction between invasive plants: the influence of *Pyraecanthus angustifolia* on the recruitment of native and exotic woody species. *Austral Ecology* 31, 293–300. <https://doi.org/10.1111/j.1442-9993.2006.01557.x>.
- The Nature Conservancy (TNC), Fundación Vida Silvestre Argentina (FVSA), Fundación para el Desarrollo Sustentable del Chaco (DeSDelChaco) y Wildlife Conservation Society Bolivia (WCS), 2005. *Evaluación ecorregional del gran chaco americano/ Gran chaco Americano ecorregional assessment*. Buenos Aires, Argentina 2005, 28.
- Torrella, S., Ginzburg, R., Galetto, L., 2015. Forest fragmentation in the argentine chaco: Recruitment and population patterns of dominant tree species. *Plant Ecology* 216, 1499–1510. <https://doi.org/10.1007/s11258-015-0532-2>.

- Torres, R., Giorgis, M., Trillo, C., Volkman, L., Demaio, P., Heredia, J., Renison, D., 2013. Post-fire recovery occurs overwhelmingly by resprouting in the chaco serrano forest of central argentina. *Austral Ecology* 39. <https://doi.org/10.1111/aec.12084>.
- Torres, R.C., Renison, D., 2017. Human-induced vegetation changes did not affect tree progeny performance in a seasonally dry forest of central argentina. *Journal of Arid Environments* 147, 125–132.
- Ubeda, X., Sarricolea, P., 2016. Wildfires in chile: A review. *Global and Planetary Change* 146, 152–160. <https://doi.org/10.1016/j.gloplacha.2016.10.004>.
- Vergara-Tabares, D.L., Badini, J., Peluc, S., 2016. Fruiting phenology as a “triggering attribute” of invasion process: Do invasive species take advantage of seed dispersal service provided by native birds? *Biological Invasions* 18, 667–687. <https://doi.org/10.1007/s10530-015-1039-4>.
- Villalba, L., Ortiz, B., Gengler, N., 2018. Principales mamíferos del chaco central. WCS, WWF, USAID, p. 68.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Zeballos, S. R., Giorgis, M. A., Cabido, M. R., Acosta, A. T. R., Iglesias, M. del R., & Cantero, J. J. (2020). The lowland seasonally dry subtropical forests in central Argentina: Vegetation types and a call for conservation. *Vegetation Classification and Survey*, 1, 87–102. 10.3897/VCS/2020/38013.
- Zeballos, S.R., Giorgis, M.A., Cingolani, A.M., Cabido, M., Whitworth-Hulse, J.I., Gurvich, D.E., 2014. Do alien and native tree species from central argentina differ in their water transport strategy? *Austral Ecology* 39, 984–991. <https://doi.org/10.1111/aec.12171>.
- Zouhar, K., Smith, J.K., Sutherland, S., Brooks, M.L. (2008). Wildland fire in ecosystems. Fire and nonnative invasive plants. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA. 355 pp.

4.2 CHAPTER 2. ARTICLE 2: SPATIOTEMPORAL ANALYSIS OF WILDFIRES AND THEIR RELATIONSHIP TO CLIMATE AND LAND-USE IN THE GRAN CHACO AND PANTANAL ECOREGIONS

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Spatiotemporal analysis of wildfires and their relationship with climate and land use in the Gran Chaco and Pantanal ecoregions

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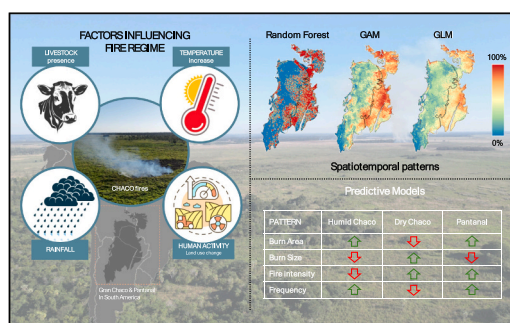
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HIGHLIGHTS

- This comprehensive approach assesses fire patterns in the Gran Chaco and Pantanal
- Our approach is based on remote data acquisition and spatiotemporal modelling
- Spatiotemporal patterns indicate an irregular trend in fire activity
- Climate, livestock and tree cover patterns are main drivers of fire activity
- Higher temperatures, lower rainfall, and livestock presence increase fire incidence

GRAPHICAL ABSTRACT



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ABSTRACT

The Gran Chaco and Pantanal ecoregions are the largest remaining dry forest areas in South America. Supporting diverse savanna, woodland and wetland ecosystems, these ecoregions are experiencing rapid changes in land use and fire occurrence with implications for ecosystem integrity. Our study characterizes the spatiotemporal patterns of wildfires in the Gran Chaco and Pantanal, and then examines the relationship between patterns of fire occurrence and climatic and anthropogenic drivers. We evaluated fire data of the last two decades (2001–2020) using the MODIS Collection 6.1 and the Global Fire Atlas products. Results of the fire pattern characterization were then used to model the probability of fire occurrence across each ecoregion (Random Forest, Generalized Linear Model, and Generalized Additive Model).

Our results indicated that most of the total burned area belonged to the Humid Chaco, while the largest individual burned areas were mainly observed in the Pantanal. Fires primarily occurred during the dry season, with the majority of burned areas recorded during this period. Findings from the three modelling approaches consistently illustrated the spatial distribution of fire occurrence, depicting a declining probability of fire

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occurrence from East to West. All models underscored the importance of three variables to predict fire occurrence: temperature, livestock abundance and forest cover. Fire occurrence increased with increasing maximum temperatures and livestock presence and decreased with tree cover. This research helps to clarify the potential consequences of changes in land use, rainfall regime and temperature, and uncontrolled burning practices on the current fire activity in the Gran Chaco and Pantanal ecoregions. Understanding the spatiotemporal patterns of fire occurrence and their relationship with climatic, environmental and anthropogenic drivers can help to design more effective management strategies to mitigate fire impacts and to preserve the ecological integrity of these highly diverse regions

1. Introduction

Fire plays a pivotal role in shaping natural ecosystems worldwide (Bowman et al., 2009; Armenteras and De la Barrera, 2023). The general impacts of fire on vegetation composition, structure, and hydrological cycles are well documented (Morgan et al., 2001; Falk et al., 2007; McLauchlan et al., 2020). To fully understand how these impacts manifest, it is essential to examine the specific dynamics and consequences of fire regimes, including their frequency, size, intensity, and interactions with vegetation and fuel availability (Whelan, 1995; Whitlock et al., 2010; Archibald et al., 2018). Furthermore, fire risk, hazard, and seasonality are critical factors in assessing the broader impacts of fire on ecosystems (Bond and Keeley, 2005; Giglio et al., 2006).

Given changing climatic conditions, fire activity is expected to increase, with extreme events becoming more frequent globally (Flannigan et al., 2006; Bowman et al., 2017; United Nations Environment Programme, 2022). This trend is already evident, with fire being recognized as a major cause of forest loss between 2010 and 2020, particularly in savannas and grassland ecosystems (FAO, 2020). As temperature and aridity increase, especially in fire-prone regions, understanding the specific impacts of these changes on fire dynamics is essential (Eskandari et al., 2020; Butsic et al., 2015; Marchal et al., 2017).

The South American Chaco (Gran Chaco) consists of an extensive semi-arid lowland dry broadleaf tropical forest that supports a diverse assemblage of flora and fauna. It is considered the second largest forested region in South America after the Amazon rainforest (Rodríguez and Morello, 2009; Assine et al., 2016). The Gran Chaco acts as an important corridor connecting species assemblages from the tropical (Amazon) regions and assemblages from the temperate belt (Atlantic forest) regions (Mereles et al., 2020). In addition, it is considered as one of the last extensive dry forest systems on earth (De la Sancha et al., 2021). The Gran Chaco consists of two distinct ecoregions: the Humid Chaco and the Dry Chaco. It is interlinked with the Pantanal, one of the largest protected tropical wetlands globally, where >84 % of the territory is recognized for its high ecological integrity (Libonati et al., 2020). Both aforementioned biomes are biodiversity hotspots that provide unique ecosystem services including critical water and soil resources (Thielen et al., 2021; Guerra et al., 2022).

Anthropogenic activities have significantly altered the natural vegetation in both the Gran Chaco and Pantanal. In the Gran Chaco, large-scale deforestation to enable expansion of agriculture and livestock has led to habitat fragmentation and loss of native species (Gasparri et al., 2008; Mosciaro et al., 2022). Although livestock grazing represents the primary land use across all regions, other economic activities include cultivation of monoculture crops, mostly soybean, sugarcane, wheat and corn (Baumann et al., 2016; Machado and Costa, 2018; Tomas et al., 2019) and also rice in wetter areas of these ecoregions (Laino et al., 2022). Intensive land management often involves the use of fire as an integral part to prepare land for pasture and agriculture, removing undesirable woody vegetation and promoting pasture renovation. Across the area, fire represents a vital disturbance process mediating the balance between grasses, shrubs and woody vegetation, given by complex interactions between factors such as moisture content, soil type and grazing (Delegido et al., 2017; Leal Filho et al., 2021; Vidal-

Riveros et al., 2023). The introduction of non-native species and the conversion of land to monoculture plantations have further disrupted the native ecosystems, reducing biodiversity and contributing to modifying fire regimes (Nogueira Junior et al., 2019). In the Pantanal, agricultural expansion, infrastructure development and wetland drainage have degraded natural habitats, increasing the frequency and intensity of fires, especially during drier periods (Marengo et al., 2021; Pott, 2020; Magalhães and Evangelista, 2022).

Although fire is an integral type of disturbance in the Gran Chaco, few studies have examined the specific role of fire in the system (Kunst, 2011). Bravo et al. (2010) explored temporal trends of fire by using tree rings and fire scars in relation to rainfall variability. Previous remote sensing studies have identified different spatiotemporal patterns of fire activity relating to climate, land cover and vegetation at multiple scales (Arganaraz et al., 2015, 2020; Maillard et al., 2022; San Martín et al., 2023). For instance, Correa et al. (2022) assessed the inter-annual variability in fire and land cover changes in the Pantanal between 2000 and 2021 by using the MCD64A1 V.6 product and Landsat LULC data. Naval et al. (2023) used Sentinel 2 imagery to map the 2020 fires and compared the data with historical data from 1987 to 2019, analyzing fire metrics such as number, size and frequency. Moreover, Marengo et al. (2021) used hydroclimatic data to analyze the impacts of the 2019–2020 drought in the Brazilian Pantanal. However, few studies have explored interactions and feedback between fire activity, ecosystem characteristics and the consequences in the Gran Chaco and Pantanal ecoregions. Indeed, recent studies indicate that fire activity in the Pantanal is expected to increase in the near future (Marques et al., 2021; Menezes et al., 2022; Libonati et al., 2022). Furthermore, in recent decades, increased anthropogenic burn frequency in these grassland and savanna environments is changing ecosystem dynamics in ways that are not well understood.

This study seeks to address the scarcity of information on historical patterns of fires, the drivers of fire activity and future projections for fire occurrence in the Gran Chaco and Pantanal. More specifically, we aim to better understand the spatiotemporal patterns of fire occurrence and intensity and how these patterns are related to climatic, environmental and anthropogenic drivers. Given the importance of fire as a disturbance process and the complex interplay between climatic, environmental and anthropogenic factors, we hypothesize that fire occurrence and intensity are strongly influenced by these drivers in the Gran Chaco and Pantanal ecoregions. To test this hypothesis, we analyzed the relationships between fire patterns and potential drivers over the past two decades (2001–2020) using remote sensing data and statistical models. We characterized fire activity—such as fire occurrence, burned area, and intensity—using data from the Fire Information for Resource Management System (FIRMS), MODIS Collection 6.1, and the Global Fire Atlas (GFA). We then explored the links between fire activity and factors like climate, topography, fuel, and land use, employing three statistical models (Random Forest, GAMs, GLMs) to predict fire occurrence in the three ecoregions. This approach enabled us to cross-validate data and gain deeper insights into fire dynamics in the Gran Chaco and Pantanal.

2. Materials and methods

2.1. Study area

This study focuses on the Gran Chaco and Pantanal ecoregions, which are ecologically diverse, fire-prone regions in South America spanning Paraguay, Brazil, Argentina and Bolivia. The study area includes three ecoregions following [Dinerstein et al. \(2017\)](#): the Dry Chaco (793,219 km²), the Humid Chaco (291,677 km²) and the Pantanal (170,452 km²), which together cover a total area of approximately 1,255,348 km² ([Fig. 1](#)). The Gran Chaco is a vast basin that extends across Argentina, Bolivia, Paraguay and southwestern Brazil ([Olson et al., 2001](#)), characterized by a subtropical climate with extreme summer temperatures (> 40 °C) and cool winter temperatures (< -10 °C). Precipitation decreases from east to west, ranging from a maximum of 1500 mm and a minimum of 700 mm ([Naumann et al., 2006](#)), and distributed in two clearly differentiated seasons: a dry season (July to September) and a rainy season (October to June) ([Arganaraz et al., 2015](#)). The differences in the rainfall regimes define the two clearly distinguished sub regions driven by the water availability gradient: the Humid Chaco and the Dry Chaco. Natural vegetation in the Gran Chaco is a direct result of climate, fire and topography, mainly consisting of a broad mosaic of different formations that includes closed dry forests, open forests, scrublands, and palm savannas ([Gasparri et al., 2008](#)). Representative species in the Dry Chaco include *Aspidosperma quebracho-blanco* and *Schinopsis lorentzii*, both of which are known for their fire-resistant characteristics, such as thick bark and deep roots ([Prado, 1993](#); [Rodríguez and Morello, 2009](#)). By contrast, the Humid

Chaco supports species like *Schinopsis balansae* and *Astronium urundeuva* in elevated areas with deep soils, while *Copernicia alba* appears in areas with greater water availability ([Mereles et al., 2020](#)).

In addition to the Humid and Dry Chaco, the study area includes a vast tropical mosaic of wetlands, grasslands and forests called the Pantanal. The Pantanal is located at the NE of the Gran Chaco, extending across the south of the Mato Grosso in Brazil, Bolivia and Paraguay ([Evans and Costa, 2013](#)). Known for its high diversity and richness of aquatic, wetland and many terrestrial species, the Pantanal is a large alluvial plain with various ecosystems characterized by periodic flooding. These ecosystems predominantly include savannas with aquatic plants, riparian and dry forests, forest islets, woodlands, grasslands and numerous monodominant formations ([Pott, 2020](#)). Representative species in the Pantanal include *Paspalum spp.*, *Cyperus spp.*, *Mimosa spp.*, *Eugenia spp.* and *Tabebuia aurea*, species adapted to survive in the fluctuating water conditions and periodic fires typical of the region ([Pott, 2020](#); [Manrique-Pineda et al., 2021](#)).

2.2. Data acquisition and fire regime characterization

To characterize a specific fire regime, several products are currently available for burnt areas, including Global Burnt Area 2000 (GBA, 2000) ([Grégoire et al., 2003](#)), L3JRC ([Tansey et al., 2008](#)), ATSR Global Burned Forest Mapping (GLOBSCAR) ([Simon et al., 2004](#)), Global Land Products for Carbon Model Assimilation (GLOBCARBON) ([Plummer et al., 2006](#)), Globfire ([Artés et al., 2019](#)), Global Fire Atlas (GFA) ([Andela et al., 2019](#)) and the MODIS MCD64A1 Collection 6.1 (MODIS; [Giglio et al., 2018](#)). We used GFA in conjunction with the MODIS to characterize fire

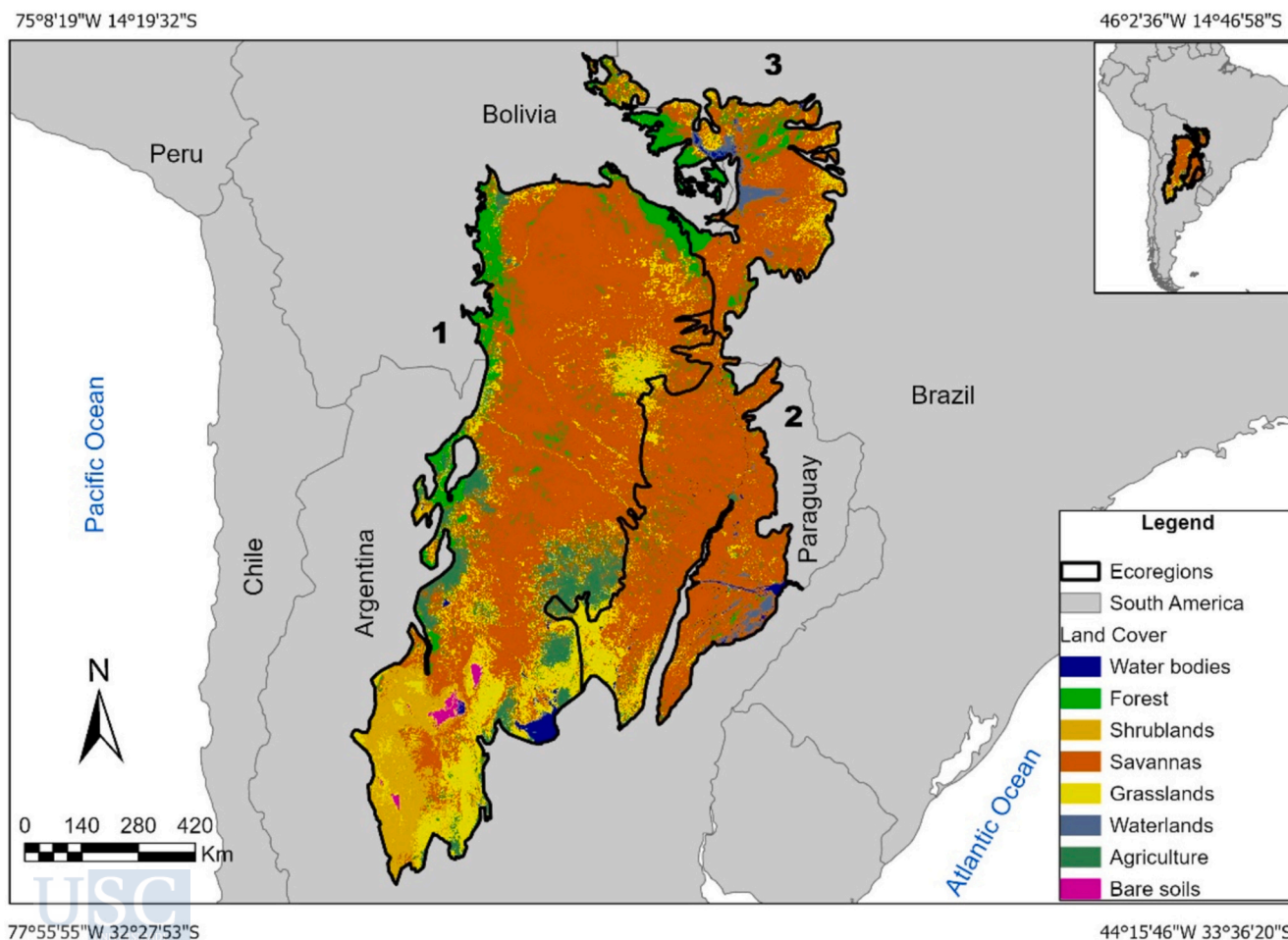


Fig. 1. Map of the study area with land cover types based on MODIS Land Cover Dynamics (MCD12Q1) Version 6.1, derived from the classification of the University of Maryland (UMD). The three studied ecoregions are labelled in black color as follows: 1 Dry Chaco; 2 Humid Chaco and 3 Pantanal.

patterns (Table 1). The GFA is a comprehensive dataset that provides detailed information about the timing, location and progression of individual fires worldwide, based on active fire detection and burned area data from the MODIS sensor. It provides high-resolution data on fire dynamics at the global scale, making it invaluable for fire regime characterization. The GFA dataset is publicly available through NASA's Earth Data platform, providing a crucial resource for fire activity studies. MODIS 6.1 is a monthly product, with spatial and temporal resolutions of 500 m and two days, respectively, and it has been successfully used in previous studies carried out in the region (Arganaraz et al., 2016; Landi et al., 2017; Maillard et al., 2022; Correa et al., 2022). Due to its higher temporal resolution, this dataset is a valuable data source, particularly in tropical conditions where post-fire signals are quickly obscured by sensors, and persistent cloud cover affects image quality (Chuvieco et al., 2018). For consistency, all product layers were projected to the WGS 1984 UTM 21 S coordinate system.

Fire frequency was calculated using GFA for 2003–2016 and the MODIS 6.1 product for the remaining study years (2001, 2002, and 2017–2020). Subsequently, all layers were converted to a binary raster (2.5 km² spatial resolution) categorizing 0 as the absence and 1 as the presence of fire. A frequency map (1 to 20) was created by adding all layers using raster; frequencies were then grouped into major categories: 0 (no fire event), 1 (low frequency, 1–2 fire events in the studied period), 2 (medium frequency, 3–4 fire events) and 3 (high frequency; > 4 fire events). This classification was then adapted to reflect local conditions. Fire Radiative Power (FRP) was used as a proxy for fire intensity (Laurent et al., 2018; Silva et al., 2021), with a 70 % confidence level. The zonal statistics tool in ArcGIS PRO 2.9 software was used to obtain an average intensity signal in 6.25 km² quadrants.

Similar to previous research (Silva et al., 2021), the burned area was categorized into small (<1000 ha), medium (1000–5000 ha) and large (>5000 ha) fire scars. Climate seasons were divided according to precipitation (wet and dry) and defined using the date of fire (date of year, DOY) obtained from GFA and MODIS 6.1 products. Monthly and yearly frequencies of occurrence were analyzed to identify patterns during the study period.

2.3. Modelling approach

The relationship between fire activity and potential drivers, including climate, topography, fuel and land use was examined by using three statistical models: Generalized Linear Models (GLM), Generalized Additive Models (GAM), and the decision tree classification algorithm Random Forest (RF), to predict the probability of fire occurrence for the Gran Chaco and Pantanal ecoregions. This combined approach using different statistical models enabled us to infer the spatial probability of fire occurrence (McWethy et al., 2018). These models were selected due to their proven effectiveness in predicting fire occurrence across various regions and their ability to offer distinct perspectives on the factors influencing fire dynamics (Bustillo Sánchez et al., 2021; Rodríguez-Pérez et al., 2020; Sydorenko et al., 2024). Random Forest (RF) is particularly useful for managing complex interactions between variables and has been successfully applied globally, in Mediterranean ecosystems, temperate forests and tropical regions (e.g. Rodríguez-Galiano et al., 2012; Eskandari et al., 2020). GLMs (Celebrezze et al., 2024; Beltrán-Marcos et al., 2024) and GAMs (Lindenmayer et al., 2023)

Table 1
Products used to characterize spatiotemporal patterns of fires.

| Variable | Format | Unit | Source |
|---|-----------|-------------------------------------|--------|
| Fire intensity | shapefile | Mega wats (MW) | FIRMS |
| Burnt area (2001, 2002, 2017, 2018, 2019, 2020) | shapefile | Date of year (DOY) | MODIS |
| Burnt area (2001–2020) | shapefile | Square kilometer (Km ²) | GFA |

complement RF by providing insights into linear and non-linear relationships, respectively. By adopting a multi-model approach, we not only enhance the reliability of our predictions but also provide a comprehensive analysis of the factors influencing fire occurrence. Each model has unique strengths: Random Forest for capturing complex interactions, GLMs for understanding linear relationships and GAMs for modelling non-linear dynamics (Breiman, 2001; Cutler et al., 2007; Dobson and Barnett, 2018; Wood, 2017).

2.4. Statistical analysis

We calculated the total accumulated annual Burned Area (BA) for each ecoregion. To compare the impact of fire occurrence, we also estimated the yearly Normalized Burned Area (NBA) for each of the ecoregions. The NBA is defined as the ratio between the total amount of BA (Ha) in each ecoregion and its respective total area (Ha). The normalization enabled us to account for differences in ecoregion sizes when assessing fire impact. To model the relationship between fire occurrence and human, climate and environmental variables, we used GLM, GAM, and RF. To compare classification categories among the models we used the Kappa statistic (κ), which quantifies the agreement between observed and predicted classifications (values 1 to 0) and it is particularly useful for assessing the accuracy of categorical models and provides a robust measure of model performance (Viera and Garrett, 2005).

The presence/absence of fires was the dependent variable. A set of 8 variables, categorized under topography, climate, fuel composition and land use criteria, was selected as explanatory factors for model input (Table 2). These variables were selected after a comprehensive literature review (Vidal-Riveros et al., 2023) for the study area and on the basis of expert criteria. The GEE platform was used to gather all variables using various algorithms developed for the study area, resulting in the calculation of averages for each variable for the 2001–2020 period. Livestock information for 2010 was sourced from the global product by Gilbert et al. (2018). In all instances, information was retrieved in raster format at a resolution of 1 km². Bilinear interpolation was used to rescale fire occurrence (originally at a 2.5 km² resolution) to assure consistency in the spatial scale across all variables. The statistical models were derived using R software Version 4.2.2 and Random Forest, Terra and Raster packages.

3. Results

3.1. Characteristics of the fire regime

Within the study period (2001–2020), the largest area was burned in 2020 (11.78 × 10⁶ ha) throughout the entire study area, followed by 2002 and 2007 (8.41 and 8.29 × 10⁶ ha, respectively) (Fig. 2). The burned area in 2020 was almost twice the mean value for the entire time series (6 × 10⁶ ha), accounting for 9.38 % of the area burned. Conversely, the smallest burned area was recorded in 2014 and 2018, affecting 1.98 % and 2.61 % of the study area respectively. Throughout the study period, the burned area fluctuated yearly with no discernible trend. The Humid Chaco contributed on average 40.45 % of the total burned area annually, followed by Dry Chaco (32.92 %) and Pantanal (26.63 %) (Fig. 3 a).

Analysis of the Normalized Burned Area (NBA) revealed that in each ecoregion, on average >2 % of the area was burned during the study period (Fig. 3 b). Notably, the NBA for the Pantanal was approximately five times greater than that of the Dry Chaco (10.15 % vs 2.39 %) reaching a peak value of 23.71 % in 2020. This year marked the highest recorded NBA for both the Humid Chaco and the Pantanal, while the lowest NBA occurred in 2018 in both ecoregions. In the Dry Chaco the peak of NBA was reached in 2003 (3.33 %), while the lowest rate was recorded in 2018 (1.49 %).

Fires predominantly occurred during the dry season (July to

Table 2
Predictive variables used to model fire drivers.

| Variable type | Variable name | Code | Units | Source |
|------------------|-------------------------|--------|---------------------------------------|--------------------------------------|
| Topographic | Elevation | DEM | Meter (m) | NASA ASTER GDEM |
| Climatic | Vapour pressure Deficit | VPD | Kilo pascal (kpa) | Abatzoglou et al., 2018 |
| | Precipitation | pr | Millimeter (mm) | Abatzoglou et al., 2018 |
| | Max. Temperature | Tmax | Degree Celsius | Abatzoglou et al., 2018 |
| Fuel composition | Net primary production | NPP | kgC/m ² /year | MODIS-MOD17A3 (Heinsch et al., 2003) |
| | Tree cover | TC | Percentage (%) | MODIS-006-MOD44B |
| | Land Cover | LC | University of Maryland Classification | MODIS-006-MCD12Q1 |
| Land use | Livestock | cattle | Number of animal head | Gilbert et al., 2018 |

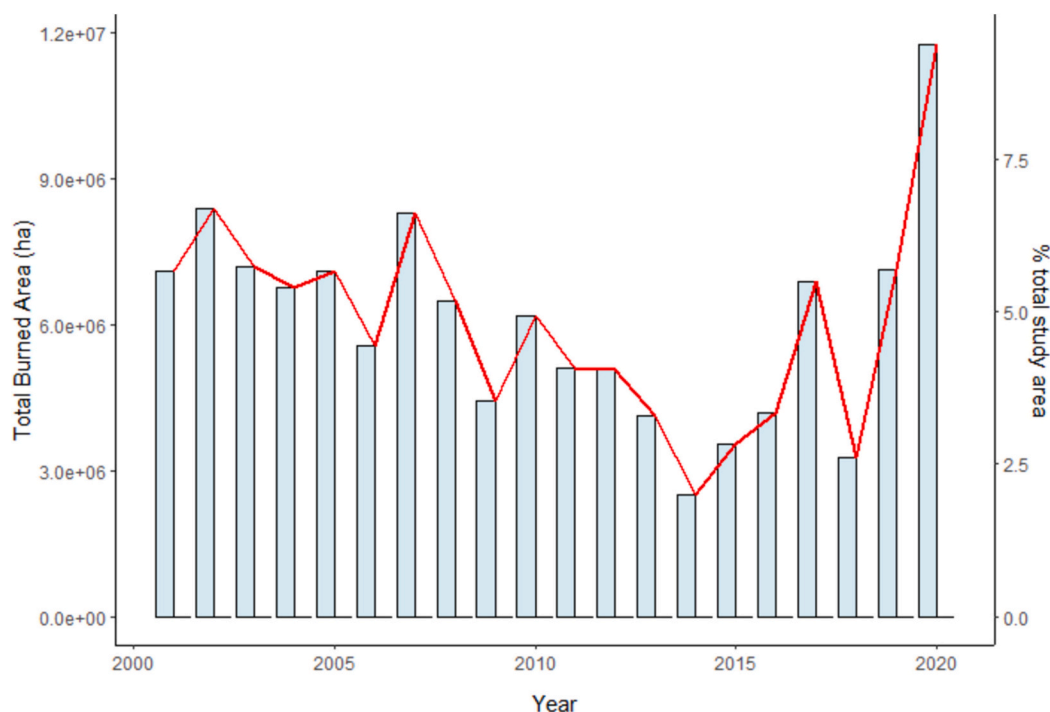


Fig. 2. Total burned area annually across the Gran Chaco and Pantanal: burned area (ha) during the time-span of the study separated by year (left axis in light blue bars) and percentage (%) of total study area burned annually (right axis in red line).

October), with >70 % of annual burned areas recorded during this four-month period (Fig. 3 c). Detailed observation of the patterns of burned area based on ecoregions revealed a slight increase in burned areas during the rainy season (January to March) in the Humid Chaco. On the other hand, an increase in fire patterns was observed in October and November in the Dry Chaco.

Considering the spatial distribution of fire scars, small fires (<1000 ha) accounted for 61.48 % of the total burned area during the study period, with medium (1000–5000 ha) and large fires (>5000 ha) representing 21.78 % and 16.74 %, respectively. Small and medium sizes were more prevalent in the Humid Chaco, while large fires occurred more frequently in the Pantanal (Fig. 4). The study area ecoregions exhibited different patterns in fire frequency (Pantanal > Humid Chaco > Dry Chaco) (Fig. SM1). Fires were most frequent in the Pantanal, occurring more than five times during the 2001–2020 period, followed by the Humid Chaco (3 to 4 fire occurrences) and the Dry Chaco (1 to 2 occurrences), indicating a lower occurrence than in the other ecoregions. No clear trend in fire intensity was observed throughout the time series (Fig. 5). Spatial analysis revealed that fire intensity was highest (1.3294×10^7 kW) in the Dry Chaco in 2010. On average, fire intensity in the Humid Chaco can be considered low, while in the Dry Chaco and the Pantanal fire intensity ranged from moderate to high.

3.2. Predictive models

Among the three models tested, Random Forest (RF) yielded the highest precision (87 %), with a Kappa concordance index of 0.74 (Fig. 6). The best performing general additive model (GAM) yielded a precision of 73 % and a Kappa concordance index of 0.43, while the best performing generalized linear model (GLM) yielded values of 70 % and 0.39, respectively. Based on variable importance, the RF model identified maximum temperature, tree cover and livestock as the most important variables affecting fire occurrence in the Chaco Region (Fig. 3-a).

While the RF model provided the best predictive performance, the relationship between individual predictor variables and the probability of fire occurrence is difficult to interpret. By contrast, although the GLM and GAM models performed less well than the RF model, they provided useful information on the relationship between predictor variables and fire activity (Fig. 6). The GLM model revealed positive correlations between temperature and fire occurrence and negative correlations between precipitation and Vapour Pressure Deficit (VPD) (Table 3-b). VPD was generally higher in the dry Chaco and lower in the Humid Chaco. Additionally, analysis of topographic variables showed that lower altitude above sea level increased fire probability. High net primary productivity (NPP) was positively correlated with fire occurrence. The percentage of tree cover was negatively correlated with fire probability,



Fig. 3. Burning area patterns in the three ecoregions for the study period (2001–2020): a) stacked bar chart representing the individual percentage (0–100 %) of the burned area attributed to each ecoregion (Dry Chaco, Humid Chaco and Pantanal); b) Average Normalized Burned Area (NBA) per year and c) distribution of accumulated burned area per month.

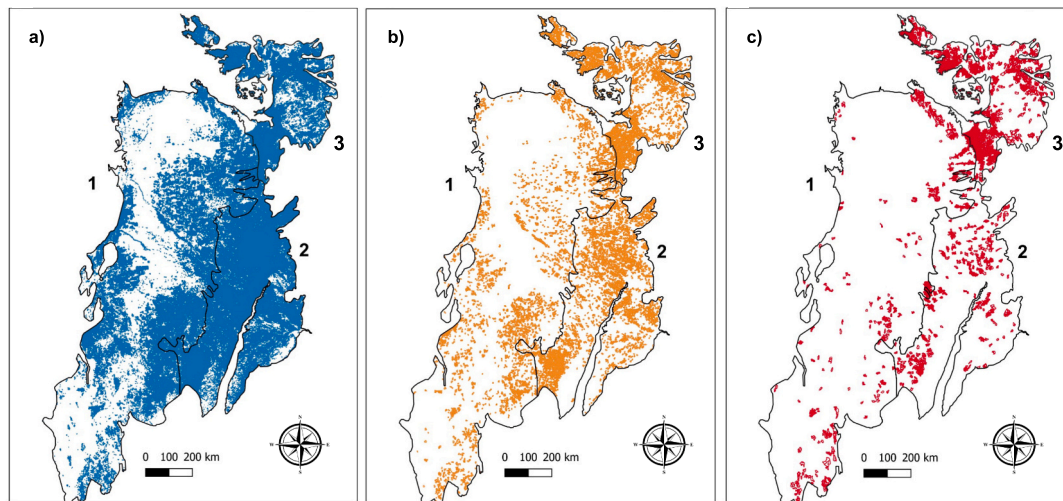


Fig. 4. Spatial distribution of fire scar size class over the 2001–2020 period in the three ecoregions: a) Small: < 1000 ha; b) Medium: 1000–5000 ha; c) Large: > 5000 ha. Ecoregions are labelled as follows: 1-Dry Chaco; 2-Humid Chaco; and 3-Pantanal.

while land use variables related to savannas and grasslands were positively correlated. Livestock was also positively correlated with fire occurrence. The GAM model yielded similar results but with higher prediction probabilities than the GLM. Unlike GLM, which uses simple coefficients, the GAM model uses smoothed functions to capture complex, non-linear relationships between the predictor variables and fire occurrence, providing more nuanced predictions (Table 3c).

Results of the three modelling approaches were consistent in depicting the spatial pattern of fire occurrence, indicating a decrease in fire probability from east to west. This indicates that fire occurrence was most pronounced in the Humid Chaco and the Pantanal.

4. Discussion

4.1. Characterizing fire patterns

Our study provides a comprehensive analysis of fire patterns over a 20-year period in the Gran Chaco and Pantanal regions, providing valuable insights into the spatial and temporal distribution of fire events. This characterization is crucial for understanding the dynamics of fire in these biodiverse and ecologically sensitive areas.

The prevalence of burning activity in the last two decades highlights the ubiquitous nature of fire as an important disturbance process shaping environmental conditions across the three ecoregions. Fire occurrence was most pronounced in all regions during the dry season,

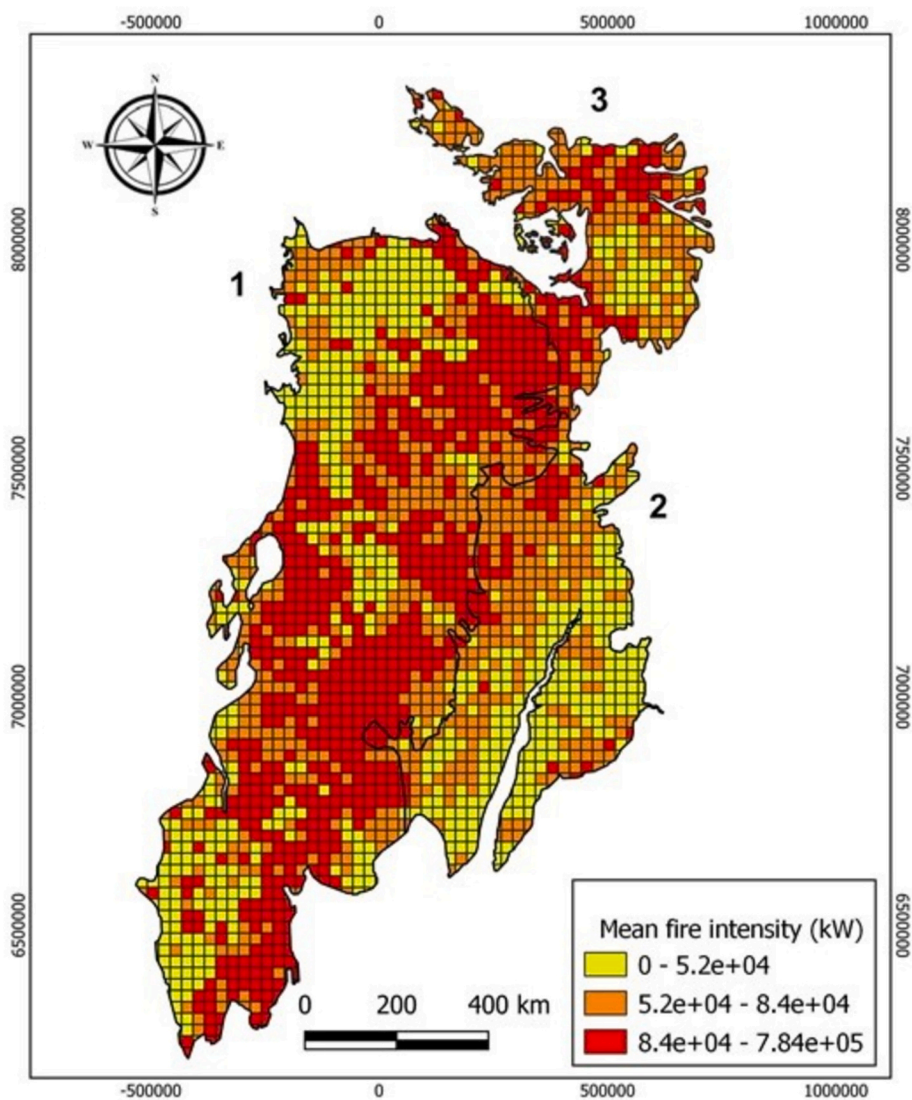


Fig. 5. Mean annual fire intensity (Kilowatts) across the three ecoregions during the last two decades. Ecoregions are divided into cells with a size of 6.25 km² and labelled as follows: 1-Dry Chaco; 2-Humid Chaco; and 3-Pantanal.

when the growth of fuels following the wet season provides abundant, connected and dry fuels. Notably, in 2020, when the highest total burned area of the decade was recorded -with almost 12 million hectares burnt- the precipitation decreased from 1433 mm to 940 mm. This reduction probably increased ignition rates and fire spread, as observed in studies attributing large fires in 2020 to extreme drought and high temperature (García and de Oliveira Roque, 2021; Mataveli et al., 2021; Marengo et al., 2021; Libonati et al., 2022). The extreme drought in 2020 greatly exacerbated fire activity, affecting almost one-third of the Pantanal region, with over 40,000 km² of natural vegetation and agricultural land burned and with severe repercussions on biodiversity (Libonati et al., 2022; Kumar et al., 2022). Additionally, the smoke from these fires contributed to increasing greenhouse gas emissions and coincided with the COVID-19 pandemic, posing an additional risk to public health by potentially exacerbating respiratory problems and interacting negatively with the ongoing epidemic (Oliveira et al., 2020).

Fire frequency was higher and fire intensity lower in the Humid Chaco and Pantanal than in the Dry Chaco, where fires were less frequent but more intense, in a pattern that is probably related, to fuel type and condition (San Martín et al., 2023). Fire intensity and behaviour are strongly influenced by several factors: land use, fuel abundance, type and condition, weather and ignition sources (Flannigan et al.,

2013). While fire frequency is higher in the Humid Chaco and Pantanal, fire intensity is comparatively lower in these ecoregions, for the following possible reasons: 1) the areas are dominated by savanna-type vegetation supporting frequent, low-severity fires and 2) higher fire occurrence reinforces the presence of more continuous, fine fuels that support low-intensity surface fires. The significant gradient in average annual precipitation (Fig. SM2), decreasing from east to west, favours water availability in Pantanal and Humid Chaco, which strongly influences the fuel type and condition. This increased rainfall regime results in eastern landscapes in the Humid Chaco and Pantanal being dominated by flooded pastures and small forest patches in small islands with an abundance of burnable fine fuel. The high rainfall regime in both ecoregions leads to high biomass accumulation, which under extreme summer temperatures (Fig. SM3) provides abundant, well-connected dry fuels that can facilitate fire spread. The increase in fire incidence during the dry season in the Humid Chaco and the Pantanal may therefore be mainly related to high biomass productivity, seasonal fuel drying and an increasing number of ignitions of anthropogenic origin (Archibald et al., 2013; San Martín et al., 2023).

By contrast, the less productive and connected fuels associated with the mosaic of woody and non-woody vegetation in the Dry Chaco results in infrequent, small fires. Here, a more heterogenous mosaic of forest,

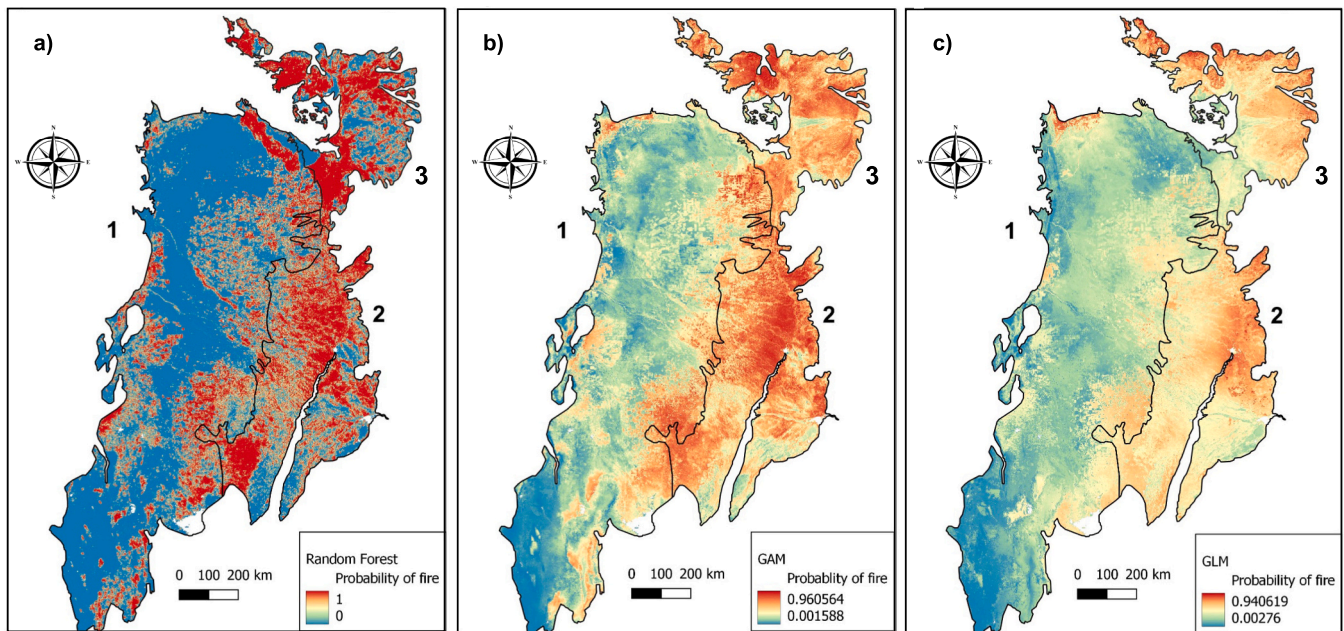


Fig. 6. Spatial distribution of the probability of fire occurrence derived from: a) Random Forest, b) GAM and c) GLM models. Values range from 0 to 1 (low to high probability of fire occurrence). Ecoregions are labelled in black as follows: 1-Dry Chaco; 2-Humid Chaco; and 3-Pantanal.

Table 3

Model results: a) Variable importance rankings for the RF model, based on Mean Decrease Accuracy and Mean Decrease Gini. Higher values for these indices indicate greater importance of the variable in predicting the outcome. b) Summary of the GLM model. c) GAM model fit statistics, including Estimated Degree of Freedom (EDF), Degree of Freedom (DF), Chi-Square, and *p*-value for continuous variables.

| Model | Variable | Mean Decrease Accuracy | Mean Decrease Gini | | |
|--------|---------------|------------------------|--------------------|------------|-----------|
| a) RF | DEM | 112.63 | 82,986.93 | | |
| | VPD | 117.71 | 60,584.17 | | |
| | Tree cover | 201.20 | 67,569.14 | | |
| | Precipitation | 104.84 | 68,108.49 | | |
| | Cattle | 177.93 | 115,101.70 | | |
| | NPP | 140.67 | 70,702.72 | | |
| | Tmax. | 210.06 | 96,127.98 | | |
| b) GLM | Variable | Estimate | Std. Error | Z Value | Pr(> z) |
| | Intercept | -2.583e+00 | 1.313e-01 | -19.673 | <2e-16*** |
| | DEM | -8.795e-04 | 1.355e-05 | -64.908 | <2e-16*** |
| | VPD | -3.294e-01 | 1.081e-02 | -30.481 | <2e-16*** |
| | Tree Cover | -2.867e-02 | 2.742e-04 | -104.541 | <2e-16*** |
| | Precipitation | -1.553e-02 | 1.094e-04 | -141.912 | <2e-16*** |
| | Cattle | 2.614e-05 | 1.750e-06 | 14.931 | <2e-16*** |
| | NPP | 8.269e-03 | 7.468e-05 | 110.729 | <2e-16*** |
| Tmax | 1.599e-01 | 1.387e-03 | 115.305 | <2e-16*** | |
| c) GAM | Variable | EDF | DF | Chi Square | p-value |
| | DEM | 8.832 | 8.98 | 5573 | <2e-16*** |
| | VPD | 8.942 | 8.99 | 2695 | <2e-16*** |
| | Tree cover | 8.5 | 8.93 | 5331 | <2e-16*** |
| | Precipitation | 8.89 | 8.99 | 3424 | <2e-16*** |
| | Cattle | 8.95 | 8.99 | 5191 | <2e-16*** |
| | NPP | 8.93 | 8.99 | 2260 | <2e-16*** |
| | Tmax. | 8.98 | 9.00 | 8349 | <2e-16*** |

scrublands, grasslands and savanna vegetation probably hinders fire spread but supports higher fire intensity when fires occur. This may result from woody vegetation accumulating under a regime of infrequent fires, which burn intensely in the presence of fire.

The irregular distribution of fire size across the Gran Chaco and Pantanal, with the predominant occurrence of small fires (<1000 ha), is a characteristic pattern of human transformed landscapes, where

deforestation and agriculture are prevalent (Archibald et al., 2013). On the other hand, larger fires were primarily concentrated in areas within the northeast region that are less impacted by grazing and agriculture, occupying a significant portion of the Pantanal ecoregion. These large fires may be the result from the interplay of an extended dry season and the presence of vast areas of well-connected fine fuels that dry seasonally (Marques et al., 2021; Bernardino et al., 2021). However, human

activities amplify environmental factors that control the presence of fire. In the Pantanal, most fires are of anthropogenic origin; only 5 % are attributed to natural causes (Menezes et al., 2022) and human activities are carried out in a large part of the burned area (84 %). Here, rangeland managers intentionally burn large areas of the Pantanal each year to improve range condition and forage availability. This intentional burning to expand rangelands for livestock farming and agriculture has a strong impact on patterns of fire activity, leading to an increase in fire frequency while decreasing fire intensity.

In the Pantanal, land use changes, infrastructure development and regional policies serve as fire precursors (Baumann et al., 2016; Leal Filho et al., 2021; Magalhães and Evangelista, 2022).

New infrastructure projects, such as roads, highways and urban expansion, are constructed in previously undeveloped areas, thus fragmenting natural habitats and introducing new ignition sources and increasing the likelihood of human-caused ignitions. Indeed, Magalhães and Evangelista (2022) suggested that the proximity of river and roads to wildland areas in the Pantanal were responsible for the worst fire episode recorded in its history. In the 2020 fire season, they found that most fire sources (60 %) were identified as being within 5 km of human infrastructures including roads, waterways, and railways.

In the Chaco ecoregions, the spatial distribution of fire is also related to human presence driven primarily by land use modification and fuel composition. In terms of structure and composition, the Humid Chaco shows some similarities with the Pantanal, where the vegetation also consists of grasslands, savannas and flooded woodlands, and fine fuels (grasses) are abundant and well-connected. Furthermore, livestock is more abundant in the Humid Chaco (1.1/km²) and in the Pantanal (0.85/km²), further promoting the predominance of grasses. Conversely, in the Dry Chaco fewer cattle (0.3/km²) and associated anthropogenic ignitions are combined sparse and less connected vegetation, limiting fire occurrence and spread (Zeballos et al., 2023). Restrictions on deforestation within the region have motivated the purchase of large areas of land in the Paraguayan Chaco, where clearing for grazing and agricultural activities are allowed (Milán and González, 2022). This situation led to increased use of fire for land clearing, cleaning, and grass renewal for cattle rearing. Therefore, regional policies may indirectly exert a strong influence on the shift in fire regimes.

4.2. Model results and predictions

The main results of all tested models (RF, GLM, GAM) reveal a consistent pattern of increasing fire occurrence across an east to west environmental gradient from the wetter Pantanal and Humid Chaco to drier Dry Chaco. Previous research has already highlighted the essential role of environmental factors in controlling fire distribution in subtropical ecosystems (Bravo et al., 2010, 2014; Roman-Cuesta et al., 2014). Grasslands and savanna systems often experience frequent fires and large burned areas after periods of fine fuel growth (increased precipitation) followed by fuel desiccation (drought) (Arganaraz et al., 2015).

Among the climatic factors influencing fire occurrence in the Gran Chaco and Pantanal regions, temperature, precipitation and vapour pressure deficit (VPD) are key variables. The Dry Chaco is characterized by higher temperatures and VPD, coupled with lower precipitation and is also the region with the lowest fire occurrence. On the other hand, the Humid Chaco and Pantanal are characterized by higher humidity. Unlike other regions where climatic factors may predominantly drive fire activity (Bradstock, 2010; Abatzoglou and Williams, 2016; Pausas and Ribeiro, 2013), the synergy with other factors, such as fuel availability and land use practices, better explains fire incidence in these ecoregions.

Therefore, climate variables alone cannot fully account for fire occurrence, as the presence of livestock and the percentage of tree cover have a notable influence on the outcome of the different models. In the GLM model, fire occurrence was positively related with the presence of cattle. During the last decades, the high global demand for meat has

promoted land use changes and increasing deforestation rates in these ecoregions (Canova et al., 2021). Livestock farmers, in turn, often use fire for pasture renewal and land clearing (Kunst, 2011). Regarding tree cover, our findings indicated an inverse relationship, with increased fire occurrence corresponding with diminished tree cover. This can probably be attributed to the increase abundance of fine herbaceous fuels in less forested areas, fine fuels that promote fire spread. In these ecoregions, several ecological studies have explored the flammability of native trees (Jaureguiberry et al., 2011; Santacruz-García et al., 2019). Although it is generally considered that dominant Chaco vegetation exhibits high to very high flammability, it is also important to note that many of the previous studies only focused on the Argentine Chaco region. As a result, the role that non-native trees play in mediating fire activity and intensity is still poorly understood and deserves to be addressed in greater detail in future studies.

Previous studies have highlighted the predominance of fire ignitions of anthropogenic origin (~90 %) in these ecoregions (Menezes et al., 2022). These human-driven ignition sources emphasize the need for future studies that address variables like land tenure, coordination of agricultural burning and burning calendars, and governance regarding burning regulation. The primary variable associated with human presence in our study was cattle. Cattle can have both positive and negative influences on fire occurrence in neotropical ecosystems. Positive feedback may arise when livestock graze on vegetation, thereby reducing fuel load and lowering the risk of large-scale wildfires (Bernardi et al., 2019). Conversely, there may be negative feedback when cattle managers contribute to human-caused ignitions by engaging in activities such as burning grasslands to clear vegetation (Pivello et al., 2021) thus preventing the regrowth of closed forests. This practice is common in these ecoregions, and when applied improperly and combined with climatic conditions, changes in land use can result in increased occurrence and intensity of wildfires. While our results indicated a positive correlation between fire occurrence and the presence of cattle, the relationship between human activity and fire needs further examination.

4.3. Uncertainties and limitations

Despite the comprehensive approach adopted in this study to analyze fire regimes and their drivers, some uncertainties and limitations remain. First, remote sensing data such as MODIS and the Global Fire Atlas, while providing extensive temporal and spatial coverage, also have some limitations in spatial resolution and underestimate both the frequency and extent of small and low-intensity fires (Giglio et al., 2006; Roy et al., 2008). MODIS sensor may miss up to 24–37 % of smaller fires and their associated burned area (Randerson et al., 2012; van der Werf et al., 2017) which is of particular importance in regions with frequent small-scale fires. Additionally, cloud cover and atmospheric conditions can obscure satellite observations, potentially affecting the accuracy of fire detection and estimation of the burned area (Roy et al., 2008). On the other hand, the temporal resolution used here may not have captured specific events that play important role in regional weather such as the South American low-level jet, upper-level jet stream, warm and cold fronts and the subtropical jet stream. These factors may influence fire occurrence and should be further studied using a more refined temporal scale.

Second, the study period (2001–2020) may not fully capture long-term trends and variability in fire activity, particularly in the context of climate change and evolving land use practices. The relatively short time frame may limit the ability to discern broader patterns and drivers of fire dynamics that operate on decadal scales. Future prospects should include extending the study period to encompass a longer time frame, which would provide more comprehensive insights into fire ecology trends and enhance the accuracy of conclusions about fire dynamics in these ecoregions.

Third, even though all models used in the study (RF, GLM, GAM) produced a good response, they also have some inherent limitations.

While Random Forest provided the best predictive performance, it is a black-box model making it difficult to interpret the relationships between predictor variables and fire occurrence. Conversely, GLM and GAM, though more interpretable, showed lower predictive accuracy. In the present study predictor variables were selected on the basis of a comprehensive literature review and expert criteria. Notwithstanding, models will probably benefit from the inclusion of socioeconomic variables, which are useful for relating wildfire risk and social vulnerability (Chas-Amil et al., 2022). Unfortunately, this type of data is not available or is difficult to access for the region.

Finally, as in most of the studies that consider climatic variables, there is some degree of uncertainty associated with the climatic and environmental data used as inputs for the models. Climate variables may yield different results depending on specific variables related to temperature and precipitation. Additionally, livestock data is very coarse and may not accurately reflect the current land use situation, leading to potential misinterpretations in model outputs.

4.4. Implications for management

The findings of this study have important implications for fire management in the Gran Chaco and Pantanal regions. Understanding the spatiotemporal patterns of fire occurrence and intensity and their relationship with climatic, environmental and anthropogenic drivers can provide relevant information for developing more effective fire management strategies.

At local scale and for landowners, the study findings highlight the importance of integrating climate change projections into fire management planning. With a potential increase in fire activity and extreme fire events under changing climatic conditions, managers need to develop adaptive strategies including enhancing firebreaks, implementing controlled burns under safer conditions during the appropriate season (Martins et al., 2022) or fostering land restoration using fire-resistant species adapted to local conditions. It is also important to implement preventive measurements to protect fire-sensitive moist forest such as gallery and riparian forests (Lapola et al., 2023) or sensitive species such as *Alchornea castaneifolia*, *Bactris glaucescens* and *Genipa americana* (Pott, 2020; Damasceno-Junior et al., 2021).

Forest degradation and changes in fuel composition to more homogeneous, continuous and highly susceptible to ignition landscapes also play a crucial role across these ecoregions. In the past two decades, there has been a significant increase in Eucalyptus plantations in Paraguay, Argentina, and Brazil, driven by the demand for pulp production (Grossman, 2015; Denegri et al., 2021; Florêncio et al., 2022). As observed elsewhere, the conversion of sparse, heterogeneous native vegetation to highly flammable, continuous and homogeneous eucalypt plantations, known for their highly susceptibility to ignition, can promote fire spread (Paritsis et al., 2018; McWethy et al., 2018). Additionally, the introduction of non-native grasses and shrubs in livestock and agricultural production increases the combustible biomass, diminishes tree cover, and promotes fire spread, resulting in a more frequent occurrence of large fires (Silvério et al., 2013; Maillard et al., 2020).

This study demonstrated that most fires occurred in the Humid Chaco and Pantanal ecoregions, which comprise a greater proportion of the land transformed by human activity, especially for livestock farming.

The significant role of anthropogenic factors in driving fire activity suggests that management efforts should also focus on regulating land use practices and the need for targeted fire adaptive management strategies and climate change. However, responses should be designed according to the specific needs of each country. Argentina and Paraguay face similar challenges, mainly related to deforestation for agricultural and livestock expansion. Although sustainable forest management and reforestation programs exist in Argentina, they are limited by resource shortages and fragmented policies (De Marzo et al., 2022). Similarly, the

enforcement of environmental laws is limited in Paraguay, where fire prevention programs require greater investment in infrastructure, funding and community participation (Coronel et al., 2021). In both cases, encouraging community involvement in fire prevention programmes, strengthening collaboration between government agencies and local communities and improving enforcement of environmental laws through adequate resources and training for local authorities are essential.

Bolivia faces similar challenges with land burning mainly due to agricultural expansion. Here, the “Law of Mother Earth” aims for sustainable management but struggles with enforcement due to lack of infrastructure and funding (Romero-Muñoz et al., 2019). Effective enforcement of environmental laws, investment in infrastructure and integrating traditional land-use practices with modern fire prevention strategies could help mitigate fire risks. Finally, the Pantanal has experienced devastating fires exacerbated by agricultural expansion and extreme climatic conditions in Brazil. Despite efforts like the Program for Prevention and Combating Fires in the Pantanal, coordination among local actors remains challenging (Libonati et al., 2022; Marengo et al., 2021). Improving coordination between federal, state and local authorities in fire prevention and integrating fire monitoring systems with land use planning are crucial. Although specifically indicated for the Brazilian case, there is a need for coordinated fire management across the Gran Chaco and Pantanal regions. Transboundary cooperation and sharing sustainable practices, data and resources could enhance the effectiveness of fire management strategies. Establishing regional fire management plans that account for the unique ecological and socio-economic contexts of each ecoregion could help mitigate the impacts of fire and preserve the ecological integrity of these highly diverse ecoregions.

5. Conclusions

Our study is the first spatiotemporal analysis of fire patterns in the Gran Chaco and Pantanal ecoregions. The findings highlight the influence of temperature, aridity, vegetation type and land use on driving fire activity and intensity within these ecoregions. The main findings suggest that conditions within the Humid Chaco and Pantanal ecoregions foster frequent large and less intense fires, whereas less frequent but more intense fires are favoured in the Dry Chaco ecoregion. Recurrent fires in the Humid Chaco and Pantanal are mainly of anthropogenic origin and are sustained by the abundance of fine fuels that in turn support recurrent and low-intensity fires. Higher temperatures, longer dry seasons and an increasing number of ignition sources (given by land use transformation), could amplify the prevalence of fire activity in the future, given the strong seasonality that promotes fuel drying and fire spread.

Our findings indicate that fire occurrence has remained relatively constant over the last two decades, with recurrence mainly depending on climatic and anthropic variables. Although an increase in fire occurrence was not observed, it is essential to focus on current management practices and environmental conditions that may influence future fire activity. Such practices include continued application of intentional burning to manage pastures, lack of management controls for intentional burning, and projected variation in precipitation and temperatures. Considering the positive correlation between fire occurrence and the presence of cattle, further studies should carry out detailed exploration of the relationship between human activity and fire, or the role of non-native grasses introduced for livestock production.

Predictive models are useful for understanding the distribution of historical fire events and exploring the variables responsible for its occurrence. These may be valuable tools that should be taken into consideration in the development of fire prevention and management systems. Unravelling the components of the fire regime and understanding their relationship with climate and anthropogenic variables are essential for developing effective fire management strategies in these

fire-prone ecoregions. By using GLM, GAM and Random Forest models, we also contribute to the growing body of literature on fire ecology by demonstrating the strengths and limitations of different statistical approaches in predicting fire occurrence. Our findings highlight the importance of using a combination of models to enhance the reliability and robustness of fire predictions and as valuable tools to develop fire prevention and fire management systems.

CRedit authorship contribution statement

Cristina Vidal-Riveros: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bryce Currey:** Visualization, Validation, Supervision, Software, Methodology, Formal analysis, Data curation. **David B. McWethy:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Conceptualization. **Marie Ange Ngo Bieng:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Pablo Souza-Alonso:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176823>.

Data availability

Data will be made available on request.

References

- Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A., Hegewisch, K.C., 2018. Terra climate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data* 5 (1), 170191. <https://doi.org/10.1038/sdata.2017.191>.
- Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci.* 113 (42), 11770–11775. <https://doi.org/10.1073/pnas.1607171113>.
- Andela, N., Morton, D.C., Giglio, L., Paugam, R., Chen, Y., Hantson, S., van der Werf, G.R., & Randerson, J.T. (2019). The global fire atlas of individual fire size, duration, speed, and direction. *Earth System Science Data*, 11(2), 529–552. doi:<https://doi.org/10.5194/essd-11-529-2019>.
- Archibald, S., Lehmann, C., Belcher, C., Bond, W., Bradstock, R., Daniau, A.-L., Dexter, K., Forrester, E., Greve, M., He, T., Higgins, S., Hoffmann, W., Lamont, B., McGlenn, D., Moncrieff, G., Osborne, C., Pausas, J., Price, O., Ripley, B., Zanne, A., 2018. Biological and geophysical feedbacks with fire in the earth system. *Environ. Res. Lett.* 13. <https://doi.org/10.1088/1748-9326/aa9ead>.
- Archibald, S., Lehmann, C., Gomez-Dans, J., Bradstock, R., 2013. Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci. USA* 110. <https://doi.org/10.1073/pnas.1211466110>.
- Arganaraz, J., Cingolani, A., Bellis, L., Giorgis, M., 2020. Fire incidence along an elevation gradient in the mountains of Central Argentina. *Southern Ecology* 30, 268–281.
- Arganaraz, J., Gavier-Pizarro, G., Zak, M., Bellis, L., 2015. Fire regime, climate, and vegetation in the sierras de Córdoba, Argentina. *Fire Ecol.* 11, 55–73. <https://doi.org/10.4996/fireecology.1101055>.
- Arganaraz, J., Landi, M., Bravo, S., Gavier-Pizarro, G., Scavuzzo, C., Bellis, L., 2016. Estimation of Live Fuel Moisture Content From MODIS Images for Fire Danger Assessment in Southern Gran Chaco. *IEEE J. Sel. Top. Appl. Earth Obs. Remote. Sens.* 9, 5339–5349. <https://doi.org/10.1109/JSTARS.2016.2575366>.
- Armenteras, D., De la Barrera, F., 2023. Landscape management is urgently needed to address the rise of megafires in South America. *Communications Earth & Environment* 4. <https://doi.org/10.1038/s43247-023-00964-6>.
- Artés, T., Oom, D., de Rigo, D., Durrant, T.H., Maianti, P., Libertà, G., San-Miguel-Ayanz, J., 2024. A global wildfire dataset for the analysis of fire regimes and fire behaviour. *Scientific Data* 6 (1), 296. <https://doi.org/10.1038/s41597-019-0312-2>.
- Assine, M., Merino, E., Pupim, F., Warren, L., Guerreiro, R., & McGlue, M. (2016). Geology and geomorphology of the Pantanal Basin. *En Handbook of Environmental Chemistry* (pp. 23–50). https://doi.org/10.1007/698_2015_349.
- Baumann, M., Piquer-Rodríguez, M., Fehlenberg, V., Gavier-Pizarro, G., & Kuemmerle, T. (2016). Land-use competition in the south American Chaco: (pp. 215–229). doi:https://doi.org/10.1007/978-3-319-33628-2_13.
- Beltrán-Marcos, D., Suárez-Seoane, S., Fernández-Guisuraga, J.M., Azevedo, J.C., Calvo, L., 2024. Fire regime attributes shape pre-fire vegetation characteristics controlling extreme fire behavior under different bioregions in Spain. *Fire Ecol.* 20 (1), 47. <https://doi.org/10.1186/s42408-024-00276-w>.
- Bernardi, R., Staal, A., Xu, C., Scheffer, M., Holmgren, M., 2019. Livestock herbivory shapes fire regimes and vegetation structure across the global tropics. *Ecosystems* 22, 1457–1465. <https://doi.org/10.1007/s10021-019-00349-x>.
- Bernardino, P. N., Dantas, V. L., Hirota, M., Pausas, J. G., & Oliveira, R. S. (2021). Savanna–Forest Coexistence Across a Fire Gradient. *Ecosystems*, 25, 279–290. doi:<https://doi.org/10.1007/s10021-021-00654-4>.
- Bond, W., Keeley, J., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J. E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Pyne, S.J., 2009. Fire in the earth system. *Science* 324, 481–484. <https://doi.org/10.1126/science.1163886>.
- Bowman, D.M.J.S., Williamson, G.J., Abatzoglou, J.T., Kolden, C.A., Cochrane, M.A., Smith, A.M.S., 2017. Human exposure and sensitivity to globally extreme wildfire events. *Nature Ecology & Evolution* 1. <https://doi.org/10.1038/s41559-016-0058>.
- Bradstock, R.A., 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Glob. Ecol. Biogeogr.* 19 (2), 145–158. <https://doi.org/10.1111/j.1466-8238.2009.00512.x>.
- Bravo, S., Kunst, C., Grau, R., Aráoz, E., 2010. Fire-rainfall relationships in Argentine Chaco savannas. *J. Arid Environ.* 74, 1319–1323. <https://doi.org/10.1016/j.jaridenv.2010.04.010>.
- Bravo, S., Kunst, C., Leiva, M., Ledesma, R., 2014. Response of hardwood tree regeneration to surface fires, western Chaco region, Argentina. *For. Ecol. Manag.* 326, 36–45. <https://doi.org/10.1016/j.foreco.2014.04.009>.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45 (1), 5–32. <https://doi.org/10.1023/A:1010933404324>.
- Bustillo Sánchez, M., Tonini, M., Mapelli, A., & Fiorucci, P. (2021). Spatial assessment of wildfires susceptibility in Santa Cruz (Bolivia) using random forest. *Geosciences*, 11 (5), Article 5. <https://doi.org/10.3390/geosciences11050224>.
- Butsic, V., Kelly, M., Moritz, M.A., 2015. Land use and wildfire: a review of local interactions and teleconnections. *Land* 4, 140–156. <https://doi.org/10.3390/land4010140>.
- Canova, E., García-Calabrese, M., Kriese, J., Cabral, N., Pérez de Molas, L., Alvarenga, M., Caceres, A., Gali, A., García, V., Morinigo, L., Ríos, M., Salinas, A., 2021. Understanding 34 years of Forest cover dynamics across the Paraguayan Chaco: characterizing annual changes and Forest fragmentation levels between 1987 and 2020. *Forests* 13, 25. <https://doi.org/10.3390/f13010025>.
- Celebrezze, J.V., Franz, M.C., Andrus, R.A., Stahl, A.T., Steen-Adams, M., Meddens, A.J. H., 2024. A fast spectral recovery does not necessarily indicate post-fire forest recovery. *Fire Ecol.* 20 (1), 54. <https://doi.org/10.1186/s42408-024-00288-6>.
- Chas-Amil, M.L., Nogueira-Moure, E., Prestemon, J.P., Touza, J., 2022. Spatial patterns of social vulnerability in relation to wildfire risk and wildland-urban interface presence. *Landsc. Urban Plan.* 228, 104577. <https://doi.org/10.1016/j.landurbplan.2022.104577>.
- Chuvieco, E., Lizundia-Loiola, J., Pettinari, M.L., Ramo, R., Padilla, M., Tansey, K., Mouillot, F., Laurent, P., Storm, T., Heil, A., Plummer, S., 2018. Generation and analysis of a new global burned area product based on MODIS 250 m reflectance bands and thermal anomalies. *Earth System Science Data* 10 (4), 2015–2031. <https://doi.org/10.5194/essd-10-2015-2018>.
- Coronel, G., Pastén, M., Breuer, N., Celeste, A., Rejalaga, L., Monte Domecq, F., Nagy, G. J., 2021. Wildfires in Paraguay: Environmental and human impacts. In: Leal Filho, W., Azeiteiro, U.M., Setti, A.F.F. (Eds.), *Sustainability in Natural Resources Management and Land Planning*. Springer, Cham, pp. 419–437. https://doi.org/10.1007/978-3-030-76624-5_25.
- Correa, D.B., Alcántara, E., Libonati, R., Massi, K.G., Park, E., 2022. Increased burned area in the Pantanal over the past two decades. *Sci. Total Environ.* 835, 155386. <https://doi.org/10.1016/j.scitotenv.2022.155386>.
- Cutler, D.R., Edwards Jr., T.C., Beard, K.H., Cutler, D.R., Hess, K.T., Gibson, J., Lawler, J. J., 2007. Random forests for classification in ecology. *Ecology* 88 (11), 2783–2792. <https://doi.org/10.1890/07-0539.1>.
- Damasceno-Junior, G. A., Pereira, A. de M. M., Oldeland, J., Parolin, P., & Pott, A. (2021). Fire, flood and Pantanal vegetation. In G. A. Damasceno-Junior & A. Pott (Eds.), *Flora and Vegetation of the Pantanal Wetland* (pp. 661–688). Springer International Publishing. doi:https://doi.org/10.1007/978-3-030-83375-6_18.
- De La Sancha, N., Boyle, S., McIntyre, N., Brooks, D., Yanosky, A., Soto, E., Mereles, M., Camino, M., Stevens, R., 2021. The disappearing dry Chaco, one of the last dry forest

- systems on earth. *Landsc. Ecol.* 36, 2997–3012. <https://doi.org/10.1007/s10980-021-01291-x>.
- De Marzo, T., Gasparri, N., Lambin, E., Kuemmerle, T., 2022. Agents of Forest disturbance in the Argentine dry Chaco. *Remote Sens.* 14. <https://doi.org/10.3390/rs14071758> **Cornel** 2021.
- Delegido, J., Pezzola, A., Casella, A., Winschel, C., Urrego, E.P., Jiménez-Muñoz, J.C., Soria, J., Sobrino, J., A. y Moreno, J., 2017. Potencialidad de índices de severidad de incendios utilizando Sentinel2 y su análisis comparativo con Landsat8 en el Sur de la provincia de Buenos Aires (Argentina) 2016–2017. XVII Congreso de la Asociación Española de Teledetección, XVII Congreso de la Asociación Española de Teledetección, Murcia.
- Denegri, G., Aguerre, M., Acciari, G., Denegri, G., Aguerre, M., Acciari, G., 2021. La expansión de las plantaciones forestales y su incidencia en la reducción de la superficie de bosques nativos en tres regiones de la República Argentina. *SaberEs* 13 (2), 137–158.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6), 534–545. <https://doi.org/10.1093/biosci/bix014>.
- Dobson, A.J., Barnett, A.G., 2018. *An Introduction to Generalized Linear Models*, 4th ed. Chapman and Hall/CRC. <https://doi.org/10.1201/9781315182780>.
- Eskandari, S., Pourghasemi, H.R., Tiefenbacher, J.P., 2020. Relations of land cover, topography, and climate to fire occurrence in natural regions of Iran: applying new data mining techniques for modeling and mapping fire danger. *For. Ecol. Manag.* 473, 118338. <https://doi.org/10.1016/j.foreco.2020.118338>.
- Evans, T.L., Costa, M., 2013. Landcover classification of the lower Nhecolândia subregion of the Brazilian Pantanal wetlands using ALOS/PALSAR, RADARSAT-2 and ENVISAT/ASAR imagery. *Remote Sens. Environ.* 128, 118–137. <https://doi.org/10.1016/j.rse.2012.09.022>.
- Falk, D.A., Miller, C., McKenzie, D., Black, A.E., 2007. Cross-scale analysis of fire regimes. *Ecosystems* 10, 809–823.
- FAO, 2020. *Global Forest resources assessment 2020 – key findings*. Rome. <https://doi.org/10.4060/ca8753en>.
- Flannigan, M., Amiro, B., Logan, K., Stocks, B., Wotton, M., 2006. Forest fires and climate change in the 21ST century. *Mitig. Adapt. Strateg. Glob. Chang.* 11, 847–859. <https://doi.org/10.1007/s11027-005-9020-7>.
- Flannigan, M., Cantin, M.D., Groot, A.S., Wotton, W.J., Newbery, M., Johnston, L., 2013. Global wildland fire season severity in the 21st century. *For. Ecol. Manag.* 294, 64–71. <https://doi.org/10.1016/j.foreco.2012.10.022>.
- Florêncio, G.W.L., Martins, F.B., Fagundes, F.F.A., 2022. Climate change on Eucalyptus plantations and adaptive measures for sustainable forestry development across Brazil. *Ind. Crop. Prod.* 188, 115538. <https://doi.org/10.1016/j.indcrop.2022.115538>.
- García, L.C., Szabo, J.K., de Oliveira Roque, F., de Matos Martins Pereira, A., Nunes da Cunha, C., Damasceno-Júnior, G.A., Morato, R.G., Tomas, W.M., Libonati, R., & Ribeiro, D.B. (2021). Record-breaking wildfires in the world's largest continuous tropical wetland: integrative fire management is urgently needed for both biodiversity and humans. *J. Environ. Manag.*, 293, 112870. doi:<https://doi.org/10.1016/j.jenvman.2021.112870>.
- Gasparri, N.I., Grau, H.R., Manghi, E., 2008. Carbon pools and emissions from deforestation in extra-tropical forests of northern Argentina between 1900 and 2005. *Ecosystems* 11, 1247–1261. <https://doi.org/10.1007/s10021-008-9190-8>.
- Giglio, L., Boschetti, L., Roy, D., Humber, M., Justice, C., 2018. The collection 6 MODIS burned area mapping algorithm and product. *Remote Sens. Environ.* 217, 72–85. <https://doi.org/10.1016/j.rse.2018.08.005>.
- Giglio, L., van der Werf, G.R., Randerson, J.T., Collatz, G.J., Kasibhatla, P., 2006. Global estimation of burned area using MODIS active fire observations. *Atmos. Chem. Phys.* 6 (4), 957–974. <https://doi.org/10.5194/acp-6-957-2006>.
- Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T.P., Vanwambeke, S.O., Wint, G.R.W., Robinson, T.P., 2018. Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Scientific Data* 5 (1), 180227. <https://doi.org/10.1038/sdata.2018.227>.
- Grégoire, J.-M., Tansey, K., Silva, J., 2003. The GBA2000 initiative: developing a global burnt area database from SPOT-VEGETATION imagery. *Int. J. Remote Sens.* 24, 1369–1376. <https://doi.org/10.1080/0143116021000044850>.
- Grossman, J.J., 2015. Eucalypts in agroforestry, reforestation, and Smallholders' conceptions of "Nateness": A multiple case study of plantation owners in eastern Paraguay. *Small-Scale Forestry* 14 (1), 39–57. <https://doi.org/10.1007/s11842-014-9272-8>.
- Guerra, C., Berdugo, M., Eldridge, D., Eisenhauer, N., Singh, B., Cui, H., Abades, S., Alfaro, F., Bamigboye, A., Bastida, F., Blanco-Pastor, J., De los Ríos, A., Durán, J., Grebenc, T., G. Illan, J., Liu, Y.-R., Makhalanyane, T., Mamet, S., Molina-Montenegro, M., & Delgado-Baquerizo, M., 2022. Global hotspots for soil nature conservation. *Nature* 610, 693–698. <https://doi.org/10.1038/s41586-022-05292-x>.
- Heinsch, F., Reeves, M., Votava, P., Kang, S., MMilessi, C., Zhao, M., Glassy, J., Jolly, W., Loehman, R., Bowker, C., Kimball, J., & Nemani, R. (2003). User's guide GPP and NPP (MOD17A2/A3) products NASA MODIS land algorithm. Version 2.0.
- Jaureguiberry, P., Bertone, G., Díaz, S., 2011. Device for the standard measurement of shoot flammability in the field. *Austral Ecol.* 36 (7), 821–829. <https://doi.org/10.1111/j.1442-9993.2010.02222.x>.
- Kumar, S., Getirana, A., Libonati, R., Hain, C., Mahanama, S., & Andela, N. (2022). Changes in land use enhance the sensitivity of tropical ecosystems to fire-climate extremes. *Scientific reports*, 12(1). Scopus. doi:<https://doi.org/10.1038/s41598-022-05130-0>.
- Kunst, C., 2011. Ecology and use of fire in the Chaco region of Argentina. *Bulletin informative CIDEU* 10, 81–105.
- Laino, R., Musalem, K., Laino, L.D., Caballero-Gini, A., Bueno-Villafina, D., Aranda, L., Esquivel, A., Riveros, M.F., Nardelli, L.R., Cantero, N., Irala, R., 2022. Islands of forests among savannas: Key elements for conservation and production in the Paraguayan humid Chaco. In: Montagnini, F. (Ed.), *Biodiversity Islands: Strategies for Conservation in Human-Dominated Environments*, vol. 20. Springer International Publishing, pp. 185–205. https://doi.org/10.1007/978-3-030-92234-4_8.
- Landi, M., Di Bella, C., Ojeda, S., Salvatierra, P., Arganaraz, J., Bellis, L., 2017. Selecting control sites for post-fire ecological studies using biological criteria and MODIS time series data. *Fire Ecol.* 13, 1–17. <https://doi.org/10.4996/fireecology.130274623>.
- Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E.O.C., Berenguer, E., Carmenta, R., Liddy, H.M., Seixas, H., Silva, C.V.J., Silva-Junior, C.H.L., Alencar, A.A.C., Anderson, L.O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M.H., Faria, B.L., Walker, W.S., 2023. The drivers and impacts of Amazon forest degradation. *Science* 379 (6630), eabp8622. <https://doi.org/10.1126/science.abp8622>.
- Laurent, P., Mouillot, F., Yue, C., Ciais, P., Moreno, M.V., Nogueira, J.M.P., 2018. FRY, a global database of fire patch functional traits derived from space-borne burned area products. *Scientific Data* 5. <https://doi.org/10.1038/sdata.2018.132>.
- Leal Filho, W., Azeiteiro, U.M., Salvia, A.L., Fritzen, B., Libonati, R., 2021. Fire in paradise: why the Pantanal is burning. *Environ. Sci. Pol.* 123, 31–34. <https://doi.org/10.1016/j.envsci.2021.05.005>.
- Libonati, R., Dacamara, C., Peres, L., Sander de Carvalho, L., Garcia, L., 2020. Rescue Brazil's burning Pantanal wetlands. *Nature* 588, 217–219. <https://doi.org/10.1038/d41586-020-03464-1>.
- Libonati, R., Geirinhas, J., S. Silva, P., Russo, A., Rodrigues, J., Belém, L., Nogueira, J., Roque, F., Dacamara, C., Nunes, A., Marengo, J., & Trigo, R. (2022). Assessing the role of compound drought and heatwave events on unprecedented 2020 wildfires in the Pantanal. *Environ. Res. Lett.*, 17, 015005. doi:<https://doi.org/10.1088/1748-9326/ac462e>.
- Lindenmayer, D., Taylor, C., Blanchard, W., Zylstra, P., Evans, M.J., 2023. What environmental and climatic factors influence multidecadal fire frequency? *Ecosphere* 14 (8), e4610. <https://doi.org/10.1002/ecs2.4610> **Viera & Garrett**, 2005.
- Machado, R.X., Costa, E.A., 2018. O turismo de pesca em Corumbá, na fronteira oeste do Brasil. *RITUR-Revista Iberoamericana de Turismo* 8 (1), 36–48.
- Magalhães, N., Evangelista, H., 2022. Human activity behind the unprecedented 2020 wildfire in Brazilian wetlands (Pantanal). *Front. Environ. Sci.* 10, 888578. <https://doi.org/10.3389/fevs.2022.888578>.
- Maillard, O., Herzog, S.K., Soria-Azuza, R.W., Vides-Almonacid, R., 2022. Impact of fires on key biodiversity areas (KBAs) and priority bird species for conservation in Bolivia. *Fire* 5 (1), 4. <https://doi.org/10.3390/fire5010004>.
- Maillard, O., Vides-Almonacid, R., Flores-Valencia, M., Coronado, R., Vogt, P., Vicente-Serrano, S.M., Azurduy, H., Anívarro, R., Cuellar, R.L., 2020. Relationship of Forest cover fragmentation and drought with the occurrence of Forest fires in the Department of Santa Cruz. *Bolivia. Forests* 11 (9), 910. <https://doi.org/10.3390/f11090910>.
- Manrique-Pineda, D.A., de Souza, E.B., Paranhos Filho, A.C., Cáceres Encina, C.C., Damasceno-Junior, G.A., 2021. Fire, flood and monodominance of *Tabeuia aurea* in Pantanal. *For. Ecol. Manag.* 479, 118599. <https://doi.org/10.1016/j.foreco.2020.118599>.
- Marchal, J., Cumming, S.G., McIntire, E.J.B., 2017. Land cover, more than monthly fire weather, drives fire-size distribution in southern Québec forests: implications for fire risk management. *PLoS One* 12 (6), e0179294. <https://doi.org/10.1371/journal.pone.0179294>.
- Marengo, J., Cunha, A.P., Cuartas, L., Deusdará-Leal, K., Broedel, E., Seluchi, M., Michelin, C., Baião, C., Chuchón Angulo, E., Almeida, E., Kazmierczak, M., Mateus, N., Silva, R., Bender, F., 2021. Extreme drought in the Brazilian Pantanal in 2019–2020: characterization, causes, and impacts. *Frontiers in Water* 3, 639204. <https://doi.org/10.3389/frwa.2021.639204>.
- Marques, J., Alves, M., Silveira, C., Amaral e Silva, A., Silva, T., Santos, V., & Calijuri, M., 2021. Fires dynamics in the Pantanal: impacts of anthropogenic activities and climate change. *J. Environ. Manag.* 299, 113586. <https://doi.org/10.1016/j.jenvman.2021.113586>.
- Martins, P.I., Belém, L.B.C., Szabo, J.K., Libonati, R., Garcia, L.C., 2022. Prioritising areas for wildfire prevention and post-fire restoration in the Brazilian Pantanal. *Ecol. Eng.* 176, 106517. <https://doi.org/10.1016/j.ecoleng.2021.106517>.
- Mataveli, G.A.V., Pereira, G., de Oliveira, F., Seixas, H.T., Cardoso, F.d.a S., Shimabukuro, Y.E., Kawakubo, F.S., Brunell, N.A., 2021. 2020 Pantanal's widespread fire: short- and long-term implications for biodiversity and conservation. *Biodivers. Conserv.* 30 (11), 3299–3303. <https://doi.org/10.1007/s10531-021-02243-2>.
- McLachlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Topley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Battlori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Watts, A.C., 2020. Fire as a fundamental ecological process: research advances and frontiers. *J. Ecol.* 108 (5), 2047–2069. <https://doi.org/10.1111/1365-2745.13403>.
- McWethy, D.B., Pauchard, A., García, R.A., Holz, A., González, M.E., Veblen, T.T., Stahl, J., Currey, B., 2018. Landscape drivers of recent fire activity (2001–2017) in south-Central Chile. *PLoS One* 13 (8), e0201195. <https://doi.org/10.1371/journal.pone.0201195>.
- Menezes, L.S., de Oliveira, A.M., Santos, F.L.M., Russo, A., de Souza, R.A.F., Roque, F.O., Libonati, R., 2022. Lightning patterns in the Pantanal: unglancing natural and anthropogenic-induced wildfires. *Sci. Total Environ.* 820, 153021. <https://doi.org/10.1016/j.scitotenv.2022.153021>.

- Mereles, M., Céspedes, G., De Egea, J., Spichiger, R., 2020. Estudios fitosociológicos en el gran Chaco: Estructura, composición florística y variabilidad del bosque de *Schinopsis balansae* en el Chaco húmedo boreal, Paraguay. *Bonplandia* 29, 39–55. <https://doi.org/10.30972/bon.2914108>.
- Milán, M., González, E., 2022. Beef–cattle ranching in the Paraguayan Chaco: typological approach to a livestock frontier. *Environ. Dev. Sustain.* 25, 5185–5210. <https://doi.org/10.1007/s10668-022-02261-2>.
- Morgan, P., Hardy, C., Swetnam, T., Rollins, M., Long, D., 2001. Mapping fire regimes across time and space: understanding coarse and fine-scale fire patterns. *Int. J. Wildland Fire* 10, 329–342. <https://doi.org/10.1071/WF01032>.
- Mosciaro, M., Calamari, N., Peri, P., Montes, N., Seghezzi, L., Ortiz, E., Rejalaga, L., Barral, M., Villarino, S., Mastrangelo, M., Volante, J., 2022. Future scenarios of land use change in the Gran Chaco: how far is zero-deforestation? *Reg. Environ. Chang.* 22. <https://doi.org/10.1007/s10113-022-01965-5>.
- Naumann, C.M., Maldonado, P., Höhne, E., 2006. Atlas del Gran Chaco Sudamericano. In: Sociedad Alemana de Cooperación Técnica (GTZ). Buenos Aires. *ErreGé & Asoc. Argentina*, p. 92.
- Naval, C., Albornoz, J., Bellis, L., Baldini, C., Arcamone, J., Silveti, L., Alvarez, M., Arganaraz, J., 2023. Megaincendios 2020 en Córdoba: Incidencia del fuego en áreas de valor ecológico y socioeconómico. *Ecol. Austral* 33, 136–151. <https://doi.org/10.25260/EA.23.33.1.0.2120>.
- Nogueira Junior, F.C., Pagotto, M.A., Aragão, J.R.V., Roig, F.A., Ribeiro, A.S., Lisi, C.S., 2019. The hydrological performance of *Prosopis juliflora* (Sw.) growth as an invasive alien tree species in the semiarid tropics of northeastern Brazil. *Biol. Invasions* 21, 2561–2575. <https://doi.org/10.1007/s10530-019-01994-y>.
- Oliveira, G., Chen, J., Stark, S., Berenguer, E., Moutinho, P., Artaxo, P., Anderson, L., Aragão, L., 2020. Smoke pollution's impacts in Amazonia. *Science* 369, 634–635. <https://doi.org/10.1126/science.abd5942>.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., et al., 2001. Terrestrial ecoregions of the world: A new map of life on earth. *BioScience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2).
- Paritsis, J., Landesmann, J., Kitzberger, T., Tiribelli, F., Sasal, Y., Quintero, C., Dimarco, R., Barrios-García, M.N., Iglesias, A., Diez, J., Sarasola, M., Nuñez, M., 2018. Pine plantations and invasion Alter fuel structure and potential fire behavior in a Patagonian Forest-steppe ecotone. *Forests* 9 (3), 117. <https://doi.org/10.3390/f9030117>.
- Pausas, J.G., Ribeiro, E., 2013. The global fire-productivity relationship. *Glob. Ecol. Biogeogr.* 22 (7), 728–736. <https://doi.org/10.1111/geb.12043>.
- Pivello, V., Guimarães Vieira, I., Christianini, A., Ribeiro, D., Menezes, L., Berlinck, C., Melo, F., Marengo, J., Tornquist, C., Tomas, W., Overbeck, G., 2021. Understanding Brazil's catastrophic fires: causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation* 19 (3), 233–255. <https://doi.org/10.1016/j.pecon.2021.06.005>.
- Plummer, S., Arino, O., Simon, M., Steffen, W., 2006. Establishing a earth observation product service for the terrestrial carbon community: the Globcarbon initiative. *Mittg. Adapt. Strateg. Glob. Chang.* 11 (1), 97–111. <https://doi.org/10.1007/s11027-006-1012-8>.
- Pott, A., 2020. What is the Flora of the Pantanal wetland? *Wetland Science & Practice* 37, 261–266. <https://doi.org/10.1672/UCRT083-203>.
- Prado, D.E., 1993. What is the Gran Chaco vegetation in South America? I: A review. Contribution to the study of flora and vegetation of the Chaco. V. (n.d.). Retrieved August 28, 2024, from: <https://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=4876384>.
- Randerson, J.T., Chen, Y., van der Werf, G.R., Rogers, B.M., Morton, D.C., 2012. Global burned area and biomass burning emissions from small fires. *Journal of geophysical research. Biogeosciences* 117 (G4). <https://doi.org/10.1029/2012JG002128>.
- Rodríguez, A.F., Morello, J.H. (Eds.), 2009. *El Chaco sin bosques: la pampa o el desierto del futuro*. GEPAMA, Universidad de Buenos Aires.
- Rodríguez-Galiano, V.F., Chica-Olmo, M., Abarca-Hernandez, F., Atkinson, P.M., Jegathanan, C., 2012. Random Forest classification of Mediterranean land cover using multi-seasonal imagery and multi-seasonal texture. *Remote Sens. Environ.* 121, 93–107. <https://doi.org/10.1016/j.rse.2011.12.003>.
- Rodríguez-Pérez, J.R., Ordóñez, C., Roca-Pardiñas, J., Vecín-Arias, D., Castedo-Dorado, F., 2020. Evaluating lightning-caused fire occurrence using spatial generalized additive models: A case study in Central Spain. *Risk Anal.* 40 (7), 1418–1437. <https://doi.org/10.1111/risa.13488>.
- Roman-Cuesta, R.M., Carmona-Moreno, C., Lizcano, G., New, M., Silman, M., Knoke, T., Malhi, Y., Oliveras, I., Asbjørnsen, H., Vuille, M., 2014. Synchronous fire activity in the tropical high Andes: an indication of regional climate forcing. *Glob. Chang. Biol.* 20 (6), 1929–1942. <https://doi.org/10.1111/gcb.12538>.
- Romero-Muñoz, A., Fernández-Llamazares, Á., Moraes, M.R., et al., 2019. A pivotal year for Bolivian conservation policy. *Nature Ecology & Evolution* 3 (6), 866–869. <https://doi.org/10.1038/s41559-019-0893-3>.
- Roy, D.P., Boschetti, L., Justice, C.O., Ju, J., 2008. The collection 5 MODIS burned area product—global evaluation by comparison with the MODIS active fire product. *Remote Sens. Environ.* 112 (9), 3690–3707. <https://doi.org/10.1016/j.rse.2008.05.013>.
- San Martín, R., Ottlé, C., Sörensson, A., 2023. Fires in the south American Chaco, from dry forests to wetlands: response to climate depends on land cover. *Fire Ecol.* 19, 57. <https://doi.org/10.1186/s42408-023-00212-4>.
- Santacruz-García, A.C., Bravo, S., del Corro, F., Ojeda, F., 2019. A comparative assessment of plant flammability through a functional approach: the case of woody species from Argentine Chaco region. *Austral Ecol.* 44 (8), 1416–1429. <https://doi.org/10.1111/aec.12815>.
- Silva, P., Nogueira, J., Rodrigues, J., Lemos, F., Pereira, J., Dacamara, C., Daldegan, G., Pereira, A., Peres, L., Schmidt, I., Libonati, R., 2021. Putting fire on the map of Brazilian savanna ecoregions. *J. Environ. Manag.* 296, 113098. <https://doi.org/10.1016/j.jenvman.2021.113098>.
- Silvério, D., Brando, P., Balch, J., Putz, F.E., Nepstad, D., Oliveira-Santos, C., Bustamante, M., 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 368, 20120427. <https://doi.org/10.1098/rstb.2012.0427>.
- Simon, M., Plummer, S., Fierens, F., Hoelzemann, J.J., Arino, O., 2004. Burnt area detection at global scale using ATSR-2: the GLOBSCAR products and their qualification. *J. Geophys. Res. Atmos.* 109 (D14). <https://doi.org/10.1029/2003JD003622>.
- Sydorenko, S., Gumeniuk, V., De Miguel-Díez, F., Soshenskiy, O., Budzinskiy, I., Koren, V., 2024. Assessment of the surface forest fuel load in the Ukrainian Polissia. *Fire Ecol.* 20 (1), 35. <https://doi.org/10.1186/s42408-024-00265-z>.
- Tansey, K., Grégoire, J.-M., Defourny, P., Leigh, R., Pekel, J.-F., van Bogaert, E., Bartholomé, E., 2008. A new, global, multi-annual (2000–2007) burnt area product at 1 km resolution. *Geophys. Res. Lett.* 35 (1). <https://doi.org/10.1029/2007GL031567>.
- Thielen, D., Ramoni-Perazzi, P., Puche, M.L., Márquez, M., Quintero, J.I., Rojas, W., Soto-Werschitz, A., Thielen, K., Nunes, A., Libonati, R., 2021. The pantanal under siege—on the origin, dynamics and forecast of the megadrought severely affecting the largest wetland in the world. *Water (Switzerland)* 13 (21). <https://doi.org/10.3390/w13213034>.
- Tomas, W. M., de Oliveira Roque, F., Morato, R. G., Medici, P. E., Chiaravallotti, R. M., Tortato, F. R., Penha, J. M. F., Izzo, T. J., Garcia, L. C., Lourival, R. F. F., Girard, P., Albuquerque, N. R., Almeida-Gomes, M., Andrade, M. H. da S., Araujo, F. A. S., Araujo, A. C., Arruda, E. C. de, Assunção, V. A., Battirola, L. D., ... Junk, W. J. (2019). Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. *Tropical Conservation Science*, 12, 1940082919872634. doi:<https://doi.org/10.1177/1940082919872634>.
- United Nations Environment Programme, 2022. *Spreading like Wildfire – The Rising Threat of Extraordinary Landscape Fires*. A UNEP Rapid Response Assessment, Nairobi.
- van der Werf, G.R., Randerson, J.T., Giglio, L., van Leeuwen, T.T., Chen, Y., Rogers, B.M., Mu, M., van Marle, M.J.E., Morton, D.C., Collatz, G.J., Yokelson, R.J., Kasibhatla, P. S., 2017. Global fire emissions estimates during 1997–2016. *Earth System Science Data* 9 (2), 697–720. <https://doi.org/10.5194/essd-9-697-2017>.
- Vidal-Riveros, C., Souza-Alonso, P., Bravo, S., Laino, R., Ngo Bieng, M.A., 2023. A review of wildfires effects across the Gran Chaco region. *For. Ecol. Manag.* 549, 121432. <https://doi.org/10.1016/j.foreco.2023.121432>.
- Viera, A.J., Garrett, J.M., 2005. Understanding interobserver agreement: the kappa statistic. *Fam. Med.* 37 (5), 360–363. <https://pubmed.ncbi.nlm.nih.gov/15883903/>.
- Whelan, R.J., 1995. *The Ecology of Fire*. Cambridge University Press, Cambridge United Kingdom.
- Whitlock, C., Higuera, P.E., McWethy, D.B., Briles, C.E., 2010. Paleocological perspective on fire ecology: revisiting the fire regime concept. *The Open Ecology Journal* 3, 6–23.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R*, 2nd ed. Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>.
- Zeballos, S., Acosta, A., Agüero, W., Ahumada, R., Almirón, M., Argibay, D., Arroyo, D., Blanco, L., Biurrun, F., Cantero, J., Márquez, J., Quiroga, A., Quiroga, E., Cabido, M., 2023. Vegetation types of the arid Chaco in Central-Western Argentina. *Vegetation Classification and Survey* 4, 167–188. <https://doi.org/10.3897/VCS.100532>.

4.3 CHAPTER 3. ARTICLE 3: ASSESSING FIRE REGIMES IN THE PARAGUAYAN CHACO: IMPLICATIONS FOR ECOLOGICAL AND FIRE MANAGEMENT

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f.- Names and affiliations of all the co-authors: The first author (Cristina Vidal-Riveros) is a PhD. student in at the University of Santiago de Compostela. The co-author Pablo Souza-Alonso is a Professor at the University of Santiago de Compostela and the thesis supervisor/tutor; and the co author Marie Ange Ngo Bieng is the thesis supervisor, she is affiliated at Center for International Cooperation in Agricultural Research (CIRAD) and the Tropical Agricultural Research & Higher Education Center-CATIE.

Assessing Fire Regimes in the Paraguayan Chaco: Implications for Ecological and Fire Management

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Abstract: This study analyzed the fire regime in the highly diverse Paraguayan Chaco, focusing on different aspects of fire patterns, including spatial (area burned) and temporal (frequency) aspects and magnitude (severity). We focused on fire as it is a natural phenomenon that drives ecosystem change and has significant economic, ecological and social impacts of particular concern in vulnerable ecosystems. Using the K-means clustering technique, we identified four distinct fire regimes in the study region: High (H), Moderately High (MH), Moderately Low (ML) and Low (L). On the one hand, the Dry Chaco predominantly featured Low and Moderately High regimes, characterized by a low fire frequency due to arid conditions. On the other hand, the Humid Chaco was particularly affected by agricultural burning, driven by extensive livestock activity and higher biomass productivity. Finally, in the Pantanal, the variations in fire intensity were influenced by flood pulses and rainfall patterns. Our findings highlight the distinct fire regimes across the Paraguayan Chaco and detail the differences in the regimes. The study's findings are valuable for developing efficient management strategies that account for fire behaviour during agricultural burning in this poorly studied region.

Keywords: fire regime; severity; frequency; area burned; land use change; climate change; fire management



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1. Introduction

Fire is a natural phenomenon in flammable landscapes, acting as a significant driver of ecological change with economic, ecological and social impacts [1]. These impacts are determined by the fire's behaviour within a specific time and space, known as the fire regime [2]. Fire regimes can generally be defined by spatial and temporal attributes and their magnitude, which collectively describe the role of fire in different ecosystems [3].

Spatial attributes are represented by the size of the burnt area and also include information regarding fire location [4]. Temporal attributes are represented by the seasonal distribution or fire frequency, i.e., the number of fires that occurred in a given period [5]. Variations in these attributes include the fire return interval, which is the time between fires at a specific point, expressed as a mean, median, minimum or maximum [3]. Fire frequency generally represents the temporal dimension in fire regime studies, but variations depend on the study objectives. For instance, the fire return interval is more informative for studying ecosystem degradation or resilience. Finally, fire magnitude is generally represented by fire intensity or fire severity, which represent distinct aspects of fire, although they are sometimes used interchangeably in non-specific studies. Fire severity is defined as the impact of fire on the ecosystem [6]. It is generally defined by burn indices such as the normalized burn ratio (NBR), differences in the NBR (dNBR) and relative differences in the NBR (RdNBR), using datasets to capture a wide range of fire conditions and characterize

landscape-to-regional-scale fire severity [7–9]. However, severity can also be assessed in the field by using observational data such as species composition and structure [10], seasonality [11] and the fire weather index [12].

Fire regime studies are common at global and continental scales [13]. For example, European pyroregions have been defined on the basis of burnt area, fire frequency, climate and fire seasonality [14]. In other cases, burnt area, number of fires and land cover types have been used to describe fire patterns [15]. In the mountainous regions of the US, fire regimes are characterized by severity and frequency [16], whereas in Australia, fire regimes have been shaped based on frequency and intensity [17].

In South America, several recent studies have expanded the understanding of fire regimes through diverse data sources and methodologies. For example, in Chile, the spatial and temporal dynamics of fires have been described using the national wildfire database provided by the Chilean Forest Service (CONAF) combined with monthly burned area (MODIS) data [18]. In Brazil, fire frequency and return intervals were analyzed over a 12-year period in a protected area of the Cerrado [19]. The drivers and effects of fire were assessed in the Argentinean Chaco, clearly highlighting differences between the Humid and the Dry Chaco, as well as revealing significant variations in fire behaviour and the impacts in different countries [20].

Despite the wealth of literature on fire regimes in fire-prone regions of South America, significant knowledge gaps remain, particularly in areas such as the Gran Chaco Americano in some of its regions, such as the Paraguayan Chaco, the most unexplored region within the Gran Chaco in terms of fire behaviour [21]. During the period 1999–2015, Paraguay had the fourth largest number of wildfires in South America, even surpassing Brazil in terms of the average number of fire outbreaks, thus indicating the very high incidence of fires in the country [22]. This issue highlights the urgent need for fire regime studies to understand impacts, propose management actions and preserve land. This study aimed to model the fire regime in the Paraguayan Chaco, considering spatial (area burnt) and temporal (frequency) attributes and magnitude (severity).

2. Materials and Methods

2.1. Description of Study Area

The study area encompasses three ecoregions in the South American continent (Figure 1a): the Dry Chaco, the Humid Chaco and the Pantanal, collectively known as the Gran Chaco Americano, which spans an area of 1,141,000 km² (Figure 1b). These ecoregions are shared by four countries: Argentina (60%), Paraguay (27%), Bolivia (11%) and Brazil (2%) [23].

Climatically, the Chaco region experiences a pronounced dry season (May to September) with average monthly temperatures reaching 29 °C. The rainfall gradient varies between 1200 mm in the east to 450 mm in the centre, resulting in highly heterogeneous vegetation. The eastern Chaco, the wettest part, comprises extensive wetlands and is mainly dominated by wet savannas, comprising a mosaic of dense or open woodland patches interspersed with grasslands [24].

The Paraguayan Chaco (Figure 1c) represents a large portion of the Gran Chaco, covering an area of 230,000 km² and including the departments of Boquerón, Alto Paraguay and Presidente Hayes [25]. It is located to the west of the Paraguay river, which serves as a natural border dividing the country into two distinct regions. The climate is semi-arid, with an average rainfall of 400 mm. Rainfall distribution is uneven, with the north and northwest receiving between 400 and 800 mm/year, mostly during spring and summer. By contrast, the northeast, east and southeast, closer to the Paraguay River, receive 1300–1400 mm of rainfall a year, with more regular distribution. Consequently, there is a pronounced east–west gradient in precipitation and humidity, with increasing aridity towards the west, culminating in the driest areas near the Andean foothills [26]. Winters are extremely dry, with rainfall in July–August not exceeding 34 mm/year. Average temperatures range between 13 and 34 °C, with summer peaks of 45–48 °C and winter lows of –3 to –7 °C [27].

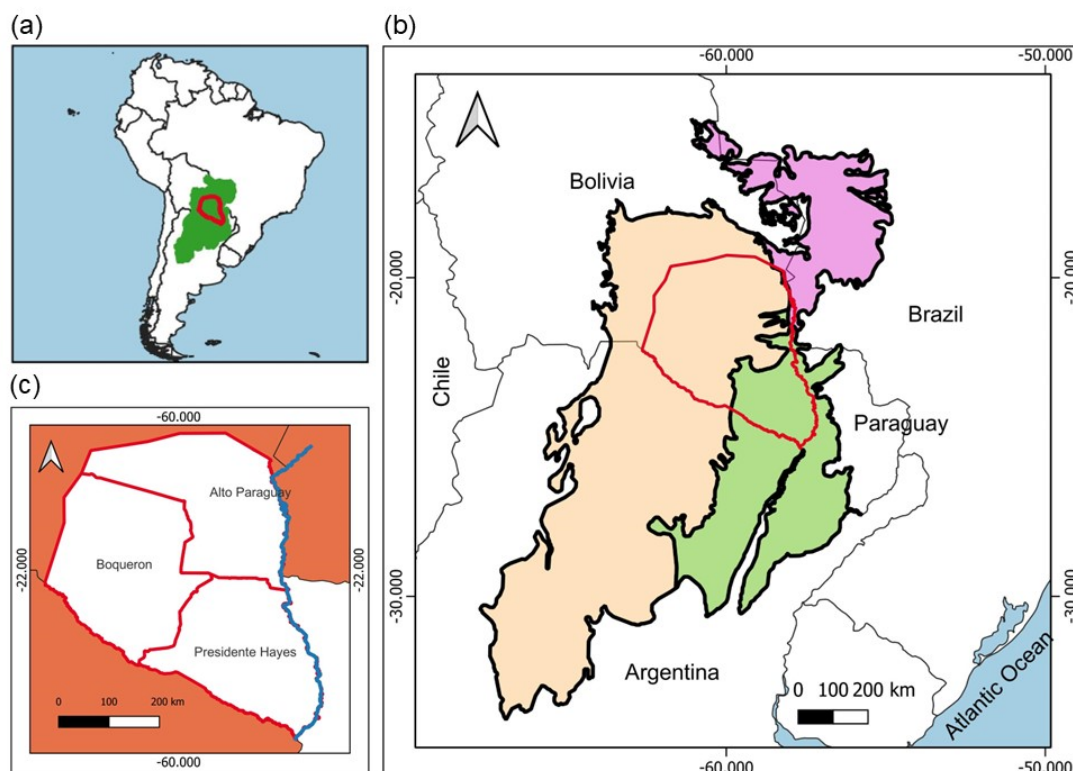


Figure 1. Map of the study area: (a) Gran Chaco and Pantanal ecoregions (green) and Paraguayan Chaco (red) within South America. (b) Map representing the three ecoregions: Humid Chaco (green); Dry Chaco (orange); and Pantanal (purple); the red line denotes the perimeter of the Paraguayan Gran Chaco. (c) Political division of the Paraguayan Chaco region, with the Paraguayan River (blue) dividing the country into two distinct regions: The Eastern Region and the Western Region (also known as Chaco).

The vegetation distribution is influenced by climate, with denser woodlands occurring in areas receiving precipitation of 800–1300 mm/year, and shrublands of varying densities found in regions receiving less than 800 mm/year. The primary socioeconomic activities are cattle ranching and soybean and dairy production. In the past decade, these industries (especially cattle ranching) have expanded greatly and have become major drivers of deforestation in the country [28]. Consequently, the forest ecosystems are highly fragmented and degraded. Fire is an essential tool for agricultural practises, such as renewing pastures for cattle and clearing fields for various activities. Furthermore, these ecoregions are prone to fire, as indicated by other studies in the same areas [29–31].

2.2. Data Collection and Remote Sensing Products

The pyroregions were defined on the basis of the selection of the most important variables after an extensive literature review of fire regime attributes. Thus, fire frequency, burn severity and burnt area were selected as fire variables. Two different satellite products, the MODIS MCD64A1 (Version 6) Burned Area database and the MOSEV database were then selected according to their time spans and temporal scale resolutions. MODIS MCD64A1 is a product that provides monthly per-pixel burned area and quality information on a 500 m global grid that uses 500 m MODIS Surface Reflectance imagery coupled with 1 km MODIS active fire observations [32]. MCD64A1 was selected due to its temporal resolution (1–2 days) to detect fire spots and because it has recently been used in South American ecosystems for different purposes, e.g., post-fire restoration [33], examining fire impact on biodiversity [34] and fire mapping in Brazilian savannas [35]. The MOSEV database (derived from MODIS) includes the most commonly used indices of severity for the period from 2000 to 2020. The product relies on the combination on Terra MOD09A1 and Aqua

MYD09A1 surface reflectance products to obtain dense time series of the NBR spectral index, and the MCD64A1 product was used to identify BA and the date of burning [36]. MOSEV also provides the dNBR and the RdNBR, both considered fire severity metrics that are suitable for characterizing fire impacts.

MODIS MCD64A1 was obtained from the NASA Land Processes Distributed Active Archive Center (<https://lpdaac.usgs.gov>, accessed on 11 November 2022) and the MOSEV database was obtained from <https://zenodo.org/record/4265209#.Y3dbG3bMK3A> (accessed 10 November 2022).

2.3. Data Quality Control

To ensure the reliability of the satellite data, we implemented several quality control measures. For the MODIS MCD64A1 dataset, the product's internal quality assurance (QA) flags were used to exclude low-quality observations, such as those affected by cloud cover, atmospheric disturbances and sensor anomalies. These QA flags provide pixel-level information on the reliability of the data, enabling the identification and exclusion of pixels flagged as having low confidence in burned area detection. Only pixels that provided reliable burned area detection were included in the analysis to minimize false positives or missed detections.

For the MOSEV dataset, we validated the burn severity metrics (dNBR and RdNBR) by cross-referencing them with active fire detections from the MODIS Fire and Thermal Anomalies (MOD14A1) product, ensuring temporal alignment between the burned area and fire severity data.

2.4. Fire Regime Characterization

The fire regimes in the Gran Chaco and Pantanal were characterized using K-means clustering analysis (Figure 2), an unsupervised data mining method that groups data with similar characteristics. This technique does not require training or testing data and does not require a target output. K-means is effective in grouping fire regimes with distinct fire characteristics and is flexible enough to handle the spatial–temporal dynamics of fire patterns in the study area, where predefined classes of fire regimes do not exist. Use of this unsupervised approach enabled us to explore hidden patterns and establish well-defined fire regime clusters, enhancing our understanding of the fire dynamics in the region. Before running the cluster, we used MODIS to determine the fire frequency and area burnt. The fire frequency was calculated as the total number of times that the area represented by a pixel was burnt within a year. Additional frequency variables were also computed, including the time span between fires, minimum time span, maximum time span and 2 to 5 consecutive time spans.

We selected the total fire frequency year⁻¹ as the primary frequency variable, to maintain consistency with the literature and to align with the data aggregation within each cluster. The total burnt area was calculated using a circular window of 7 × 7 pixels with a maximum of 49 pixels per window, also serving as a proxy for the burnt area. Severity was calculated using a function of the terra package for spatial data manipulation (R program, version 4.2.2). This enabled us to obtain the mean fire severity for the study period (2001–2020). Data were retrieved from MOSEV tiles and cropped to the local scale. We opted to use the dNBR index, which reflects the post-fire impacts on vegetation reflectance relative to the pre-fire condition [9]. The twenty-year time series was summarized in a raster file representing the severity index for the study area.

For the cluster analysis, we rescaled the variables into Z-scores with a zero mean and unit variance, as recommended in most clustering approaches. The K-means clustering approach consisted of an unsupervised learning method that iteratively partitions the dataset into a predefined number of non-overlapping clusters or subgroups [37]. The number of clusters was defined using the elbow method, which provided an estimate based on the within-cluster sum of squares (WCSS) between data points and the centroids of the assigned clusters. We chose k at the point where the WCSS curve starts to flatten and

forms an elbow (SM1). We ran the K-means clustering with the three selected variables (fire frequency, fire severity and burnt area) ten times using different centroids as references until the model converged. Additionally, we performed a sensitivity analysis by running K-means clustering with different values of $k = 2, 3, 5, \text{ and } 10$. We recalculated the WCSS for k ranging from 1 to 10 to assess the efficiency of each clustering solution. Then, we created box plots for each k to visualize the behaviour of the variables (SM2) and selected the value of k that best aligned with the ecological conditions of the study area. The thresholds for each variable within each cluster were visualized using the ggplot2 and patchwork packages in R software.

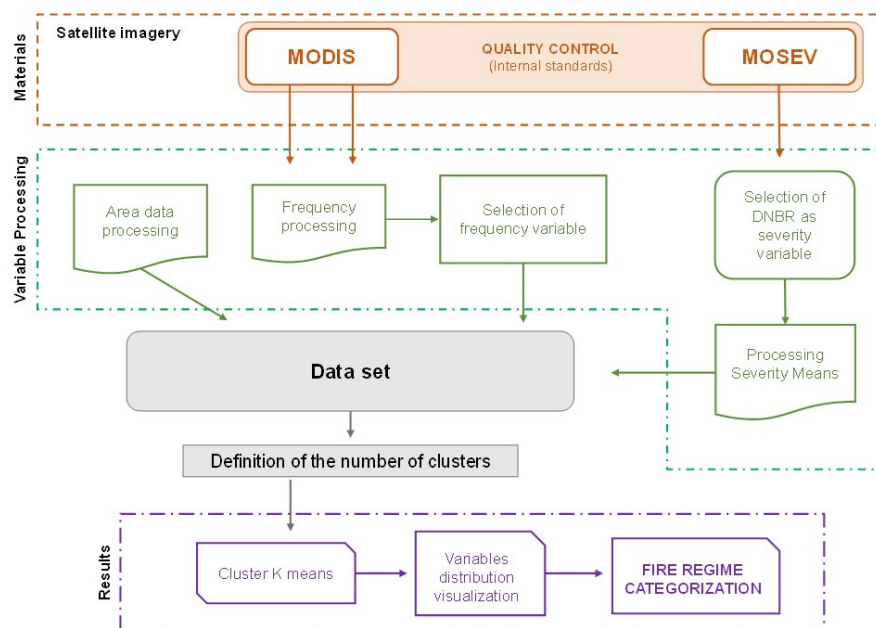


Figure 2. Flow chart of the fire regime characterization. The materials (remote sensing products of MODIS and MOSEV, see the text for detailed information) used are indicated in the orange box; different steps during variable preprocessing and processing are represented in green, and results in purple boxes.

3. Results

The K-means results suggest that the appropriate number of clusters is between three and four (SM1). Based on the box plot analysis (Figure 3) and the ecological background of the study area, we identified four distinct clusters that can be attributed to four different fire regimes in the Paraguayan Chaco: High (H), Moderate High (MH), Moderate Low (ML) and Low (L) (Figure 3). The most prevalent regimes at the scale of the Paraguayan Chaco were L (45.76%) and MH (28.96%) (Figure 4), while the least represented cluster was H (5.98%). However, the dominance of each fire regime varied between the ecoregions (Dry Chaco, Humid Chaco and Pantanal).

Clusters L and MH predominated within the Dry Chaco ecoregion (Figure 4). These regimes indicate a higher frequency of fires and smaller burned areas. Fire severity, however, varied between the clusters, with MH being the most severe. This MH cluster is concentrated in the north of the Paraguayan Chaco, particularly in the Alto Paraguay department, and shows significant aggregations in the northeast of the Dry Chaco (37%). The L cluster was also predominant in the northwest of the Chaco (52%) and was scattered in the northern part of the Humid Chaco. Fires in the L cluster were characterized by low severity, less extensive burned areas and, in contrast to MH, a low frequency of fires. Regime L was the most prevalent (39.43%) in the Humid Chaco, followed by areas classified as belonging to the ML regime (31.73%). The High regime (H) was mainly concentrated close to the Paraguay river, and was characterized by high-frequency, high-severity fires

and large burned areas. Finally, higher proportions of the ML (37.53%) and H regimes (34.05%) were found in the Paraguayan Pantanal. The highest concentrations of the H regime were observed in the northern area of the Pantanal, while the ML regime was predominantly present in the southern zone.

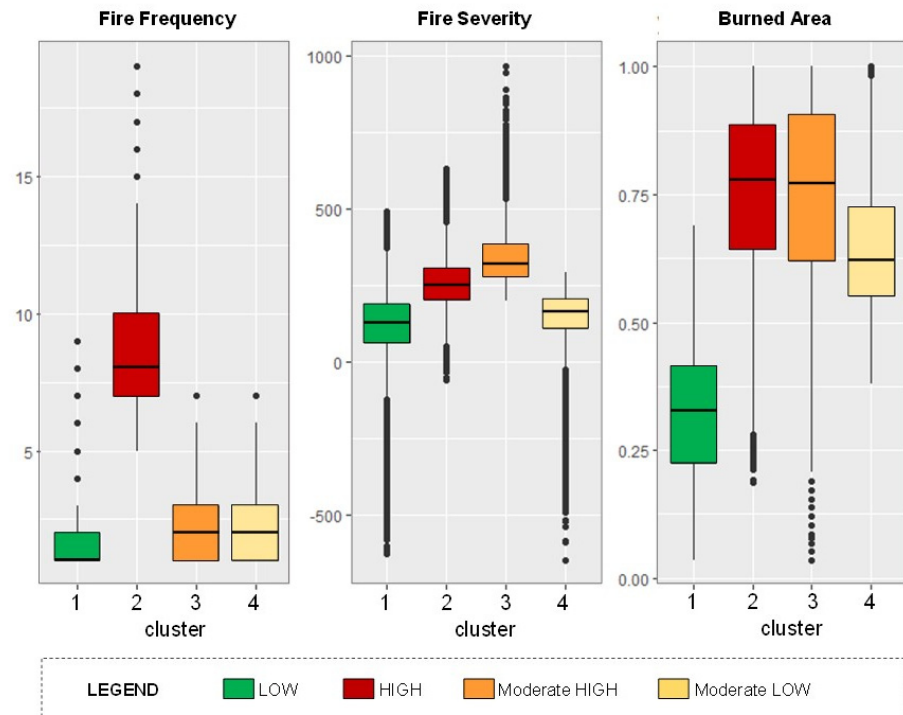


Figure 3. Classification of the four distinct clusters based on the variables “fire frequency”, “fire severity” and “burned area”. Each cluster represents a fire regime based on a group of pixels with similar characteristics as determined by the input variables. The category of each fire regime was assigned by the intra-cluster variations and inter-cluster differences.

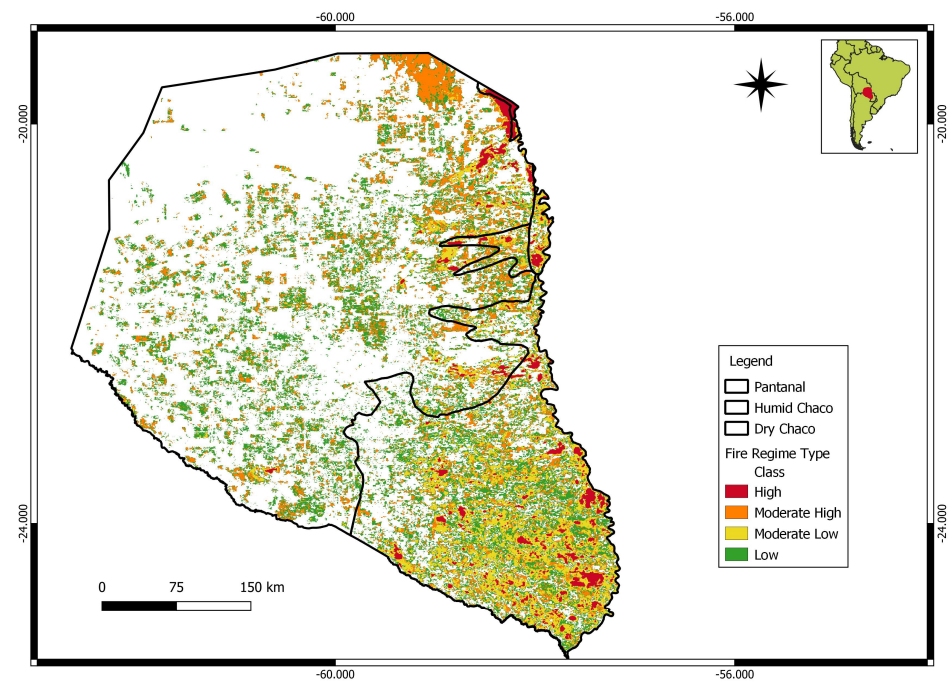


Figure 4. Map of the Paraguayan Gran Chaco reflecting the spatial distribution of the different clusters according to the selected variables “fire frequency”, “fire severity” and “burned area”.

4. Discussion

Our cluster analysis categorized the fire regimes in the Paraguayan Chaco into four clusters based on fire severity, fire frequency and burnt area. Interestingly, the cluster analysis revealed distinct fire regimes that might not be apparent from simple observations or the use of traditional methods. The cluster analysis reflected a spatial separation, identifying four well defined groups of increasing fire regime, ranging from the relatively small, less frequent and less severe fires included in the Low category (L) to the large areas, high severity and relatively low frequency included in the High (H) cluster.

One of the key contributions of this research is the clear identification of how fire regimes vary spatially across the ecological subregions. The L and MH regimes predominated in the Dry Chaco, with regime L predominating in the Humid Chaco, and regimes ML and H in the Pantanal. In this regard, the Dry Chaco exhibited a Low fire regime in the northwest and a Moderately High one in the north, sharing a low fire frequency as a common feature characterizing this subregion. This may be associated with arid and semi-arid regions, where dry conditions throughout the year limit the biomass growth necessary for fire ignition or spread [38]. In the Humid Chaco, Low and Moderate Low regimes prevailed, mainly due to agricultural burning driven by extensive livestock activity in this subregion [39]. These fires also correspond to high vegetation productivity, influenced by a pronounced precipitation gradient and abundant availability of fine fuel (biomass) treated with fire for renewal [40]. Conversely, the Pantanal was characterized by High and Moderate Low regimes, influenced by the flood pulses, rainfall patterns and biomass produced during the flooding period, which becomes available as fuel for burning in the subsequent dry season [41]. Additionally, cattle ranching, a primary economic activity in the biome [42], is closely linked to fire. Much of the pasture is managed using fire, and many of the wildfires may be a consequence of these practises [43].

A second major contribution lies in the application of these findings for fire management, particularly for highly diverse regions with limited information about their fire regime, such as the Paraguayan Chaco. With this unsupervised classification, we gained a clearer understanding of the spatial and temporal fire patterns [44], which helped us to identify areas with higher fire risks and varying fire behaviours and thus facilitate targeted fire management strategies and resource allocation related to fire prevention and control. Although these findings are preliminary and must be validated in the field with supervised techniques, this information is very valuable for the initial planning of experimental designs or sampling strategies based on the best available information on fire characteristics. The findings can also guide local authorities and stakeholders in developing more effective fire prevention and mitigation strategies. For example, areas within the H or MH clusters can be prioritized for increased surveillance, early warning systems or the implementation of prescribed burns to reduce fuel loads. Conversely, areas within the L cluster may require adaptive management such as promoting fire-adapted vegetation.

Fire regime characterization facilitates the development of predictive models to forecast fire behaviour and dynamics, especially considering expected changes in temperature, precipitation or land use, which are essential for long-term planning and adaptation strategies. Cluster separation can also serve as the basis for interdisciplinary studies to explore ecological, social and economic impacts of different fire regimes, e.g., how varying fire regimes affect forest recovery or biodiversity conservation [45], soil health [46] or regional greenhouse gas (GHG) emissions [47]. In socioeconomic terms, cluster categorization can allow us to explore the relationships between fire regimes and changes in land use practises, the financial costs associated with different fire regimes and the potential benefits of mitigation strategies.

In summary, the findings of this research contribute to identifying different fire regimes and also provide valuable insights into fire management and long-term fire risk planning. These findings can be immediately applied to improve fire management practises in the Paraguayan Chaco and similar fire-prone regions, providing a foundation for future research and decision-making in fire prevention, mitigation and ecological recovery.

5. Conclusions

Cluster analysis provides a robust framework for understanding and managing fire regimes, particularly in regions where fire dynamics are not well documented, as in the Paraguayan Chaco. Our study revealed the complex interaction between spatial, temporal and magnitude attributes that shape fire patterns in this large, highly diverse region.

In regions where available information is scarce, such as the Paraguayan Chaco, cluster analysis provided significant advantages to enhance our understanding of spatial and temporal fire patterns. This classification aids in identifying high-risk areas and facilitates targeted fire management strategies. These findings may guide local authorities in developing effective prevention and mitigation measures, e.g., increased surveillance and prescribed burns in high-risk areas and promotion of fire-adapted vegetation in lower-risk areas.

Overall, the characterization of fire regimes provides a foundational basis for developing fire management strategies adapted to the specific geographical, climatic and socioeconomic conditions in the Paraguayan Chaco, contributing to future mitigation of fire impacts at different levels in this fire-prone region within the context of a changing climate.

Author Contributions: Conceptualization, C.V.-R. and P.S.-A.; methodology, C.V.-R.; software, W.J.W.R.; validation, C.V.-R., P.S.-A. and M.A.N.B.; formal analysis, C.V.-R.; investigation, C.V.-R.; resources, P.S.-A.; data curation, C.V.-R.; writing—original draft preparation, C.V.-R.; writing—review and editing, P.S.-A.; visualization, M.A.N.B.; supervision, P.S.-A.; project administration, C.V.-R.; funding acquisition, P.S.-A. All authors have read and agreed to the published version of the manuscript.

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References

1. Bowman, D.M.J.S.; Murphy, B.P.; Williamson, G.J.; Cochrane, M.A. Pyrogeographic Models, Feedbacks and the Future of Global Fire Regimes. *Glob. Ecol. Biogeogr.* **2014**, *23*, 821–824. [[CrossRef](#)]
2. Morgan, P.; Hardy, C.; Swetnam, T.; Rollins, M.; Long, D. Mapping Fire Regimes across Time and Space: Understanding Coarse and Fine-Scale Fire Patterns. *Int. J. Wildland Fire* **2001**, *10*, 329–342. [[CrossRef](#)]
3. van Wagtenonk, J.; Lutz, J. Fire Regime Attributes of Wildland Fires in Yosemite National Park, USA. *Fire Ecol.* **2007**, *3*, 34–52. [[CrossRef](#)]
4. Fernández, V.; Quintano, C.; Taboada, A.; Marcos, E.; Calvo, L.; Fernandez-manso, A. Remote Sensing Applied to the Study of Fire Regime Attributes and Their Influence on Post-Fire Greenness Recovery in Pine Ecosystems. *Remote Sens.* **2018**, *10*, 733. [[CrossRef](#)]
5. Bond, W.; Keeley, J. Fire as a Global ‘Herbivore’: The Ecology and Evolution of Flammable Ecosystems. *Trends Ecol. Evol.* **2005**, *20*, 387–394. [[CrossRef](#)]
6. Lentile, L.; Holden, Z.; Smith, A.; Falkowski, M.; Hudak, A.; Morgan, P.; Lewis, S.; Gessler, P.; Benson, N. Remote Sensing Techniques to Assess Active Fire Characteristics and Post-Fire Effects. *Int. J. Wildland Fire* **2006**, *15*, 319–345. [[CrossRef](#)]
7. Bowman, D.M.J.S.; Kolden, C.A.; Abatzoglou, J.T.; Johnston, F.H.; van der Werf, G.R.; Flannigan, M. Vegetation Fires in the Anthropocene. *Nat. Rev. Earth Environ.* **2020**, *1*, 500–515. [[CrossRef](#)]
8. Estes, B.L.; Knapp, E.E.; Skinner, C.N.; Miller, J.D.; Preisler, H.K. Factors Influencing Fire Severity under Moderate Burning Conditions in the Klamath Mountains, Northern California, USA. *Ecosphere* **2017**, *8*, e01794. [[CrossRef](#)]

9. Veraverbeke, S.; Lhermitte, S.; Verstraeten, W.W.; Goossens, R. The Temporal Dimension of Differenced Normalized Burn Ratio (dNBR) Fire/Burn Severity Studies: The Case of the Large 2007 Peloponnese Wildfires in Greece. *Remote Sens. Environ.* **2010**, *114*, 2548–2563. [[CrossRef](#)]
10. Harris, L.; Taylor, A.H. Topography, Fuels, and Fire Exclusion Drive Fire Severity of the Rim Fire in an Old-Growth Mixed-Conifer Forest, Yosemite National Park, USA. *Ecosystems* **2015**, *18*, 1192–1208. [[CrossRef](#)]
11. Miller, R.G.; Tangney, R.; Enright, N.J.; Fontaine, J.B.; Merritt, D.J.; Ooi, M.K.J.; Ruthrof, K.X.; Miller, B.P. Fire Seasonality Mechanisms Are Fundamental for Understanding Broader Fire Regime Effects. *Trends Ecol. Evol.* **2020**, *35*, 869–871. [[CrossRef](#)] [[PubMed](#)]
12. Collins, L.; Bennett, A.F.; Leonard, S.W.J.; Penman, T.D. Wildfire Refugia in Forests: Severe Fire Weather and Drought Mute the Influence of Topography and Fuel Age. *Glob. Chang. Biol.* **2019**, *25*, 3829–3843. [[CrossRef](#)]
13. García, M.; Pettinari, M.L.; Chuvieco, E.; Salas, J.; Mouillot, F.; Chen, W.; Aguado, I. Characterizing Global Fire Regimes from Satellite-Derived Products. *Forests* **2022**, *13*, 699. [[CrossRef](#)]
14. Galizia, L.F.; Curt, T.; Barbero, R.; Rodrigues, M. Understanding Fire Regimes in Europe. *Int. J. Wildland Fire* **2021**, *31*, 56–66. [[CrossRef](#)]
15. San-Miguel-Ayanz, J.; Rodrigues, M.; Oliveira, S.; Kemper Pacheco, C.; Moreira, F.; Duguay, B.; Camia, A. Land Cover Change and Fire Regime in the European Mediterranean Region. In *Post-Fire Management and Restoration of Southern European Forests-Managing Forest Ecosystems*; Springer: Berlin/Heidelberg, Germany, 2012; pp. 21–43; ISBN 978-94-007-2208-8.
16. Parks, S.; Holsinger, L.; Miller, C.; Parisien, M.-A. Analog-Based Fire Regime and Vegetation Shifts in Mountainous Regions of the Western US. *Ecography* **2018**, *41*, 910–921. [[CrossRef](#)]
17. Murphy, B.; Bradstock, R.; Boer, M.; Carter, J.; Cary, G.; Cochrane, M.; Fensham, R.; Russell-Smith, J.; Williamson, G.; Bowman, D. Fire Regimes of Australia: A Pyrogeographic Model System. *J. Biogeogr.* **2013**, *40*, 1048–1058. [[CrossRef](#)]
18. de la Barrera, F.; Barraza, F.; Favier, P.; Ruiz, V.; Quense, J. Megafires in Chile 2017: Monitoring Multiscale Environmental Impacts of Burned Ecosystems. *Sci. Total Environ.* **2018**, 637–638, 1526–1536. [[CrossRef](#)] [[PubMed](#)]
19. Júnior, A.C.P.; Oliveira, S.L.J.; Pereira, J.M.C.; Turkman, M.A.A. Modelling Fire Frequency in a Cerrado Savanna Protected Area. *PLoS ONE* **2014**, *9*, e102380. [[CrossRef](#)]
20. San Martín, R.; Ottlé, C.; Sörensson, A. Fires in the South American Chaco, from Dry Forests to Wetlands: Response to Climate Depends on Land Cover. *Fire Ecol.* **2023**, *19*, 57. [[CrossRef](#)]
21. Vidal-Riveros, C.; Souza-Alonso, P.; Bravo, S.; Laino, R.; Ngo Bieng, M.A. A Review of Wildfires Effects across the Gran Chaco Region. *For. Ecol. Manag.* **2023**, *549*, 121432. [[CrossRef](#)]
22. Bilbao, B.; Steil, L.; Urbietta, I.R.; Anderson, L.; Pinto, C.; Gonzalez, M.E.; Millán, A.; Falleiro, R.M.; Morici, E.; Ibarregaray, V.; et al. Incendios forestales. In *Adaptación Frente a Los Riesgos Del Cambio Climático en Los Países Iberoamericanos—Informe RIOCCADAPT*; Moreno, J.M., Laguna-Defior, C., Barros, V., Calvo Buendía, E., Marengo, J.A., Oswald Spring, U., Eds.; McGraw-Hill: Madrid, Spain, 2020; pp. 459–524; ISBN 9788448621643.
23. Dinerstein, E.; Olson, D.; Joshi, A.; Vynne, C.; Burgess, N.; Wikramanayake, E.; Hahn, N.; Palminteri, S.; Hedao, P.; Noss, R.; et al. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience* **2017**, *1*, 534–545. [[CrossRef](#)]
24. Baumann, M.; Levers, C.; Macchi, L.; Bluhm, H.; Waske, B.; Gasparri, N.I.; Kuemmerle, T. Mapping Continuous Fields of Tree and Shrub Cover across the Gran Chaco Using Landsat 8 and Sentinel-1 Data. *Remote Sens. Environ.* **2018**, *216*, 201–211. [[CrossRef](#)]
25. Campos Krauer, J.; Wisely, S. Deforestation and Cattle Ranching Drive Rapid Range Expansion of Capybara in the Gran Chaco Ecosystem. *Glob. Chang. Biol.* **2010**, *17*, 206–218. [[CrossRef](#)]
26. Caldas, M.M.; Goodin, D.; Sherwood, S.; Campos Krauer, J.M.; Wisely, S.M. Land-Cover Change in the Paraguayan Chaco: 2000–2011. *J. Land Use Sci.* **2015**, *10*, 1–18. [[CrossRef](#)]
27. Gill, A.; Canova, E.; Insfrán, P.; Gonzalez, R. *Atlas del Chaco Paraguayo/Atlas of the Paraguayan Chaco*; WWF: Asunción, Paraguay; DLR: Cologne, Germany, 2020; ISBN 978-99967-792-3-7.
28. Baumann, M.; Piquer-Rodríguez, M.; Fehlenberg, V.; Gavier Pizarro, G.; Kuemmerle, T. Land-Use Competition in the South American Chaco. In *Land Use Competition. Human-Environment Interactions*; Niewöhner, J., Bruns, A., Hostert, P., Krueger, T., Nielsen, J.Ø., Haberl, H., Lauk, C., Lutz, J., Müller, D., Eds.; Springer: Cham, Switzerland, 2016; pp. 215–229. [[CrossRef](#)]
29. Kunst, C.; Ledesma, R.; Navarrete, V. Fire Behavior in an Ecotonal Grassland of the Chaco Region, Argentina. *Rev. Investig. Agropecu. RIA* **2012**, *38*, 4–9. [[CrossRef](#)]
30. Ibañez Moro, A.V.; Bravo, S.J.; Abdala, N.R.; Borghetti, F.; Chaib, A.M.; Galetto, L. Heat Shock Effects on Germination and Seed Survival of Five Woody Species from the Chaco Region. *Flora* **2021**, *275*, 151751. [[CrossRef](#)]
31. Kunst, C.; Bravo, S.; Ledesma, R.; Navall, M.; Anríquez, A.; Coria, R.D.; Silberman, J.; Gómez, A.; Albanesi, A. Ecology and Management of the Dry Forests and Savannas of the Western Chaco Region, Argentina. In *Dry forest*; Nova Science Publishers, Inc.: Hauppauge, NY, USA, 2014; pp. 133–164; ISBN 978-1-63321-291-6.
32. Giglio, L.; van der Werf, G.R.; Randerson, J.T.; Collatz, G.J.; Kasibhatla, P. Global Estimation of Burned Area Using MODIS Active Fire Observations. *Atmos. Chem. Phys.* **2006**, *6*, 957–974. [[CrossRef](#)]
33. Landi, M.; Di Bella, C.; Ojeda, S.; Salvatierra, P.; Arganaraz, J.; Bellis, L. Selecting Control Sites for Post-Fire Ecological Studies Using Biological Criteria and MODIS Time Series Data. *Fire Ecol.* **2017**, *13*, 1–17. [[CrossRef](#)]
34. Maillard, O.; Herzog, S.K.; Soria-Auza, R.W.; Vides-Almonacid, R. Impact of Fires on Key Biodiversity Areas (KBAs) and Priority Bird Species for Conservation in Bolivia. *Fire* **2022**, *5*, 4. [[CrossRef](#)]

35. Silva, P.; Nogueira, J.; Rodrigues, J.; Lemos, F.; Pereira, J.; Dacamara, C.; Daldegan, G.; Pereira, A.; Peres, L.; Schmidt, I.; et al. Putting Fire on the Map of Brazilian Savanna Ecoregions. *J. Environ. Manag.* **2021**, *296*, 113098. [[CrossRef](#)]
36. Alonso-González, E.; Fernández-García, V. MOSEV: A Global Burn Severity Database from MODIS (2000–2020). *Earth Syst. Sci. Data* **2021**, *13*, 1925–1938. [[CrossRef](#)]
37. Wu, X.; Kumar, V.; Quinlan, R.; Ghosh, J.; Yang, Q.; Motoda, H.; McLachlan, G.; Ng, S.K.A.; Liu, B.; Yu, P.; et al. Top 10 Algorithms in Data Mining. *Knowl. Inf. Syst.* **2007**, *14*, 1–37. [[CrossRef](#)]
38. Archibald, S.; Lehmann, C.; Gomez-Dans, J.; Bradstock, R. Defining Pyromes and Global Syndromes of Fire Regimes. In Proceedings of the National Academy of Sciences of the United States of America 2013, Washington, DC, USA, 20 August 2013. [[CrossRef](#)]
39. Mereles, M.; Rodas, O. Assessment of Rates of Deforestation Classes in the Paraguayan Chaco (Great South American Chaco) with Comments on the Vulnerability of Forests Fragments to Climate Change. *Clim. Chang.* **2014**, *127*, 55–71. [[CrossRef](#)]
40. Negri Bernardino, P.; Dantas, V.; Hirota, M.; Pausas, J.; Oliveira, R. Savanna–Forest Coexistence Across a Fire Gradient. *Ecosystems* **2021**, *25*, 279–290. [[CrossRef](#)]
41. Damasceno-Junior, G. Lessons to Be Learned from the Wildfire Catastrophe of 2020 in the Pantanal Wetland. *Wetl. Sci. Pract. WSP* **2021**, *38*, 107–115. [[CrossRef](#)]
42. Teodoro, P.E.; Maria, L.D.S.; Rodrigues, J.M.A.; Silva, A.D.A.E.; Silva, M.C.M.D.; Souza, S.S.D.; Rossi, F.S.; Teodoro, L.P.R.; Della-Silva, J.L.; Delgado, R.C.; et al. Wildfire Incidence throughout the Brazilian Pantanal Is Driven by Local Climate Rather Than Bovine Stocking Density. *Sustainability* **2022**, *14*, 10187. [[CrossRef](#)]
43. Menezes, L.S.; de Oliveira, A.M.; Santos, F.L.M.; Russo, A.; de Souza, R.A.F.; Roque, F.O.; Libonati, R. Lightning Patterns in the Pantanal: Untangling Natural and Anthropogenic-Induced Wildfires. *Sci. Total Environ.* **2022**, *820*, 153021. [[CrossRef](#)] [[PubMed](#)]
44. McLauchlan, K.K.; Higuera, P.E.; Miesel, J.; Rogers, B.M.; Schweitzer, J.; Shuman, J.K.; Tepley, A.J.; Varner, J.M.; Veblen, T.T.; Adalsteinsson, S.A.; et al. Fire as a Fundamental Ecological Process: Research Advances and Frontiers. *J. Ecol.* **2020**, *108*, 2047–2069. [[CrossRef](#)]
45. Müller, S.C.; Overbeck, G.E.; Pfadenhauer, J.; Pillar, V.D. Plant Functional Types of Woody Species Related to Fire Disturbance in Forest–Grassland Ecotones. *Plant Ecol.* **2007**, *189*, 1–14. [[CrossRef](#)]
46. Pellegrini, A.F.A.; Ahlström, A.; Hobbie, S.E.; Reich, P.B.; Nieradzic, L.P.; Staver, A.C.; Scharenbroch, B.C.; Jumpponen, A.; Anderegg, W.R.L.; Randerson, J.T.; et al. Fire Frequency Drives Decadal Changes in Soil Carbon and Nitrogen and Ecosystem Productivity. *Nature* **2018**, *553*, 194–198. [[CrossRef](#)] [[PubMed](#)]
47. Rogers, B.M.; Veraverbeke, S.; Azzari, G.; Czimczik, C.I.; Holden, S.R.; Mouteva, G.O.; Sedano, F.; Treseder, K.K.; Randerson, J.T. Quantifying Fire-Wide Carbon Emissions in Interior Alaska Using Field Measurements and Landsat Imagery. *J. Geophys. Res. Biogeosci.* **2014**, *119*, 1608–1629. [[CrossRef](#)]

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4.4 CHAPTER 4 : FOREST RESPONSES TO FIRE REGIME IN THE HUMID CHACO OF PARAGUAY

This chapter was submitted to the *Journal of Austral Ecology*. Its current status is under review. Quality indexes: The journal in which this article is published corresponds to level 2 (quartile Q2 of the SCImago Journal Rank). In this case, this journal is indexed in the SCImago in the category of Ecology. It has an impact factor of 1.6 in the 2023 ranking (latest available year), and Cite score (2023) of 2.9.

Abstract

The responses of vegetation to fluctuations in fire regimes are increasingly important in the context of the global increase in fire pressure. This is particularly important in poorly studied, fire-prone regions such as the Gran Chaco, a vast ecoregion with diverse ecosystems about which information on fire behaviour is limited. This study examined the impact of fire regimes on plant functional traits, diversity and community assembly in the Humid Chaco forests in Paraguay. Thirty-one experimental plots were established in fragmented forest areas to assess species composition, vegetation structure and fire-adaptive traits across low, moderate and no-fire regimes. Functional diversity indices, including functional richness, evenness, divergence and dispersion, were calculated to examine the community responses to fire.

Species taxonomic composition, distribution and structure were similar across the different fire regimes. Species of the Fabaceae family were dominant, and typical mesoxerophytic forest species were also present. In terms of functional response, evidence of increased resprouting was observed in individuals in fire-affected regimes. While the vegetation structure remained consistent across fire regimes, the functional dispersion varied, indicating a more homogeneous trait assemblage in the no-fire regime. This study is the first of its kind in the region, providing valuable insights into vegetation responses to fire regimes and emphasizing the importance of preserving forest patches to prevent fire spread in the fire-prone landscapes of the Humid Chaco of Paraguay.

Resumen (Castellano)

Las respuestas de la vegetación a las fluctuaciones en los regímenes de incendios son cada vez más importantes en el contexto del aumento global de la presión de incendios. Esto es especialmente relevante en regiones poco estudiadas y propensas al fuego, como el Gran Chaco, una vasta ecorregión con diversos ecosistemas sobre los cuales la información sobre el comportamiento del fuego es limitada. Este estudio analizó el impacto de los regímenes de incendios en los rasgos funcionales de las plantas, la diversidad y la estructura de la comunidad en los bosques del Chaco Húmedo en Paraguay. Se establecieron treinta y una parcelas experimentales en áreas de bosque fragmentado para evaluar la composición de especies, la estructura de la vegetación y los rasgos adaptativos al fuego en regímenes de fuego bajo, moderado y sin fuego. Se calcularon índices de diversidad funcional, como la riqueza, la equidad, la divergencia y la dispersión funcional, para determinar las respuestas de la comunidad al fuego.

La composición taxonómica de especies, su distribución y estructura fueron similares entre los diferentes regímenes de incendios. Las especies de la familia Fabaceae fueron dominantes, y

también estuvieron presentes especies típicas de bosques mesoxerofíticos. En términos de respuesta funcional, se observó un aumento en el rebrote de individuos en los regímenes afectados por el fuego. Aunque la estructura de la vegetación se mantuvo consistente entre regímenes de fuego, la dispersión funcional varió, indicando una agrupación de rasgos más homogénea en el régimen sin fuego. Este estudio es el primero de su tipo en la región, proporcionando información valiosa sobre las respuestas de la vegetación a los regímenes de incendios y enfatizando la importancia de preservar los fragmentos de bosque para prevenir la propagación de incendios en los paisajes propensos al fuego del Chaco Húmedo en Paraguay

Keywords

fire regime; dry forests; adaptative traits; functional diversity; fire resistance

4.4.1 Introduction

Fire is a complex, natural process within the Earth's system that has shaped many ecosystems, playing a key role in the composition and distribution of plants and animals (Bond et al., 2005; Grau-Andrés et al., 2024). In fire-prone ecosystems such as dry forests, savannas and grasslands, the dynamics, functioning and maintenance of these systems are closely associated with fire activity (Bowman et al., 2009). Fire stimulates processes such as plant resprouting and seed bank expression, which are essential for ecosystem dynamics and the persistence of species that have evolved in response to fire (Pausas and Keeley, 2014). Thus, fire is recognized as a selective pressure, favouring the morphological adaptations that enable species to survive both fire and environmental fluctuations (Dantas et al., 2013). Fire probably contributes to a range of ecosystem services, as it accounts for a high proportion of the variability in biodiversity (Ponisio et al., 2016; Pausas and Ribeiro, 2013). In flammable ecosystems, species are adapted to specific conditions of the fire regime, i.e. the frequency, intensity, size, seasonality and type of fire (Keeley et al., 2011). However, in the past decade, there has been a global increase in extreme fires, marked by greater frequency and intensity, largely driven by human-induced global warming (Intergovernmental Panel on Climate Change, 2021; Jolly et al; 2015; Cunningham et al; 2024). It is therefore of utmost importance to study how ecosystems adapt to fluctuations in fire regimes in the context of increasing fire dynamics. Changes in fire regimes represent a major source of change for fire-adapted and non-adapted communities. In this respect, fire regimes may affect the resistance and resilience of plant communities (Karavani et al., 2018) and their responses are directly related to fire adaptations that are mainly expressed by functional traits. Considering the evolutionary basis of the functional traits, studying fire regimes, rather than single fire events, is a more reliable approach to examining changes in vegetation communities (Keeley et al., 2012).

Functional differences are among the most notable characteristics distinguishing tropical biomes (Ratnam et al., 2011; Dantas et al., 2013, 2016). Each biome is characterized by species with specific functional traits, which result from the contrasting selective processes that have shaped communities (Ratnam et al., 2011; Dantas et al., 2013). Thus, functional traits serve as proxies that help to clarify the ecological strategies by which plants respond to environmental factors, affect other trophic levels and influence ecosystem properties (Kattge et al., 2011). For instance, traits such as relative stem height, bark thickness, resprouting and spines are used to

differentiate fire-adapted ecosystems (Pausas and Fernández-Muñoz 2011; Zupo et al; 2020; Pausas 2014). Analysis of functional traits and functional diversity thus offers insights into ecological processes within ecosystems, such as productivity, resilience to disturbance and colonization/invasion dynamics (Villéger et al., 2013), as well as species responses to environmental change (Salgado-Negret and Paz, 2015).

Paraguay is one of the smallest countries in South America and it has a high deforestation rate (347,000 ha/year) (FAO 2020) accompanied by a gradual increase in forest degradation (Gasparri and Grau, 2009; Fehlenberg et al., 2017). Although forest degradation is a complex mixture of different factors, fires intentionally started by humans (usually in pastures) must be considered in order to understand this phenomenon in Paraguay and many other areas in South America (Argañaraz et al., 2015). A large part of Paraguay (> 60%) is occupied by a globally important biome: the Gran Chaco (GC). The GC is an alluvial sedimentary plain covering more than 647,500 km² across Northern Argentina, Bolivia and Paraguay. Two subregions can be distinguished within the Paraguayan Chaco: the dry Chaco and the humid Chaco (Mereles et al., 2020). The latter occupies the lowest areas of the GC (Rumbo 2010), located in the Paraguay and Paraná river basins. Most of the subregion is subject to periodic flooding due to heavy rainfall (900-1400 mm per year) and overflow from rivers.

The landscape of the GC consists of dense forest islands immersed in savannas, palm groves and wetlands, resulting in the development of different types of forest (Laino et al., 2022). These islands are often situated in flood-prone landscapes where water levels fluctuate due to seasonal rains and droughts, creating a dynamic aquatic-terrestrial transition zone (Mereles et al., 2020). The forests include the Dense Subtropical Forest, which occurs naturally on islands associated with palm groves in the floodplain of the Paraguay River (Pérez de Molas 2015); the Dense Mesoxerophytic Forest, where the dominant tree species is *Schinopsis balansae* (quebracho colorado) (Mereles et al., 2020); and the Riparian Forest, which appears along the riverbeds in strips of 50-100 metres wide (Maturro et al., 2005). Despite its large extension, location and importance at regional levels and in terms of biodiversity, little is known about the GC (especially in Paraguay and Bolivia) beyond some regions (e.g. Argentina), where most of the existing studies have been conducted. Although this ecoregion has experienced severe, intense fires in the last two decades, little research has been conducted regarding the effects of wildfires at different levels (Vidal-Riveros et al., 2023). As indicated above, fire regimes influence the plant community response, and increased fire frequency and intensity can thus alter the delicate balance between species composition and ecosystem functioning, leading to shifts from forested areas to more open, savanna-like ecosystems (Dantas and Pausas, 2013). Across this region, the interactions between climate variability, land use changes and fire dynamics cause strong challenges for conservation efforts. Considering the evolutionary basis of the functional traits, changes in fire regimes provide a reliable approach to examining changes in vegetation communities (Keeley et al., 2012). Understanding how fluctuations in fire regimes interact with vegetation responses within forest islands in the Paraguayan Chaco is essential for developing effective management strategies to preserve the ecological integrity of the area. This is of particular importance in this fire-prone region as information on fire behaviour and related vegetation responses is scarce.

In this study, we aimed to identify the responses of forest species to post-fire effects in the Humid Chaco of Paraguay. We hypothesized that fire-adaptive traits will be more prevalent in forests affected by more recurrent or intense fires. Additionally, we expected that the values of

functional diversity indices would reflect distinct responses to fire regimes, depending on the aspect of functional diversity they measure. Specifically, we expected functional dispersion (FDis) to increase under moderate fire regimes, indicating coexistence of species with contrasting fire-adaptive traits. Functional evenness (FEve), however, was expected to decrease under intense fire regimes, as these may promote the dominance of certain fire-adapted traits. Functional divergence (FDiv) was hypothesized to increase in communities where extreme trait values confer advantages in fire-prone environments. The specific aims of the study were as follows: 1) to determine the differences in structure and composition of native species within forest patches along identified fire regimes at a local scale; 2) to assess fire functional traits within communities along a gradient of fire regimes; and 3) to compare functional diversity among fire regimes by using functional diversity indices.

4.4.2 Materials and Methods

4.4.2.1 Study area

The study was conducted in the Presidente Hayes department of the Western Region of Paraguay (coordinates: 24°57'41" S; 57°22'10" O) (**Figure 4**), along a heterogeneous landscape formed by islands of mesoxerophytic forests and riparian forests typical of the region, within a landscape dominated by dry savannas (**Figure 5**). The forest plots were located in 8 private cattle ranches mostly dedicated to livestock rearing and that span an area of 14,000 hectares. The ranches are very large (>1000 ha), pasture-based, with fragmented forests randomly distributed across the landscape, and they are highly specialized in rearing beef cattle. The climate is tropical savanna transitioning to humid subtropical, according to the Köppen classification. The annual average rainfall in this region is 1200 mm, and the average temperature stands at 24°C (Mereles et al., 2013). The study area has experienced extreme weather leading to periodic flooding and occasional droughts. Throughout the year, approximately half of the area is submerged in floodwater and is then subjected to a period of intense drought in the following season (Laino et al., 2022).

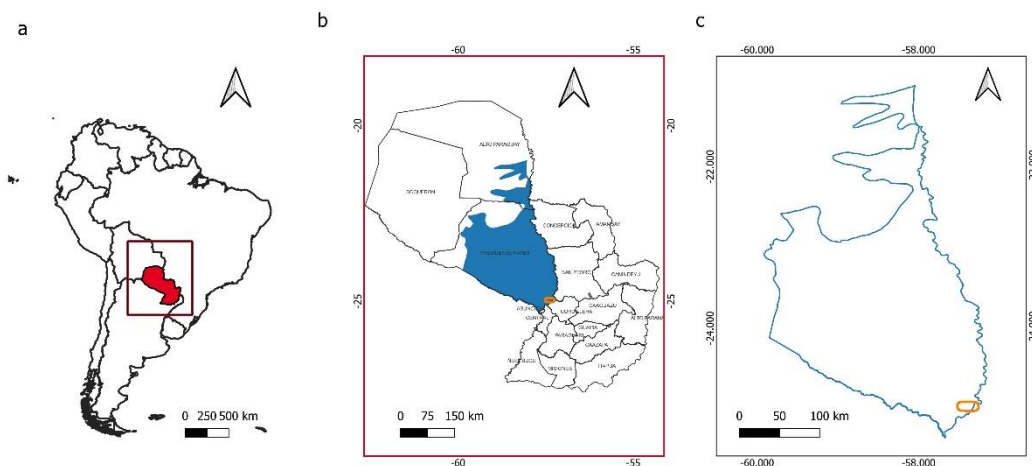


Figure 4. Map of the study area. a) Location of Paraguay in South America (red square), b) Country map including the studied ecoregion c) detail of the Humid Chaco area where the study area is placed.

The study area is a convergence of species that occur exclusively in the GC, such as the *Schinopsis balansae*, *Caesalpinia paraguariensis* *Neltuma nigra*, species from the Eastern region, such as *Astronium fraxinifolium* and *Patagonula americana*, and species that are present in both regions, such as the *Enterolobium contortisiliquum* and *Handroanthus heptaphyllus*. The landscape is considered to be relatively stable regarding forest cover, where periods of extensive cattle ranching have occurred without deforestation, mainly utilizing natural grasslands (Gonzalez et al., 2018). However, different types of human disturbance have occurred on pristine vegetation both in the past and in current time. The most important of these is fire, mainly control burning to renew natural pasture for cattle rearing. Wildfires also occur, especially in the dry season (June-September), where uncontrolled agricultural burning may spread and impact forest cover (**Figure 5**).



Figure 5. a) Aerial image of a typical forest stand in the region, with the transition zone and a fire caused by a prescribed burn in the background, and b) detail of the interior of one of the Mesoxerophytic forests studied.

4.4.2.2 Fire regimes in the study area

The sampling strategy was based on identifying forest patches that suffered different fire regimes during the past few decades. Thus, selection was based on a detailed fire regime classification map constructed using remote sensing data (2001-2020) from the Paraguayan Gran Chaco (Vidal-Riveros et al., 2024). The classification was based on the integration of different fire magnitude, spatial and temporal patterns, using variables such as area burned, fire frequency and fire severity to identify four major fire regime intensities: High (H), Moderately High (MH), Moderately Low (ML) and Low (L). For this chapter, the original fire regime map was reclassified into three categories to simplify sampling and address logistical constraints, as well as to ensure sufficient plot representation across fire regimes. This map was reclassified into three categories by merging the MH and ML classes into a single Moderate (M) fire regime intensity class. The resulting map showed that H intensity fire regimes were carried out in 3.47% of the area, M intensity regimes in 54.21% of the area, and L intensity regimes in 42.32% of the area. For the present study, we selected 14 forest patches that included the fire regime selected. We also selected forest patches located within clusters with no fire presence, designated as No Fire (NF) regime. No H intensity fire regime sites were identified within the forest patches. The H intensity fire regime was primarily observed at the edge of the sampling

areas, occurring in small, fragmented patches predominantly characterized by pasture and savanna ecosystems. As a result, the fire regime classification within the forest patches was restricted to the NF, L and M categories (**Figure 6**).

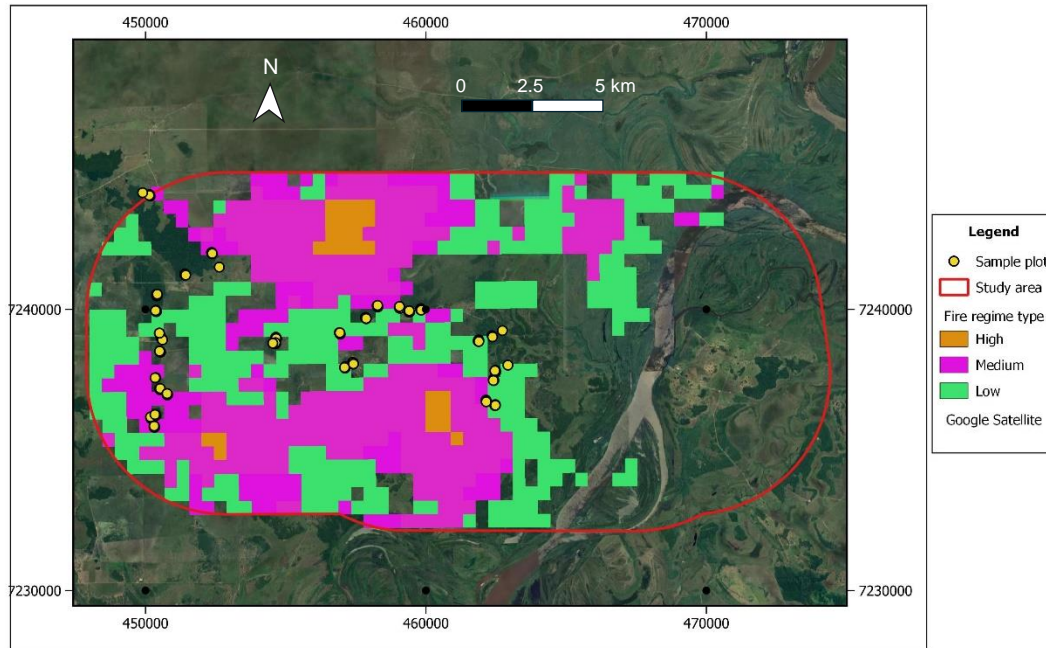


Figure 6. Detailed map of the studied area (red polygon) near the Paraguay river including sampling points (yellow circles) and different fire regimes identified. NF is the area without fire regime type within the studied area

4.4.2.3 Field data collection

Within the 14 forest patches selected, we established 31 sampling plots of 20 x 50 m along the fire regime gradient (**Figure 6**). The sampling strategy consisted of stratified sampling using unbalanced blocks, represented by the forest patches, with the fire regime classification function as the treatment. The model can be described as follows: $Y_{ij} = \mu + C_i + P_j + \varepsilon_{ij}$, where Y = response variable; μ = population mean; C = the effect of the i th treatment; P = the effect of the block; ε = Model error.

In each plot, tree vegetation data was collected from individual of diameter at breast height (DAP) of at least 10 cm. In addition, in half of the plot (20 x 25 m), vegetation was measured from 5 cm DAP. The following attributes were sampled: species taxonomy, DAP and the height of all sampled tree species, palms and lianas. This type of data provides information on the forest structure and composition. To avoid a possible edge effect, a distance from the forest edge of at least 30 m was considered to ensure that all individuals were representative of the interior forest conditions. A minimum distance of 150 m between sample plots within the same patch was also established.

Traits associated with fire resistance, including bark thickness, height, spinescence and sprouting ability, were considered functional traits (Pérez-Harguindeguy et al., 2013). These traits were assessed in the most abundant species, i.e. those with higher cumulative relative abundance appearing in at least 80% of the sampled plots.

4.4.2.4 Quantification of functional traits

The functional traits were measured in healthy plants in which foliage was exposed to the maximum amount of sunlight. The following plant traits were measured: maximum height, bark thickness, spinescence and resprouting. The two first traits were measured following Pérez-Harguindeguy et al. (2013), while spinescence and resprouting were measured following the thresholds established by Loto and Bravo (2021). Functional traits were then measured using the Community Weighted Mean (CWM), which describes the composition of an ecological community in terms of the functional traits of the species therein. Specifically, the CWM is calculated as the weighted average of the values of a functional trait for all species present in the community, where the weights correspond to the relative abundance of each species (Lavorel et al., 2008).

4.4.2.4.1 Calculation of Functional Diversity Indices (FDI)

In general, indices can be classified in ranges that consider a single trait and a single species to multi-trait and multi-species indices (Pla et al., 2010). Here, we focused on multi-trait and multi-species indices, which also consider relative species abundance e.g. in the form of individuals (n), basal area (%) (Grime 1997) and biomass (Villéger et al., 2008). We calculated common functional diversity indices (FDI) (Pla et al., 2010) along the fire regime gradient, including functional richness (Fric), functional evenness (Feve), functional divergence (Fdiv) and functional dispersion (Fdis). FRic indicates the diversity and range (extreme values) of functional traits within a community (Fischer et al., 2007), which can be influenced by species richness to the extent that species are functionally different (Villéger et al., 2008; Mouchet et al., 2010). FEve describes the equity in the distribution of the relative abundance of species across functional space (Pla et al., 2010) enabling quantification (values from 0 to 1) of how close or distant species cluster together in terms of functional traits, according to vegetation cover. FDiv represents the divergence (0 to 1) between the clusters generated for each species across the trait space (Schleuter, 2010). Finally, FDis measures the average distance of species in the functional space from the centroid, weighted by abundance, across the entire community. In comparison to functional richness, this index reduces sensitivity to extreme values and also takes into account the relative abundance of species (Laliberté and Legendre, 2010).

4.4.2.5 Statistical analysis

We used Generalized Linear Modelling (GLM) to test the effects of variables such as maximum height and bark thickness. For categorical variables, we used the Chi square test. We used the dbFD () command available in the “FD” package of the R software version 4.2.1 (Laliberté et al., 2015) to calculate the indices. This command enables calculation of all indices, requiring as input parameters the matrix corresponding to the values of the functional traits and the matrix of relative abundances of each species, which in this case were taken from the 80% most abundant species. We used ANOVA and Fisher’s test to examine differences in Functional Diversity indices between the three fire regime categories (NF and L and M fire regimes). All analyses were carried out using the R software (version 4.2.1).

4.4.3. Results

4.4.3.1 General taxonomic features

4.4.3.1.1 Species composition and taxonomic diversity

We recorded a total of 3,254 individuals in the three sites representing the different fire regimes, including 75 woody species belonging to 19 botanical families. Among these, the Fabaceae, Ulmaceae (10%) and Euphorbiaceae (9%) families were the most abundant (**Figure 7**). Considering the numerical abundance and the distribution, which varied depending on the type of fire regime, *Phyllostylon rhamnoides*, *Syagrus romanzoffiana*, *Gymnanthes discolor*, *Trichilia catigua*, *Diplokeleba floribunda*, *Eugenia uniflora*, *Ruprechtia laxiflora* and *Sorocea saxicola* were the dominant species.

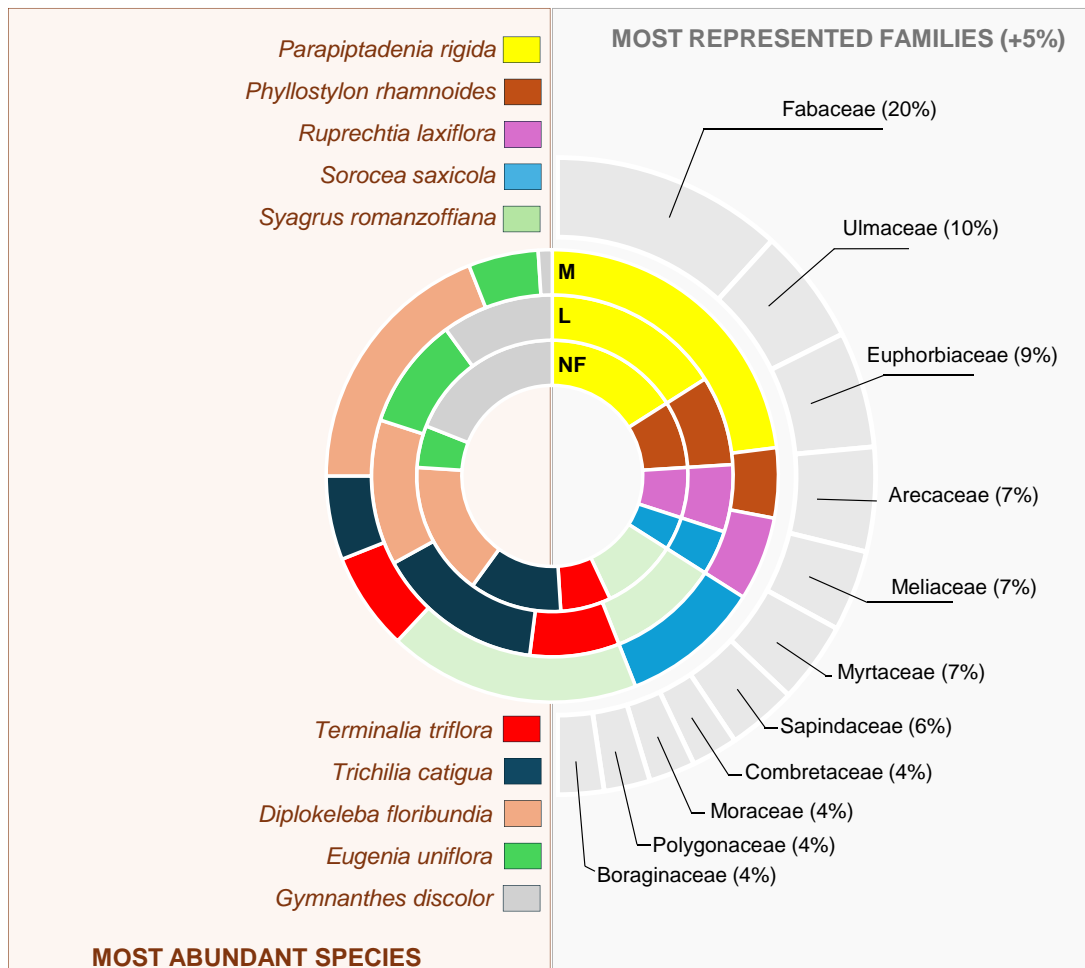


Figure 7. Left panel and the different concentric circles represent the proportion (in different colours) and species composition (10 most abundant species) between the different fire regimes; from the inside out: no fire (NF), low (L) and medium (M) fire regime. Grey semicircle in the right panel represent the proportions of the most abundant families (> 5% of the total individuals identified)

Thus, we observed that in the NF regime sites, the most predominant species were *Gymnanthes discolor*, *Phyllostylon rhamnoides* and *Trichilia catigua*, whereas in the L and M fire regime sites, *Parapiptadenia rigida* and *Syagrus romanzoffiana* were the most abundant; the latter was also present in the M fire regime sites. *Eugenia uniflora* and *Terminalia triflora* were abundant in all three fire regime sites (**Figure 7**).

Regarding representativeness by basal area, we found that *Gymnanthes discolor* predominated in the NF community composition but less so in the L and M fire regime sites. By contrast, *Parapiptadenia rigida* and *Siagrus rommanzofianun* were more abundant in the L and M fire regimes plots, although also present in the NF plots.

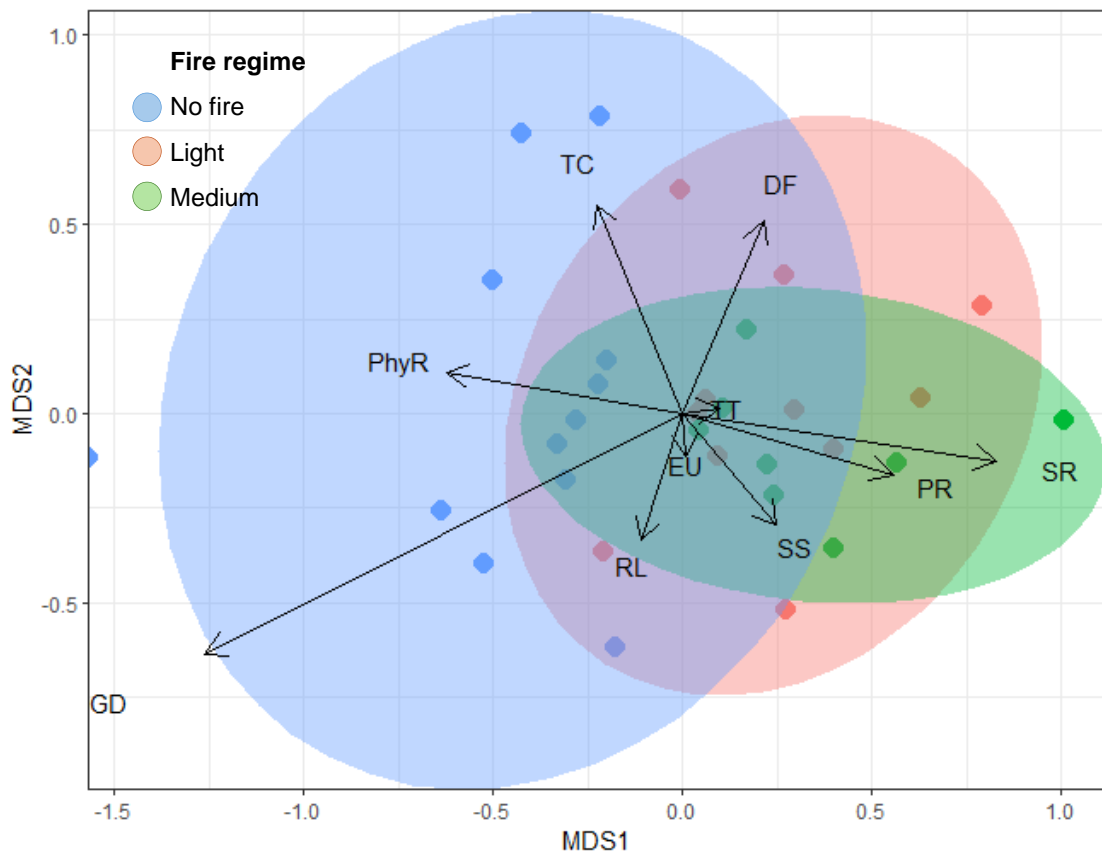


Figure 8. Multidimensional scaling representing the spatial relationship between the 10 most abundant species and the different fire regimes considered: No fire, light and medium

The MDS ordination representation based on the association between the presence of the most abundant species and the fire regime showed a considerable overlap between the different fire regimes (**Figure 8**). Although the spatial distribution was heterogeneous across the NF regime, the L and M intensity fire regime plots, values associated with the plots with fire tended to be distributed towards more positive values on the 1st MDS axis while the control plots were more widely distributed, being more associated with neutral and negative values on this first axis. The 2nd MDS axis values revealed greater dispersion and heterogeneity the

control plots, while the L and M fire regime sites tended to present a greater concentration around neutral values (0.0).

The stress value of the MDS ordination was 0.145, which is below the commonly accepted threshold of 0.2, indicating that the two-dimensional representation provides a reasonable approximation of the original multivariate distances. However, the stress level also suggests that some fine-scale details of the community structure may not be fully captured in this reduced space. This is particularly relevant for interpreting patterns of overlap between fire regimes, as the ordination might slightly underrepresent subtle differences in species composition. Despite this limitation, the stress value is within acceptable bounds for ecological studies and supports the use of the ordination to identify general patterns associated with fire regimes.

At the community level, there was a notable increase in the Shannon index, from 1.7 to 2.9, which indicates low to medium ecological diversity. For the Simpson index, the gradient was 0.61 to 0.93 and the species abundance did not differ among the three fire regime types (**Table 2**).

Table 2. Statistic for taxonomic diversity indices

| Taxonomic Index | Regime type | Mean | Minimum | Maximum | P- Value |
|-----------------|-------------|----------------------|---------|---------|----------|
| Richness | No Fire | 20.50 (± 2.61) | 16 | 25 | 0.4209 |
| | Light | 21.27 (± 3.58) | 17 | 27 | |
| | Medium | 22.50 (± 3.74) | 15 | 28 | |
| Shannon | No Fire | 2.47 (± 0.31) | 1.7 | 2.77 | 0.6331 |
| | Light | 2.58 (± 0.27) | 1.91 | 2.90 | |
| | Medium | 2.55 (± 0.25) | 2.16 | 2.89 | |
| Simpson | No Fire | 0.86 (± 0.10) | 0.61 | 0.92 | 0.6005 |
| | Light | 0.89 (± 0.06) | 0.71 | 0.93 | |
| | Medium | 0.89 (± 0.04) | 0.84 | 0.93 | |

4.4. 3.2 Community structure

4.4.3.2.1. Horizontal Structure

Of a total of 3254 individuals, 1597 (49%) had a diameter at breast height (DBH) of between 10 and 25 cm. Species with a DBH greater than 45 cm accounted for 54 (1.66%) of the total. The results for individual diameters by regime are summarized in **Figure 9 a**. The diameter class contributing most to basal coverage was DBH > 25 cm in all three fire regimes, while trees with a DBH between 5 and 10 cm were most abundant in the NF and L regimes. However, in the M fire regime, the highest number of individuals were associated with the DBH

10 to 20 cm class. The results of the mixed linear model did not show any significant differences in terms of basal area by regime.

4.4.3.2.2 Vertical structure

Three different strata were clearly distinguished according to plant height within the forest plots considered. The lower stratum (1 to 15 m) was represented by species such as *Cynophalla retusa*, *Eugenia uniflora*, *Machaerium hirtum*, *Myrcianthes pungens*, *Pisonia aculeata*, *Trichilia catigua* and *Sorocea saxicola*. The intermediate stratum (16 to 20 m) was represented by *Terminalia triflora*, *Ruprechtia laxiflora*, *Aspidosperma quebracho-blanco*, *Chloroluma gonocarpa*, *Schinopsis balansae* and *Neltuma nigra*. Finally, the upper stratum (> 20 m) was represented by *Parapiptadenia rigida*, *Calycophyllum multiflorum* and *Diplokeleba floribunda*. The maximum observed height was 30 m and corresponded to *Ficus sp.* individuals. In the three regimes studied (NF, L, M), the lower stratum (1-15 m) included the highest proportion of individuals (82.46, 84.65, and 88.12% respectively), indicating the reduced size of the species occupying this stratum (**Figure 9 b**). Lianas were more abundant in the NF (1,017 individuals) and L regimes (1,089 individuals) than in the M regime (0.767 individuals). Although some visual trends were inferred, there no significant differences for the height variable in the generalized linear model.

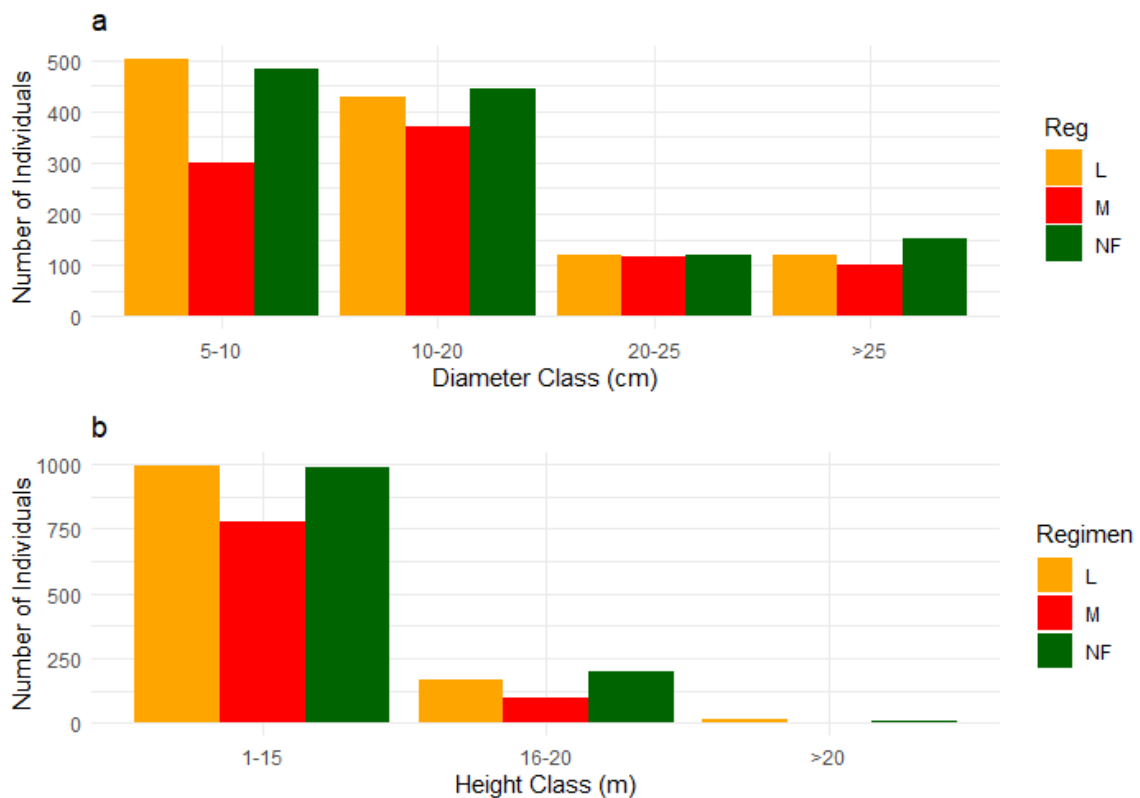


Figure 9. a) Horizontal Structure per fire regime type and b) Vertical Structure per fire regime type

4.4.3.3 Functional traits

In general, the CWM analysis revealed some differences between fire regimes within the different functional traits considered (**Table 3**). The resprouting ability of the species selected differed significantly ($F = 9.12$, $P \leq 0.001^{***}$) between NF, L and M fire regimes. Thus, Fisher's test indicated that the presence of resprouting species was higher in the plots affected by fire (L and M). On the contrary, the presence of spines, bark thickness, life form and plant height did not differ significantly across the groups (**Table 3**).

Table 3. ANOVA Test for functional traits

| CWM | No fire | Low | Medium | F value | P value |
|----------------|----------------------|----------------------|----------------------|---------|---------|
| Spine | 1.10 (± 0.15) | 1.21 (± 0.25) | 1.20 (± 0.18) | 1.12 | 0.3405 |
| Resprout | 0.83 (± 0.39) | 1.17 (± 0.23) | 1.39 (± 0.17) | 9.12 | 0.0009 |
| Height | 24.11 (± 3.42) | 22.46 (± 2.97) | 23.87 (± 3.04) | 0.86 | 0.4321 |
| Bark thickness | 8.16 (± 2.42) | 9.15 (± 2.33) | 8.65 (± 1.34) | 0.60 | 0.5548 |
| Life form | 2.96 (± 0.32) | 2.98 (± 0.32) | 3.14 (± 0.24) | 0.93 | 0.4060 |

The functional diversity analysis revealed a similar pattern for the different functional indices considered (**Figure 10**). Functional Dispersion (FDis) differed significantly between the groups, with a mean value of 1.46 ($F = 8.16$, $P \leq 0.001^{***}$). However, the remaining functional indices (Fric, Feve, FDiv) did not differ significantly across the different fire regime classes (**Figure 10**).

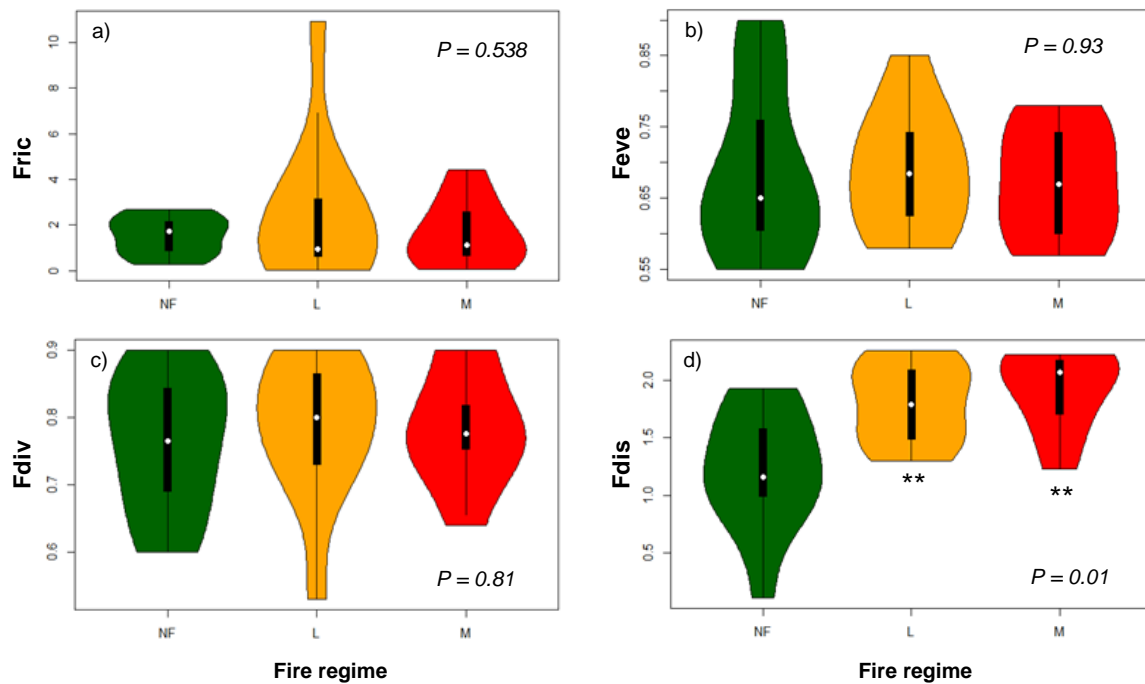


Figure 10. Functional diversity indexes for each fire regimes considered: NF =No fire, L = light and M = medium

4.4.4 Discussion

This study aimed to obtain important information related to vegetation responses to various fire regimes within the Humid Chaco of Paraguay, a fire-prone region of global importance and about which there is little scientific information available. Species composition and structure, functional traits and life form (trees, palms, lianas) were assessed in plant communities within 31 sampling plots distributed across forest patches affected by different fire regime intensities.

Classification of the fire regime highlighted the absence of high intensity fire regimes in the forest areas (within forest patches). Indeed, a high incidence of fire was not commonly observed in these forest patches, owing to the high humidity and dense forest cover, which limit the dominance of grass and the risk of fire spread (Silvério et al., 2012). These forest patches are mainly burned at their borders, but the fire does not commonly penetrate the entire forest patch. In this respect, and contrary to what might be expected from satellite information, little evidence of fire (flame evidence on standing logs, charcoal residues, tree scars) was found within these forest patches during the 3-month vegetation sampling period. This key finding emphasizes the important role of the forest patches in mitigating fire spread. The findings also mirror observations from the Chiquitania forest, where forest resilience plays a critical role in fire resistance (Maillard et al., 2020). Thus, forest patches in the Humid Chaco may provide a vital ecosystem service by preventing fire incidence. Further research into the flammability of species within these forest patches is important to enable development of locally-adapted strategies for forest restoration in fire-prone, unmanaged landscapes.

4.4.4.1 *General aspects of forest structure, composition and functional traits*

In terms of species composition, one of every five species observed in the selected sampling plots (20 %) belonged to the Fabaceae family, as indicated in previous studies in similar dry forest in neighbouring regions (Prado, 1993; Gentry et al., 1995; Tálamo et al., 2015). However, in the present study, other tree species belonging to the Eastern region were observed, i.e. *Melicoccus lepidopetalus*, *Eugenia uniflora* and *Parapiptadenia rigida*, which are typical of forests in mesoxerophytic environments (combined humid and dry environments). Our findings on species distribution, structure and diversity index are similar to those of other studies in the same type of forest in Paraguay (Mereles et al; 2020, Quevedo et al; 2021). According to our findings, diversity was intermediate (2.9), with three strata occurring: canopy, middle strata and understorey (very sparse) strata.

Although we did not observe any significant differences in vegetation responses regarding species taxonomic composition and structure, we did observe distinct patterns in species distribution across the gradient of the fire zones. For instance, *Gymananthes discolor* was more prevalent in the NF regime than in the M fire regime, indicating potential sensitivity to disturbance such as fire. Conversely, *Parapiptadenia rigida* was more abundant in both the L and M regimes, potentially indicating an association with environments characterized by higher fire incidence.

Interestingly, there were no significant differences in fire-related traits such as bark thickness, height and thorn presence among the different fire regimes. However, resprouting emerged as a significant trait, with a notable increase observed in regimes with fire presence. Several authors have reported the key role of resprouting in maintaining diversity and natural regeneration following fire in different ecosystems around the world (Lawes and Clarke, 2011; Clarke et al; 2013; Pausas and Keeley 2017), including different ecosystems in South America (Torres et al., 2013; Martins et al., 2022; Fidelis et al; 2023). Resprouting is typically considered to be associated with fire-adapted vegetation (Pausas and Keeley 2014; Clarke et al; 2013) but the forests under study are apparently not fire-adapted. Nevertheless, we provide novel information for Paraguayan forests in the Gran Chaco pointing in the same direction.

Our findings complement previous research conducted in the Gran Chaco, although variations in species structure, composition and associated traits across environments with differing levels of disturbance have been reported in the Argentinean territory (Loto and Bravo, 2020). However, we assumed that beyond fire, other factors may also affect forest structure and composition. Unlike the Argentinean region, where drier conditions predominate, the prevalence of flood pulses in the Humid Chaco could contribute to the rapid recovery observed after fire disturbance. The interaction between fire and other environmental factors, including flood dynamics, is of great importance (Damasceno-Junior et al., 2021), and also plays an important role in post-fire ecosystem recovery (Oliveira et al., 2014; Damasceno-Junior et al., 2021). In this regard, Rivaben et al. (2021) reported that the interaction between fire and flood influences the structure of forest cover and species composition in the Pantanal. These authors found that flooding favoured rapid post-fire ecosystem recovery by increasing species richness and abundance in wetter areas.

4.4.4.2 Functional response to a gradient of fire regime

The study findings indicated that resprouting was a successful strategy of the Chaco species for fire adaptation. We found that fire regimes L and M had higher average resprouting

CWM indices than the NF regime, indicating a characteristic trait in the studied communities. This is consistent with previous findings in the Argentine semi-arid Chaco (Torres et al., 2013; Bravo et al., 2019; Jaureguiberry et al., 2020). The ability of plants to resprout is an important attribute for plant survival and community resilience in frequently disturbed ecosystems (Clarke et al; 2013; Bravo et al., 2019). In woody species, resprouting after disturbance can produce changes in the growth habit, in the type and proportion of the different life forms and in different physiological processes such as nutrient assimilation rates or energy allocation (Bond and Midgley 2012). Resprouting through latent buds that utilize plant reserves is the primary post-fire regeneration strategy of woody plant species in the Chaco region of central Argentina (Torres et al., 2013; Jaureguiberry et al., 2020). However, an individual's resprouting capacity may decrease when fire is severe enough to damage meristems or frequent enough to prevent plants from regaining aboveground biomass between fires (Clarke et al., 2013). Other studies have also observed variability in pre-fire size and the incidence and type of resprouting within and among species, and between sites (Torres et al., 2013; Jaureguiberry et al., 2020). These findings highlight the need for species-specific studies to fully elucidate the factors influencing resprouting capacity in the Humid Chaco.

Our findings suggest a notable overlap in key traits such as height, life form, spines and bark thickness, all of which are critical in shaping plant community dynamics and their responses to environmental pressures, particularly fire regimes. The lack of variation in these traits contrasts with expectations based on other studies in fire-prone ecosystems (Ledesma et al., 2018; Loto and Bravo, 2020; Santacruz et al., 2021). This may imply that the study area does not exhibit the typical characteristics of a fire-prone forest, but displays certain adaptations for fire resistance, such as resprouting.

As expected in mesoxerophytic forests, trees were the predominant life form (81.45%), with a notable presence of lianas and understorey that varied from medium to sparse density, and similar taxonomic and structure composition to other forest in the region (Quevedo et al., 2021). Contrary to other studies, the fire regimes considered here did not promote evident changes in the dominant lifeform observed. In this respect, areas of higher fire frequencies in Argentina have been associated with an increasing presence of shrubs (Bravo et al; 2014; Loto and Bravo, 2020). In the present study, we assumed that the low to moderate fire incidence due to dense tree cover and humidity was not sufficient to promote changes in the dominant life forms. It is possible that prolonged and intense fire events can cause crown fires, which are necessary to promote these ecosystem changes (Silvério et al. 2013, Bernardino et al; 2021); however, this has not occurred, or at least has not occurred within the period considered (2001-2020). Other aspects include fire recurrence and time between fires, which seems to be longer in this ecosystem than other areas in the Humid Chaco, providing more time for forest species to recover.

In fire-prone areas, traits such as spines are often correlated with higher fire incidence, although they can also be an induced response to herbivory and are commonly found in arid environments like the Dry Chaco (Pérez et al., 2013; Bravo et al., 2019). However, in this study, the occurrence of spines was minimal, probably due to the dominance of species from the more humid Eastern region of Paraguay, which are less adapted to arid conditions. Similarly, although bark thickness is an important trait conferring resilience to surface fires by protecting vital tissues (Pérez et al., 2013), no significant differences in bark thickness were observed across plots with different fire regimes. The thickness of the bark ranged from 1.3 to 1.4 cm in

trees with the thickest bark (*Neltuma nigra*, *Libidibia paraguariensis* and *Sideroxylon obtusifolium*). The protective effect of bark depends on fire intensity, duration and moisture content (Lawes et al., 2011; Schubert et al., 2016).

The Humid Chaco is characterized as a subhumid ecosystem, with a well-defined seasonal regime and a water pulse that floods the savannas during a period of least six months. As stated above, the prevalent flood pulse phenomenon in the region contributes to making the different ecosystems more resilient to disturbances such as fire. However, it is also important to highlight the importance of forest conservation to protect the water pulse. Thus, the loss of or reduction in the forest area could increase forest vulnerability to fire (lower humidity, lower physical barriers, drier fuel) during the increasingly frequent periods of drought (Junk et al; 2006; Damasceno-Junior et al; 2021; Marengo et al; 2021). Besides water conservation, preservation of these forest islands is essential for maintaining the overall community integrity. Maillard et al. (2020) found that highly fragmented areas were the most affected by fires in the Department of Santa Cruz, Bolivia. Increased fragmentation, often driven by human activities, increases the vulnerability of these forests (Gasparri and Grau, 2009; Fehlenberg et al., 2017). The reduction in tree density and humidity creates conditions that facilitate fire incidence, progressively weakening forest ecosystems. Additionally, forest fragmentation significantly reduces landscape connectivity, increasing the risk of species survival and decreasing habitat quality, particularly for species most vulnerable to environmental changes (de Barros et al; 2022).

4.4.4.3 Functional diversity indexes

The study findings revealed different responses in the functional diversity indices evaluated. The significant variation in functional dispersion (FD_{is}) across fire regimes suggests differences in the regularity of the distribution of species abundance within functional spaces, probably driven by the distinct regeneration strategies prevalent in each fire regime (Mouchet et al., 2010). This finding may be attributed to the traits evaluated, which are associated with stress-tolerant species that are well-adapted to succeed in the early stages of succession. These traits enable the species to grow with minimal competition and efficiently occupy available niches to replace species lost due to disturbance.

By contrast, we did not observe any significant functional differences related to the other indices. For the Functional Richness (FR_{ic}), this could be due to a lack of variation in taxonomic richness across the sites. This is related to the concept of functional redundancy, whereby multiple species within a community perform similar functions (Fischer et al., 2007). High levels of redundancy can lead to a plateau in functional richness, as additional species do not contribute novel functions to the community (van der Sande et al., 2024). In the case of functional evenness (Feve), values greater than 0.5 were obtained for all zones, indicating a tendency towards even distribution rather than clustering. This pattern is supported by our findings on community structure and species composition, where no significant differences were detected along the fire gradient. Finally, values of functional divergence (FD_{div}) (mean value of 0.78 across the fire regimes) suggest some degree of niche specialization, with species differentiating in their roles within the community, thereby reducing direct competition for resources (Schleuter, 2010; Mason et al., 2005).

The low variation in functional indices across the fire regimes may be explained by the high productivity of the Humid Chaco ecosystem, which is largely driven by abundant water

availability. In such resource-rich environments, abiotic constraints are relaxed, leading to minimal changes in functional diversity over time (van der Sande et al., 2024). This also highlights the capacity of the ecosystem for rapid recovery following disturbance like fire, as the functional diversity is maintained despite varying fire regimes. These findings suggest that in ecosystems like the Humid Chaco, where resources are plentiful, functional diversity remains relatively stable, and community recovery after disturbances is more efficient. However, the resilience could be tested under more severe or frequent types of disturbance, indicating the importance of continuing to monitor and research these ecosystems.

4.4.4.5 Limitations of the study and future research lines.

With the data used to characterize vegetation response to various fire regimes within the Humid Chaco of Paraguay (31 plots in 14 forest patches), we did not observe any clear pattern of vegetation changes with this contrasting fire gradient. Overall, both the abundance and percentage of tree cover were similar in the three fire regimes studied, which may be due to the limited fire intensity, the rapid post-fire recovery or the presence of a hydrological regime that mitigates the impact of flames and promote a rapid ecosystem recovery. In our study, the fire regimes were constructed on the basis of a small number of variables (Vidal-Riveros et al., 2024). Despite its novelty and significance as the first classification of different fire regimes in this region, the limited set of variables considered (area, fire frequency and severity) could hamper accounting for the intrinsic ecological variability associated with this factor. This applies, for example, to the variable Time Since Last Fire (TSLF), which could play an important role, as effects may be more pronounced within shorter times in these highly productive ecosystems, given the pronounced seasonality and flood pulse. Other variables such as livestock presence, human activity and land cover changes, which have been related to changes in the fire regime in other studies (Ferrante and Fearnside 2022; Bernardi et al; 2019; Barbosa et al; 2022), should be considered for more accurate mapping.

In the future we may consider extending our research to include to other Chaco ecosystems such as savannas, the most abundant ecosystems in the ecoregion and more closely associated with high fire frequency. A comparative assessment of our results in the Humid Chaco with responses from species inhabiting the Dry Chaco, characterized by distinct environmental conditions, could yield valuable insights into ecosystem dynamics and resilience across the entire diverse vegetation subtypes and would provide more elements to understand the recovery after fire in a wide range in the Gran Chaco. Finally, although fire was the main independent variable in this study, other environmental variables of interest and that could have a significant effect on functional traits in the Chaco ecoregion could be explored, such as temperature, flood pulse, precipitation and relative humidity, all of which may interact with the functional diversity of the forest vegetation under study.

4.4.5. Conclusions

The study findings contribute to the growing, although still scarce, body of literature elucidating the intricate relationships between fire disturbance regimes, species composition and ecosystem dynamics in the Chaco region. The scarce evidence of fire incidence, together with the unclear pattern of taxonomic composition and functional diversity between the different fire regimes, suggests that preservation of forest patches is a useful strategy for

preventing fire and reducing the intensity of fire when it does occur. Similarly, the low variability in functional traits observed may be due to the limited impact of fire across the forest patches, at least in the traits evaluated. Functional overlap across the Humid Chaco, coupled with the lack of distinct taxonomic and structural distinctions, implies that microsite conditions, the influence of flood pulses and dispersal-related mechanisms may hold greater significance than the more recent fire regimes assessed in this study.

This study provides useful information on plant traits that could be used to enhance vegetation resilience and fire management strategies. On the basis of the knowledge provided, we suggest that future research should apply an interdisciplinary approach, including multiple environmental factors, to improve management of these unique and poorly studied fire-prone ecosystems.

References

- Arganaraz, J., Gavier-Pizarro, G., Zak, M., and Bellis, L. (2015). Fire Regime, Climate, and Vegetation in the Sierras de Córdoba, Argentina. *Fire Ecology*, 11, 55-73. <https://doi.org/10.4996/fireecology.1101055>
- Barbosa, M. L., Haddad, I., Nascimento, A. L., da Silva, G., Veiga, R., Hoffmann, T. B., Souza, A., Silva, R., Streher, A., Pereira, F., Aragão, L., and Anderson, L. (2022). Compound impact of land use and extreme climate on the 2020 fire record of the Brazilian Pantanal. *Global Ecology and Biogeography*, 31, Article e13563. <https://doi.org/10.1111/geb.13563>
- Bernardi, R., Staal, A., Xu, C., Scheffer, M., and Holmgren, M. (2019). Livestock herbivory shapes fire regimes and vegetation structure across the global tropics. *Ecosystems*, 22, 1212–1227. <https://doi.org/10.1007/s10021-019-00349-x>
- Bernardino, P. N., Dantas, V. L., Hirota, M., Pausas, J. G., and Oliveira, R. S. (2021). Savanna–Forest Coexistence Across a Fire Gradient. *Ecosystems*. <https://doi.org/10.1007/s10021-021-00654-4>
- Bond, W. J., and Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution*, 16(1), 45-51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4)
- Bond, W. J., & Midgley, J. J. (2012). Fire and the Angiosperm revolutions. *International Journal of Plant Sciences*, 173(6), 569–583. <https://doi.org/10.1086/665819>
- Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165(2), 525–538. <https://doi.org/10.1111/j.1469-8137.2004.01252.x>
- Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D’Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., ... Pyne, S. J. (2009). Fire in the Earth system. *Science*, 324(5926), 481–484. <https://doi.org/10.1126/science.1163886>
- Bravo, S., Kunst, C., Leiva, M., and Ledesma, R. (2014). Response of hardwood tree regeneration to surface fires, western Chaco region, Argentina. *Forest Ecology and Management*, 326, 36-45. <https://doi.org/10.1016/j.foreco.2014.04.009>
- Bravo, S., Basualdo, M., Kunst, C., and del Corro, F. (2019). Aerial Bud Bank and Structural Changes of Woody Species from Argentine Chaco in Response to Disturbances. *Journal of Environmental Science and Health - Part A Environmental Science and Engineering*, 8, 58-69. <https://doi.org/10.17265/2162-5298/2019.02.002>
- Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., and Knox, K. J. E. (2013). Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist*, 197(1), 19-35. <https://doi.org/10.1111/nph.12001>

Cunningham, C., Bowman, D., and Williamson, G. (2024, June 24). Extreme wildfires are on the rise globally, powered by the climate crisis. *The Conversation*. <http://theconversation.com/extreme-wildfires-are-on-the-rise-globally-powered-by-the-climate-crisis-229722>

Damasceno-Junior, G. A., Pereira, A. de M. M., Oldeland, J., Parolin, P., and Pott, A. (2021). Fire, Flood and Pantanal Vegetation. En G. A. Damasceno-Junior and A. Pott (Eds.), *Flora and Vegetation of the Pantanal Wetland* (pp. 661-688). Springer International Publishing. https://doi.org/10.1007/978-3-030-83375-6_18

Dantas, V. L., Batalha, M. A., and Pausas, J. G. (2013). Fire drives functional thresholds on the savanna-forest transition. *Ecology*, 94(11), 2454–2463. <https://doi.org/10.1890/13-0460.1>

Dantas, V. de L., Hirota, M., Oliveira, R. S., and Pausas, J. G. (2016). Disturbance maintains alternative biome states. *Ecology Letters*, 19(1), 12–19. <https://doi.org/10.1111/ele.12537>

De Barros, A. E., Morato, R. G., Fleming, C. H., Pardini, R., Oliveira-Santos, L. G. R., Tomas, W. M., Kantek, D. L. Z., Tortato, F. R., Fragoso, C. E., Azevedo, F. C. C., Thompson, J. J., and Prado, P. I. (2022). Wildfires disproportionately affected jaguars in the Pantanal. *Communications Biology*, 5(1), Article 1. <https://doi.org/10.1038/s42003-022-03937-1>

Fehlenberg, V., Baumann, M., Gasparri, N. I., Piquer-Rodriguez, M., Gavier-Pizarro, G., and Kuemmerle, T. (2017). The role of soybean production as an underlying driver of deforestation in the South American Chaco. *Global Environmental Change*, 45, 24–34. <https://doi.org/10.1016/j.gloenvcha.2017.05.001>

Ferrante, L., and Fearnside, P. (2022). Brazil's Pantanal threatened by livestock. *Science*, 377(6606), 720–721. <https://doi.org/10.1126/science.ade0656>

Fischer, J., Lindenmayer, D., Blomberg, S., Montague-Drake, R., Felton, A., and Stein, J. (2007). Functional Richness and Relative Resilience of Bird Communities in Regions with Different Land Use Intensities. *Ecosystems*, 10(6), 964-974. <https://doi:10.1007/s10021-007-9071-6>

Gasparri, N. I., and Grau, H. R. (2009). Deforestation and fragmentation of Chaco dry forest in NW Argentina (1972–2007). *Forest Ecology and Management*, 258(6), 913–921. <https://doi.org/10.1016/j.foreco.2009.02.024>

Gentry, A.H., Bullock, S.H., Mooney, H.A., Medina, E. (1995). Seasonally dry tropical forests. *Diversity and Floristic Composition of Neotropical Dry Forests*; Bullock, SH, Mooney, HA, Medina, E., Eds 146–194.

Gonzalez, A.M., Musálem, K., Laino, R., Benayas, J.M., Alonso, V.C., Cordero, Z.E., Moreno, V.B., Otazu, P.C., Valenzuela, A.L., González, J.D., Amarilla, S.M., Espinoza, M.L., and Enciso, C. (2018). Servicios ecosistémicos en el Chaco Húmedo Paraguayo: retos para el manejo basado en los ecosistemas. *Ecosistemas* 27(2):115-125. <https://doi:10.7818/ECOS.1531>

Grau-Andrés, R., Moreira, B., and Pausas, J. G. (2024). Global plant responses to intensified fire regimes. *Global Ecology and Biogeography*, 33(8), e13858. <https://doi.org/10.1111/geb.13858>

Grime, J. P., Thompson, K., Hodgson, J. G., Hunt, R., Cornelissen, J. H. C., Rorison, I. H., ... & Band, S. R. (1997). Integrated screening validates primary axes of specialization in plants. *Oikos*, 79(2), 259-281. <https://doi.org/10.2307/3546011>

Intergovernmental Panel on Climate Change. (2021). *Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte et al. Eds.). Cambridge University Press. <https://doi.org/10.1017/9781009157896>

Jaureguiberry, P., Cuchietti, A., Gorné, L. D., Bertone, G. A., and Díaz, S. (2020). Post-fire resprouting capacity of seasonally dry forest species – Two quantitative indices. *Forest Ecology and Management*, 473, 118267. <https://doi.org/10.1016/j.foreco.2020.118267>

Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., and Bowman, D. M. J. S. (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, 6(1), 7537. <https://doi.org/10.1038/ncomms8537>

- Karavani, A., Boer, M. M., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J., de Luis, M., Enríquez-de-Salamanca, Á., and Resco de Dios, V. (2018). Fire-induced deforestation in drought-prone Mediterranean forests: Drivers and unknowns from leaves to communities. *Ecological Monographs*, 88(2), 141-169. <https://doi.org/10.1002/ecm.1285>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van BODEGOM, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., ... Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, 17(9), 2905-2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16 (8), 406–411.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W. (2012). Fire in mediterraneanclimate ecosystems: ecology, evolution and management. Univ. of Cambridge Press, Cam-bridge, UK,515 pp.
- Laino, D.L., Musálem, K. and Laino, R. (2017). Perspectivas para un Desarrollo Sustentable: Un Estudio de Caso de Producción Ganadera en la Región del Chaco Paraguayo. *Población y Desarrollo*, 23(45): 95–106.
- Laino, R., Musalem, K., Laino, L. D., Caballero-Gini, A., Bueno-Villafña, D., Aranda, L., Esquivel, A., Riveros, M. F., Nardelli, L. R., Cantero, N., and Irala, R. (2022). Islands of Forests Among Savannas: Key Elements for Conservation and Production in the Paraguayan Humid Chaco. In F. Montagnini (Ed.), *Biodiversity Islands: Strategies for Conservation in Human-Dominated Environments* (Vol. 20, pp. 185–205). Springer International Publishing. https://doi.org/10.1007/978-3-030-92234-4_8
- Laliberté, E., and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299-305. doi: 10.1890/08-2244.1
- Laliberté, E., Legendre, P., & Shipley, B. (2015). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Retrieved from <https://cran.r-project.org/web/packages/FD/FD.pdf>
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., ... and Bonis, A. (2008). Assessing functional diversity in the field—methodology matters! *Functional Ecology*, 22(1), 134-147.
- Lawes, M. J., and Clarke, P. J. (2011). Ecology of plant resprouting: Populations to community responses in fire-prone ecosystems. *Plant Ecology*, 212(12), 1937-1943. <https://doi.org/10.1007/s11258-011-9994-z>
- Lawes, M. J., Richards, A., Dathe, J., and Midgley, J. J. (2011). Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology*, 212(12), 2057-2069. <https://doi.org/10.1007/s11258-011-9954-7>
- Ledesma, R., Kunst, C., Bravo, S., Leiva, M., Lorea, L., Godoy, J., and Navarrete, V. (2018). Developing a prescription for brush control in the Chaco region: Effects of combined treatments on the canopy of three native shrub species. *Arid Land Research and Management*, 32(3), 351–366. <https://doi.org/10.1080/15324982.2018.1430072>
- Loto, D., and Bravo, S. (2020). Species composition, structure, and functional traits in Argentine Chaco forests under two different disturbance histories. *Ecological Indicators*, 113, 106232. <https://doi.org/10.1016/j.ecolind.2020.106232>
- Maillard, O., Vides-Almonacid, R., Flores-Valencia, M., Coronado, R., Vogt, P., Vicente-Serrano, S. M., Azurduy, H., Anívarro, R., and Cuellar, R. L. (2020). Relationship of forest cover fragmentation and drought with the occurrence of forest fires in the department of Santa Cruz, Bolivia. *Forests*, 11(9), Article 9. <https://doi.org/10.3390/f11090910>
- Maillard, O., Herzog, S. K., Soria-Auza, R. W., and Vides-Almonacid, R. (2022). Impact of Fires on Key Biodiversity Areas (KBAs) and Priority Bird Species for Conservation in Bolivia. *Fire*, 5(1), Article 1. <https://doi.org/10.3390/fire5010004>

Mason, N. W. H.; Mouillot, D.; Lee, W. G.; Bastow W., J. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112-118.

Marengo, J., Cunha, A. P., Cuartas, L., Deusdará-Leal, K., Broedel, E., Seluchi, M., Michelin, C., Baião, C., Chuchón Angulo, E., Almeida, E., Kazmierczak, M., Mateus, N., Silva, R., and Bender, F. (2021). Extreme drought in the Brazilian Pantanal in 2019–2020: Characterization, causes, and impacts. *Frontiers in Water*, 3, 639204. <https://doi.org/10.3389/frwa.2021.639204>

Maturo HM, Oakley LJ, Prado DE (2005) Vegetación y posición fitogeográfica de la Reserva El Bagual. In: Di Giacomo AG, Krapovickas SF (eds) Historia natural y paisaje de la Reserva El Bagual, Formosa, Argentina. Asociación Ornitológica de La Plata, Buenos Aires, 592pp.

Mereles F, Cartes JL, Clay R, Cacciali P, Paradedda C, Rodas O, Yanosky A (2013) Análisis cualitativo para la definición de las ecorregiones de Paraguay occidental. *Paraquaria Nat* 1(2): 12–20

Mereles F, Céspedes G, De Egea-Elsam J, Spichiger R (2020) Estudios fitosociológicos en el Gran Chaco: estructura, composición florística y variabilidad del bosque de *Schinopsis balansae* en el Chaco Húmedo Boreal, Paraguay. *Bonplandia* 29(1):39–55

Mouchet, M., Villéger, S., Mason, N., and Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867-876. doi: 10.1111/j.1365-2435.2010.01695.x

Oliveira, M., Damasceno-Junior, G., Pott, A., Paranhos Filho, A., Suarez, Y., and Parolin, P. (2014). Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence. *Forest Ecology and Management*, 331. <https://doi.org/10.1016/j.foreco.2014.08.011>

Pausas, J. G., and Fernández-Muñoz, S. (2012). Fire regime changes in the Western Mediterranean Basin: From fuel-limited to drought-driven fire regime. *Climatic Change*, 110(1), 215–226. <https://doi.org/10.1007/s10584-011-0060-3>

Pausas, J. G., and Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *The New Phytologist*, 204(1), 55-65. <https://doi.org/10.1111/nph.12921>

Pausas, J. G., and Keeley, J. E. (2017). Epicormic Resprouting in Fire-Prone Ecosystems. *Trends in Plant Science*, 22(12), 1008-1015. <https://doi.org/10.1016/j.tplants.2017.08.010>

Pausas, J. G., and Ribeiro, E. (2013). The global fire-productivity relationship. *Global Ecology and Biogeography*, 22(6), 728–736. <https://doi.org/10.1111/geb.12043>

Pérez de Molas L (2015). Manual de familias y géneros de árboles del Paraguay. FAO, San Lorenzo, p 216.

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M., Cornwell, W., Craine, J., Gurvich, D., Urcelay, C., Veneklaas, E., Reich, P., Poorter, L., Wright, I., Ray, P., Enrico, L., Pausas, J., Vos, A., and Van der Heijden, M. (2013). Nuevo manual para la medición estandarizada de caracteres funcionales de plantas. *Australian Journal of Botany*, 61, 167–234.

Pla, L., Casanoves, F., and Di Rienzo, J. (2010). Cuantificación de la diversidad funcional. En L. Pla, F. Casanoves and J. Di Rienzo, Valoración y análisis de la diversidad funcional y su relación con los servicios ecosistémicos. Turrialba, Costa Rica: CATIE.

Prado, D.E. (1993). What is the Gran Chaco vegetation in South America? 1. A review. *Contribution to the study of flora and vegetation of the Chaco*: 5. *Candollea* 48,145–172.

Ponisio, L. C., Wilkin, K., M’Gonigle, L. K., Kulhanek, K., Cook, L., Thorp, R., Griswold, T., and Kremen, C. (2016). Pyrodiversity begets plant–pollinator community diversity. *Global Change Biology*, 22(5), 1794–1808. <https://doi.org/10.1111/gcb.13236>

Quevedo Fernández, M. L., Pérez de Molas, L., Folmann, W. T., Rodríguez, S. A., Gamarra Ruiz Díaz, L., Peralta-Kulik, N., Palacios, X. M. S., Nogueira Dias, A., and de Magalhaes Miranda, G. (2021). Valoración económica, composición, estructura y diversidad florística del bosque mesoxerofítico semicaducifolio de *Schinopsis balansae* Engl., Ecorregión Chaco Húmedo, Paraguay. *Investigación Agraria*, 23(2), 101-110. <https://doi.org/10.18004/investig.agrar.2021.diciembre.2302689>

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., Anderson, M. T., Higgins, S. I., and Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, 20(5), 653–660. <https://doi.org/10.1111/j.1466-8238.2010.00634.x>

Rivaben, R. C., Pott, A., Bueno, M. L., Parolin, P., Cordova, M. O., Oldeland, J., da Silva, R. H., and Damasceno-Junior, G. A. (2021). Do fire and flood interact to determine forest islet structure and diversity in a Neotropical wetland? *Flora*, 281, 151874. <https://doi.org/10.1016/j.flora.2021.151874>

Rumbo M (2010) Análisis biogeográfico de los mamíferos de Paraguay. *Bol Mus Nac Hist Parag* 16(1):18–29

Santacruz-García, A. C., Bravo, S., del Corro, F., García, E. M., Molina-Terrén, D. M., and Nazareno, M. A. (2021). How do plants respond biochemically to fire? The role of photosynthetic pigments and secondary metabolites in the post-fire resprouting response. *Forests*, 12(1), Article 56. <https://doi.org/10.3390/f12010056>

Salgado-Negret, B., and Paz, H. (2015). Escalando de los rasgos funcionales a procesos poblacionales, comunitarios y ecosistémicos (pp. 12–35). En B. Salgado-Negret (Ed.), *La ecología funcional como aproximación al estudio, manejo y conservación de la biodiversidad: Protocolos y aplicaciones* (pp. 12-35). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. Schleuter, D., Daufresne, M., Massol, F., and Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469-484. doi: 10.1890/08-2225.1

Schubert, A. T., Nano, C. E. M., Clarke, P. J., and Lawes, M. J. (2016). Evidence for bark thickness as a fire-resistance trait from desert to savanna in fire-prone inland Australia. *Plant Ecology*, 217(6), 683-696. <https://doi.org/10.1007/s11258-016-0611-z>

Silvério, D., Brando, P., Balch, J., Putz, F. E., Nepstad, D., Oliveira-Santos, C., and Bustamante, M. (2013). Testing the Amazon savannization hypothesis: Fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368, 20120427. <https://doi.org/10.1098/rstb.2012.0427>

Tálamo, A., Barchuk, A.H., Garibaldi, L.A., Trucco, C.E., Cardozo, S., Mohr, F. (2015). Disentangling the effects of shrubs and herbivores on tree regeneration in a dry Chaco forest (Argentina). *Oecologia* 178, 847–854. <https://doi.org/10.1007/s00442-015-3269-7>

Torres, R., Giorgis, M., Trillo, C., Volkmann, L., Demaio, P., Heredia, J., and Renison, D. (2013). Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina. *Austral Ecology*, 39. <https://doi.org/10.1111/aec.12084>

van der Sande, M. T., Poorter, L., Derroire, G., do Espírito Santo, M. M., Lohbeck, M., Müller, S. C., Bhaskar, R., van Breugel, M., Dupuy-Rada, J. M., Durán, S. M., Jakovac, C. C., Paz, H., Rozendaal, D. M. A., Brancalion, P., Craven, D., Mora Ardilla, F., Almeida, J. S., Balvanera, P., Becknell, J., ... Bongers, F. (n.d.). Tropical forest succession increases tree taxonomic and functional richness but decreases evenness. *Global Ecology and Biogeography*. Advance online publication. <https://doi.org/10.1111/geb.13856>

Vidal-Riveros, C., Souza-Alonso, P., Bravo, S., Laino, R., and Ngo Bieng, M. A. (2023). A review of wildfires effects across the Gran Chaco region. *Forest Ecology and Management*, 549, 121432. <https://doi.org/10.1016/j.foreco.2023.121432>

Vidal-Riveros, C., Watler Reyes, W. J., Ngo Bieng, M. A., and Souza-Alonso, P. (2024). Assessing fire regimes in the Paraguayan Chaco: Implications for ecological and fire management. *Fire*, 7(10), 347. <https://doi.org/10.3390/fire7100347>

Villéger, S., Mason, N., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290-2301. doi: 10.1890/07-1206.1

Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages: Decomposing functional β -diversity. *Global Ecology and Biogeography*, 22(6), 671–681. <https://doi.org/10.1111/geb.12021>

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>

Zupo, T., Daibes, L. F., Pausas, J. G., and Fidelis, A. (2021). Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science*, 32(1), e12968. <https://doi.org/10.1111/jvs.12968>

5 GENERAL DISCUSSION

5.1 OVERVIEW APPROACH AND RELEVANT FINDINGS

Based on the objectives outlined in this doctoral thesis, a multi-scale analysis of fire behavior and vegetation responses was conducted, encompassing three distinct scales: regional, sub-regional, and local.

At the *regional scale*, the study aimed to understand the patterns and characteristics of fire within a landscape in accordance with ecoregional classifications as proposed by Olson and Dinerstein (2003). This approach provided insight into fire dynamics within the broader context of the Gran Chaco and Pantanal, offering a detailed look at fire patterns over the past two decades and the key climatic and anthropogenic drivers influencing fire incidence. This fills a significant gap in our understanding of fire behavior at the ecoregional scale (Bowman, 2023), emphasizing how climate variability, land-use changes, and human activities collectively shape fire regimes across South America's tropical and subtropical regions.

At the *sub-regional scale*, the study focused specifically on the Paraguayan Chaco, where a fire regime analysis helped to establish a fire gradient and categorize fire behavior on an intermediate scale. This scale of analysis contributes to a more nuanced understanding of fire typologies specific to the Paraguayan Chaco—a region for which limited information exists on the ecological impacts of fire (Vidal-Riveros et al., 2023). By examining fire patterns within this sub-region, this thesis provides a differential vision of fire regimes that considers the singular biophysical and climatic factors of the Chaco ecosystem. The findings underscore the complex interplay between environmental factors and fire regimes, offering insights that are critical for developing tailored management and conservation strategies in fire-prone areas.

Finally, at the local scale, the research focused on examining the vegetation's response to fire impacts, specifically within forested areas. This component provides novel insights into the forest structure and composition in post-fire scenarios and delves into the functional traits that shape ecosystem resilience and recovery (Pausas and Keeley, 2023). Results indicate that forested areas within the Humid Chaco exhibit relatively low fire frequency, suggesting a fire regime with lower intensity in these mesoxerophytic forests. Additionally, the findings reveal the forest's potential to act as buffers against fire impacts, highlighting their importance and significant implications for fire management and ecosystem resilience. While other studies (Torres et al; 2013; Torres and Renison 2017; Herrero et al; 2016; Zeballos et al; 2014) have noted the resilience of tropical dry forests to disturbances, this thesis extends that understanding by examining fire-specific responses in a highly diverse but understudied ecosystems, as the mesoxerophytic forests of the Paraguayan Chaco.

The integrated vision of the regional, sub-regional, and local findings contributes to amplify the understanding of fire ecology within the Gran Chaco and Pantanal ecoregions. This multi-scale

approach aligns with recent research emphasizing the importance of scale in ecological and fire studies (Barbero et al; 2014; Abatzoglou et al., 2018; Pausas and Keeley, 2019). The complex spatial and temporal dynamics observed highlight how fire regimes vary significantly across scales and how vegetation responses are influenced by these shifting patterns. Furthermore, the study's emphasis on functional traits in post-fire recovery aligns with recent shifts in fire ecology towards understanding resilience mechanisms at the ecosystem level, as outlined in studies by Bowman et al. (2020, 2023) and others.

Furthermore, this thesis reinforces the need for adaptive fire management strategies that take into account regional climatic influences, land-use changes, and local vegetation characteristics, offering a roadmap for future research and conservation efforts in fire-prone biodiverse tropical regions.

5.2 HYPOTHESES VERIFICATION

Considering the results collected in chapter 2, we did not find sufficient evidence that support an increasing trend in burned area over the two decades studied across the Gran Chaco and Pantanal ecoregion, leading us to reject **Hypothesis 1**. However, it is important to highlight that a 20-year period may be relatively short for establishing strong conclusions regarding long-term trends in fire activity. Notably, we observed a slight increase in fire dynamics towards the end of the study period, with 2020 standing out as the year with the highest burned area on record in our time series. This pattern of fire activity aligns with findings from various authors (Correa et al; 2022; Marengo et al; 2021; Libonati et al; 2022; Calim Costa et al; 2023), who attribute such intensifications in fire impact to the combined effects of climatic, environmental, and anthropogenic factors. In this case, prolonged periods of high temperatures, extended droughts, reduced precipitation, and expansion of livestock activities were key drivers, contributing to a unique combination that fuelled unprecedented fire behavior across the study area (Pivello et al; 2021; Naval et al; 2023). Therefore, while we rejected Hypothesis 1, our results confirmed that factors such as high temperatures, decreased precipitation, and the influence of livestock management acted as precursors to the increased fire dynamics at ecoregional scales. In fact, considering the temperature records of the last few years, it could be possible that these trends could be exacerbated during this current decade. Regarding **Hypothesis 2**, we observed notable differences in fire regimes across distinct ecoregions within our study. Specifically, the Pantanal and Humid Chaco regions exhibited a higher propensity for ignition, while the Dry Chaco was less impacted by fire events. These differences, coupled with the widespread use of fire in livestock management practices, underscore the role of environmental and ecological diversity in mediating fire susceptibility and behavior across the landscape. In contrast, the Dry Chaco experienced fewer fire events, reflecting the arid conditions and limited fuel loads that constrain fire occurrence. These findings highlight the critical role of environmental and ecological factors—such as precipitation, fuel accumulation, and land-use practices—in shaping fire susceptibility and behavior across the landscape. This spatial heterogeneity in fire regimes underscores the importance of tailoring fire management strategies to the specific ecological contexts of each ecoregion.

Following, **Hypothesis 3**, proposed a reduced structural and compositional complexity in fire-regime areas (with a predominance of shrubby and grassy species and smaller diameter classes) as opposed to non-fire environments, our findings do not support this hypothesis. Despite exposure to fire, the forest patches selected in our study area did not exhibit significant shifts toward a more heterogeneous or savanna-like state. This indicates that fire in these patches was not intense, severe, extensive, or frequent enough to drive major structural changes in forest composition and structure. Literature suggests that higher fire frequency and severity would likely be necessary to induce such transformations in these forest types (Silvério et al; 2013; Withey et al., 2018; De Faria et al; 2021). It is also worth noting that these forest patches represent a transitional forest type, containing species from both the dry and humid Chaco regions. These findings suggest that this type of forests may play a critical ecosystem role in mitigating the spread of fire across the landscape. Regarding species composition, we found that *Diplokeleba floribunda* to be more abundant in fire-exposed areas, while others, like *Gymnanthes discolor*, were more prevalent in patches with minimal or no fire exposure. This pattern indicates certain degree of species association with the different fire regimes provides a differential vision; however, most species were found across all three fire regimes, emphasizing their adaptability and resilience to varying fire frequencies and intensities.

Turning to **Hypothesis 4**, which suggested that fire-prone environments would exhibit a prevalence of fire-tolerant traits and functional variability among plant species, our findings provide only partial support. While the literature widely recognizes that fire-prone environments favor species with fire-adaptive traits (e.g., resprouting, thick bark) (Lawes and Clarke 2011; Pausas 2015, 2017; Schubert et al; 2016; Grau-Andrés et al; 2024), our study area highlighted resprouting as the predominant adaptive trait associated with fire regime types. Although other traits were present, they did not demonstrate a significant association with specific fire regime types. This prevalence of resprouting suggests that it is a particularly effective regeneration strategy in these ecosystems, facilitating rapid recovery following disturbances.

Finally, functional diversity indices (related to fire tolerance traits) would exhibit distinct responses to fire regimes. These responses are expected to vary depending on the specific aspect of functional diversity being measured and the presence and abundance of species with fire-resistant traits. Our analysis revealed notable functional differences among traits across the sampled sites. Significant variation in functional dispersion (FD_{is}) was observed among fire regimes, indicating differences in species abundance distributions within functional space. This variation likely reflects the distinct regeneration strategies that dominate each fire regime, as species with traits suited to fire resilience occupy different niches within the functional space (Mouchet et al., 2010). The traits we evaluated, such as resprouting and others related to stress tolerance, are often associated with species adapted to early successional stages. These traits enable species to grow with minimal competition, allowing them to efficiently replace those lost due to fire or other disturbances.

In summary, while our findings did not fully support all initial hypotheses, they lead us to another scenario of work and discussion, underscoring the complex interplay between fire, environmental conditions, and vegetation responses. This study provides valuable knowledge

and novel insights into the resilience mechanisms and functional trait diversity in fire-affected ecosystems, particularly within the distinctive environmental gradients of the Gran Chaco and Pantanal regions.

5.3 CONTRIBUTION TO THE LITERATURE

This research makes a valuable contribution to the existing literature on the fire regime characterization and plants responses to fires, using a multiscale approach, and has important theoretical and practical implications. Several studies have been conducted that focus on fire behaviour across this study area (Bravo et al; 2014, 2022; Lipoma et al; 2016, 2019; Correa et al; 2022; Marengo et al; 2021), as well as characterizing plants traits within a given area (Bravo and Loto 2020; Santacruz-García et al; 2019). Nevertheless, to date and to the best of our knowledge, no comprehensive research has been conducted on the fire patterns and fire regime using a multiscale approach combining with vegetation responses at local scale in the humid Paraguayan Chaco. Therefore, this thesis contributes to the literature in several ways:

1. by **providing an overview of the state of the art of fire effects** at regional scales in the Gran Chaco region outlining the gaps and main problems considering the available literature. This contribution is particularly important given the poor and unbalanced knowledge detected across the three ecoregions, where Paraguay and Bolivia are the countries with less information related to fire studies. Here, it is also important to notice the remarkable difference between topics related to fire. In this regard, most of the advances are related to plant ecology and relatively few studies were focus on soil topics (Vidal-Riveros et al; 2023)

2. by **improving the current understanding of the seasonal fire pattern**, at regional and subregional scales. Understanding fire behaviour is crucial to propose fire management strategies for different stakeholders at national and regional levels.

3. by **identifying differences of fire patterns between the three studied ecoregions**. The analysis highlighted differences in fire frequency and intensity across sub-regions: higher frequency but lower intensity fires in the Humid Chaco and Pantanal, and lower frequency but higher intensity fires in the Dry Chaco due to variations in fuel type and connectivity.

4. by **providing a practical way to model fire regime** with few attributes which can be useful for future studies in other disciplines as soils, water, wildlife, and social issues as land use, land conversion, type of tenure and activity, among others. With this contribution, we also provided a fire regime map, being an important tool for decision-making related to adaptation and mitigation strategies, contributing to climate adaptation pathways in the Paraguayan Chaco

5. by **contributing to the scarce knowledge of fire behaviour in Paraguay** where there is a big gap of information and advances in this discipline, and especially considering that global warming conditions will favour fire recurrence in the near future (IPCC 2021)

6. by **providing a comprehensive multiscale analysis of fire dynamics** using remote sensing and combining with local field study to evaluate plants responses to fire impact.

7. by **highlighting the crucial capacity of native forest patches to mitigate fire** within the humid Paraguayan Chaco, this research offers essential information to influence decision-

makers and land managers in promoting the conservation of remaining forest islands across the landscape.

8. by **providing valuable insights into how forest vegetation responds to different fire regimes** in the humid Chaco landscape of Paraguay, this study uncovers the presence of species associated with low and medium fire regime classifications

On a practical level, the results and products (especially those provided in Chapters 2 and 3) can assist public authorities and citizens in understanding fire behavior and its drivers, evaluating how vegetation responds to fire, identifying critical restoration areas, and supporting early warning systems to prevent future wildfires.

5.4 THEORETICAL IMPLICATIONS OF THE MAIN FINDINGS

With the increasing fire weather, fire severity and extreme fire events due to climate change and the global commitment for ecosystem resilience, a new paradigm has emerged in academic research on fire ecology and management (IPCC 2021, Tedim et al; 2021; Stoof and Kettridge 2022). This research project contributes to this new paradigm emerging in academic research on fire ecology and management, highlighting the comprehension of fire dynamic at different scales and the crucial role of forest patches in preventing fire spread at local scale. In this regard, the main theoretical implications of the findings of the four chapters that make up this thesis can be summarized as follow:

The results of the **first chapter** synthesize the state of the art of the fire knowledge across the ecoregions highlighting important research topics related to fire regime, soils, herbivory and livestock, vegetation responses, invasion, wildlife, social and cultural knowledge, increasing research and transference. This finding gives the necessary background and provides the framework to support this thesis. Indeed, important gaps were covered such as modelling fire regime using a combination of area burned, severity, fire frequency and other fire metrics to understand its behaviour. Besides, the inclusion of severity in fire regime modelling is also a novelty given the predominance of using only fire frequency or burning area as the sole indicator of fire regime. Another important topic was in relation to the vegetation responses, specifically in the Paraguayan Chaco where the scientific literature is scarce and there is a need to understand the fire impact in the last decades. This chapter also highlights the evolution of fire history in the Gran Chaco, which is a key aspect to later understand the current behaviour and dynamic in different context. Another relevant issue was to collect the different contributions and identify the scarcity of information between topics and countries that comprises the Gran Chaco.

Regarding fire effects, it was highlighted that fire ecology studies has evolved in different ways within the Gran Chaco, and is especially linked to plant distribution, composition, structure and trait studies. Results are mainly focused on how ecosystems and species adapt to or are resilient to fires. It examines evolutionary adaptations in plants, such as the post-fire regeneration capacity of pyrophytic plant species and the role of fire in promoting certain fire-adapted species. However, most part of these results are limited to Argentinean and Brazilian areas of

the Gran Chaco (mainly Chaco Serrano and Pantanal, respectively), and therefore, a big scientific gap still appears in Paraguay and Bolivia.

The **second chapter** analyses fire dynamics providing a comprehensive analysis of fire patterns over a 20-year period in the Gran Chaco and Pantanal ecoregions, offering valuable insights into the spatial and temporal distribution of fire events. This characterisation is crucial for understanding the behaviour of fire in these biodiverse and ecologically sensitive areas. By providing a long-term analysis of spatial and temporal fire patterns, the study contributes to fire ecology theories on disturbance regimes, landscape resilience, and ecosystem adaptation (Mc Lauchlan et al; 2020; Kelley et al; 2023; Stoof and Kettridge 2022; Uyttewaal et al; 2024). It also underscores the importance of regional variability in fire behavior, reinforcing theoretical frameworks that address the interaction between climate, vegetation, and human activity in shaping fire regimes (Archibald et al; 2013; Bowman et al; 2014; Kelly et al; 2023). Such insights were used to predict future fire dynamics under changing environmental conditions.

In this chapter we also modelled fire patterns to understand fire activity at large scale (Gran Chaco and Pantanal Ecoregions). The main results revealed a consistent pattern of increasing fire occurrence following an east to west environmental gradient, from the wetter Pantanal and Humid Chaco to drier Dry Chaco. Previous research has already highlighted the essential role of environmental factors in controlling fire distribution in subtropical ecosystems (Bravo et al., 2014; Roman - Cuesta et al., 2014). Grasslands and savanna systems often experience frequent fires and large burned areas after fine fuel growth-desiccation alternances coinciding with an abundance of rainfall followed by drought periods (Archibald et al; 2013; Argañaraz et al., 2015b). These results also reinforce the importance of integrating climate variability and vegetation type into predictive fire models, which are essential for understanding regional fire dynamics and informing adaptive fire management strategies under climate change. However, we also found that land use is a key variable in the model, mainly given by the presence of livestock and agricultural expansion across the ecoregions. Some authors (Pivello et al; 2021; Libonati et al; 2022; Kumar et al; 2022; Barbosa et al; 2022) stressed the compound effect of climatic and land use variables in Pantanal, mainly in 2020, a year of catastrophic fire events with dramatic consequences for the studied area. Along the two decades, the last two years showed an increase pattern in fire activity which is very related to heatwaves, prolonged drought and reduced precipitation.

To further understand fire activity, we framed a medium scale where we delineated fire regime in the Gran Chaco of Paraguay, which is developed in the **third chapter**. Using a clustering technique, we combined different fire attributes (frequency, area and severity) to differentiate the fire gradient needed to identify forest areas where fire had occurred differentially. This forest selection would be fundamental for the subsequent steps of this thesis, namely the field study of the vegetation responses at the local level. In this regard, the clustering approach allowed for a nuanced categorization of fire regimes in the Paraguayan Chaco, identifying four distinct clusters that revealed a complex fire pattern not clearly inferred through traditional methods or simple observation. This analysis demonstrated a clear spatial stratification in fire regimes, with clusters progressively varying from low-severity, infrequent fires with smaller burnt areas in the Low (L) category, to high-severity fires affecting extensive areas but

occurring at a relatively lower frequency in the High (H) cluster. These findings highlight the diversity of fire behavior across the region and underscore the utility of cluster analysis for capturing variations in fire severity, frequency, and scale that may inform targeted fire management practices. Through this unsupervised classification, we achieved a more detailed perspective on the spatial and temporal patterns of fire, enabling us to pinpoint areas with elevated fire risk. Consequently, our results support more targeted strategies for fire management and allow a more efficient allocation of resources for fire prevention and fire control efforts. Although these results require field validation using supervised methods, our preliminary findings provide crucial information for planning experimental designs or sampling strategies using the most accurate fire data available. This contribution is particularly important at the academia-policy interface, where strategies are developed and assessed to prevent, mitigate, and control wildfires. In this line, our findings can contribute to the creation of early warning systems, the use of modelling tools to predict fire spread, and the design of public policies that regulate fire use and prevention in both urban and rural contexts (Stoof and Kattridge, 2022). This model classification can also support the promotion of fire management strategies aimed at reducing the risk of megafire events. In this context, the resulting map serves as a tool to guide the implementation of prescribed burning, fuel management, and the establishment of productive fuel breaks (Pulido et al., 2021). Additionally, this geographical classification enables the identification of communities that need to be prepared to coexist with fire and adapt to its presence (Tedim et al., 2021)

Afterwards, the results of this chapter served to evaluate the fire effect on vegetation and its functional responses (**fourth chapter**). We characterised species composition and structure, assessed fire-adaptive functional traits and functional diversity indices of plant communities within 31 sampling plots across the fire regime identified. The theoretical implications of this characterization are significant, as it advanced our understanding of how fire shapes species composition and community structure within a fire gradient (Kelly et al; 2023; Napier and Chipman 2021). By examining fire-adaptive functional traits across different plant communities, this research contributes to theoretical fire ecology, particularly in understanding trait-based responses and adaptations to fire (Grau-Andrés et al; 2024). This approach also improves ecological models predicting vegetation dynamics under different fire regimes, providing more detailed insights into how fire disturbances affect biodiversity and ecosystem resilience (Magnani et al., 2023). Furthermore, the identification of fire-related functional traits can provide a basis for developing conservation strategies that prioritize species and communities with varying adaptive capacities to fire (Sample et al; 2022).

Revealing that resprouting is a key trait within low and intermediate fire regime types. Additionally, functional dispersion varied across fire regime types. Despite the similarity in species composition and structure among the fire regimes, we identified some species specifically associated with both fire-prone and fire-free environments, which could be a useful insight for restoration strategies (Martins et al; 2022).

Based on the classification of different fire regimes in the Paraguayan Chaco, areas with a high fire regime were not identified within these forested regions. High fire incidences are uncommon in these patches, primarily due to their humidity and dense forest cover, which

inhibit the growth of grasses and reduce the risk of fire spread (Silvério et al., 2013). This characteristic suggests that native mesoxerophytic forests provide an essential ecosystem service, among others, by preventing fire intrusion, creating a refuge zone for wildlife during the dry season, when fires are common in the surrounding buffer zones.

5.5 IMPLICATIONS FOR FIRE MANAGEMENT

The findings of this research highlight important implications for fire management in the Gran Chaco-Pantanal ecoregions where fire has an important role in reshaping ecosystem dynamics. Effective management must consider both the historical role of fire and the recent intensification of fire events driven by climate change and land-use pressures (Mc Lauchlan et al; 2020). Traditional fire regimes, which have long played a role in sustaining biodiversity and ecosystem resilience in this region, are increasingly disrupted by factors like prolonged droughts, rising temperatures, and expanded agricultural activities (Marengo et al; 2021; Argañaraz et al; 2020). These elements underscore the need for adaptive and ecologically informed management strategies to support the resilience of native vegetation, particularly in fire-prone landscapes.

1. **Adaptive management approaches.** Given that our study identifies maximum temperature, tree cover, and livestock as key factors influencing fire incidence, fire management strategies should adopt an adaptive approach that takes these variables into account. An adaptive management framework could involve ongoing monitoring of climate variables (such as temperature and precipitation), land cover changes, and livestock densities to anticipate high-risk fire periods and adjust fire management activities accordingly. This could include setting fuel management strategies or promoting prescribed burning (McWethy et al; 2019; Pacheco et al., 2022; Kreider et al., 2023) to mitigate fire risk during periods of elevated temperature or drought, which our results suggest are associated with higher fire incidence. Engaging local communities in the monitoring process can also enhance both the accuracy of fire-risk assessments and community buy-in for management actions (Jacobs and Cramer 2017).

2. **Integrated land use and fire management.** Our results demonstrate the need to integrate land-use planning with fire management to mitigate anthropogenic pressures responsible for altered fire regimes. The presence of livestock and agricultural expansion, both linked to increased fire occurrence, suggests that land use regulations or sustainable grazing practices may be critical for reducing fire frequency and intensity. For instance, preserving buffer zones (forest islands) and incorporating more trees with less flammable vegetation around agricultural lands and grazing areas could help prevent fire from spreading and becoming more severe, such as mega fire event (Sample et al; 2022). Collaborative efforts with local landowners, including educational engagement on sustainable land practices, can support this integration by fostering a shared responsibility for fire risk management (Moore et al; 2020; Bacciu et al. 2022).

3. **Restoring and conserving fire-resilient species.** The shift in fire regimes poses risks to the structural and functional diversity of the region's forest ecosystems, with potential long-term consequences for biodiversity. Our findings indicate that fire regimes have altered functional diversity, highlighting the importance of conserving fire-resistant species and functional groups that support ecosystem stability. This could involve prioritizing the restoration of native species that have demonstrated good response to fire events and play key roles in stabilizing soils, maintaining habitat complexity, and supporting diverse faunal communities. Restoration efforts might include the enrichment of fire-adapted plant species into degraded areas (Martins et al; 2024) or developing seed banks for key native species to facilitate post-fire recovery (de Souza et al; 2021).

4. **Refining predictive fire models for proactive management.** The predictive models developed in this study have identified spatial patterns in fire occurrence that can inform management practices. By refining these models with ongoing data from remote sensing and field observations, management agencies can develop a proactive fire management approach, predicting areas of high fire risk before fire seasons begin. Mapping fire-prone zones and communicating these risks to communities can enhance early-warning systems (Bacciu et al; 2022), enabling quicker responses to fire outbreaks and reducing damage to forests and communities alike. These models can be particularly effective if integrated into national and regional fire management policies, providing a data-driven basis for resource allocation and emergency response.

5. **Community engagement and awareness.** Finally, incorporating local knowledge and practices is essential to achieving sustainable fire management (Bilbao et al; 2019). The historical use of fire for agricultural and cultural purposes in the Gran Chaco and Pantanal underscores the value of engaging local communities as partners in fire management. Educational programs that promote awareness of sustainable fire practices and provide training in fire prevention and suppression can empower local people to manage fire more effectively (Devisscher et al; 2018). This engagement can be particularly valuable in remote areas where response times for firefighting teams may be longer, and local communities are often the first line of defence against wildfire spread.

Overall, these management implications emphasize a need for a multifaceted approach that combines adaptive management, land-use planning, ecosystem restoration, predictive modeling, and community engagement. Such an approach would not only enhance the resilience of the Humid Chaco and its diverse ecosystems to fire but also mitigate the risk of large-scale ecological disruptions due to changing fire regimes. Effective fire management in this region must balance conservation goals with the socio-economic needs of local communities, ultimately fostering a sustainable relationship between people and the fire-adapted landscapes of the Gran Chaco-Pantanal ecoregions.

5.6 STUDY LIMITATIONS AND FUTURE RESEARCH LINES

This study provides valuable insights into the impacts of fire regimes on forest ecosystems in the Gran Chaco-Pantanal ecoregions, yet several limitations should be acknowledged as they offer guidance for future research.

Limitations on spatial resolution. One notable limitation is the spatial resolution of the MODIS data used for fire modeling. While MODIS provides a long-term dataset, its 500-meter resolution may lack the precision needed to detect small-scale burned areas, particularly in the heterogeneous landscapes of the Humid Chaco. Higher-resolution satellite products, such as Sentinel-2 (10–20 meters) and Landsat-8 (30 meters), could enhance burned area detection accuracy, offering a more detailed understanding of fire dynamics. Future research should prioritize the use of high-resolution satellite datasets to better capture fine-scale fire patterns, enhancing understanding across diverse vegetation types and land-use contexts.

Time scale limitations. The study period (2001–2020) may not fully capture long-term trends and variability in fire activity, especially considering the impacts of climate change and shifting land use practices. The relatively limited time frame may restrict the identification of broader patterns and underlying drivers of fire dynamics that unfold over decadal timescales. Also, this frame does not take into account the most recent (and noticeable) changes in temperature and water availability observed in last years. To gain more comprehensive insights into fire ecology trends and improve the accuracy of conclusions about fire dynamics in these ecoregions, future research should consider extending the study period to cover a longer duration.

Limited number of predictive models. Additionally, our **reliance on three predictive modeling techniques** (RF, GLM, GAM), while effective for identifying general fire patterns, may not fully capture the intricate interactions between fire regimes and environmental gradients such as temperature, precipitation, and vapor pressure deficit (VPD). Future research should explore these interactions in greater depth to better understand fire's role in shaping ecosystem dynamics.

Absence of socio-economic variables. Including socio-political variables such as land tenure, burning calendars, and governance structures, which are crucial for understanding human-driven fire ignitions, could provide a broader perspective on the complex relationship between society, nature, and fire (Smith et al., 2016). Future studies should focus on these aspects to enhance assessments of anthropogenic fire drivers and move toward a more holistic approach, recognizing that the connections between social and ecosystem resilience are essential for creating a fire-resilient landscape (Newman-Thacker et al., 2023).

The unclear role of the livestock variable. The primary variable associated with human presence in our study was cattle. Cattle can have both positive and negative influences on fire occurrence in neotropical ecosystems. Positive feedback may arise when livestock graze on vegetation, thereby reducing fuel load and lowering the risk of large-scale wildfires (Bernardi et al., 2019). Conversely, there may be negative feedback when cattle managers contribute to human-caused ignitions by engaging in activities such as burning grasslands to clear vegetation (Pivello et al., 2021), thus preventing the regrowth of closed forests. This practice is common in these ecoregions, and when applied improperly and combined with climatic conditions, changes in land use can result in increased occurrence and intensity of wildfires. While our

results indicated a positive correlation between fire occurrence and the presence of cattle, the relationship between human activity and fire needs further examination.

Limited field data. Our limited field data—31 plots across 14 forest patches—can be considered as another constraint. Although these sites provided valuable baseline information, the small sample size may not fully capture the variability in fire effects across the Humid Chaco. Additionally, the compositional similarity observed across forest patches limited our ability to discern fire-induced differences in vegetation dynamics. Expanding future research to include more diverse and extensive sampling would address this issue and improve generalizability.

What seems evident is that the work collected in this thesis can serve as a basis for further research in the region. Although the focus on forest patches in the Humid Chaco is interesting due to the important role of these systems in the region, it certainly limited the scope of this study. While our interest was focused on forest responses, other important fire-prone ecosystems like savannas and grasslands make them an ideal target for future research, especially to explore how fire impacts vary across vegetation types and environmental gradients.

Moreover, the use of averaged fire variables to classify fire regimes, while useful for an overview of impacts, may overlook key temporal dynamics such as Time Since Last Fire (TSLF). Shorter fire intervals can profoundly influence vegetation recovery, altering species composition, structure, and functional traits. Incorporating TSLF and other fire metrics would allow for a more nuanced understanding of fire's ecological impacts, particularly in ecosystems with seasonal variability and flood pulses. Hydrological dynamics, such as flood and drought pulses, are critical drivers in this ecosystem and may act as more dominant filters than fire. These factors likely influence forest recovery and species composition, potentially overshadowing fire-related effects.

On the other hand, the spatial and temporal resolution of our sampling may not fully capture the heterogeneity of this ecosystem, particularly given the patchy distribution of fire and other disturbances. Future studies should expand the sampling design and incorporate longer temporal scales to provide a more comprehensive understanding of the interplay between fire, hydrological dynamics, and successional processes.

Comparative studies between the Humid Chaco and other subtypes, such as the Dry Chaco, could provide additional insights into ecosystem resilience and post-fire recovery. Investigating the flammability of native and non-native species within forest ecosystems presents a promising avenue for informing fire management strategies. Lastly, exploring interactions between fire regimes and environmental variables like flood pulses and precipitation could offer a more comprehensive understanding of the drivers shaping functional diversity in these ecosystems. Another important topic for future research is the inclusion of regeneration in vegetation sampling. Addressing this issue could provide valuable insights into forest recovery following fire disturbances across the fire gradient.

Finally, while this study emphasized the influence of climatic factors on fire dynamics, climate alone cannot entirely explain fire occurrences in these ecoregions. Human activities such as livestock management, land clearing, and the use of fire for agricultural purposes play a significant role. Our findings highlight the need for future research to investigate the interplay

between climatic and anthropogenic factors, particularly how socio-economic variables and governance affect fire regimes.

6. CONCLUSIONS

1. This study represents a comprehensive multiscale analysis of the relationship between fire dynamics and forest resilience in the Gran Chaco and Pantanal ecoregions, providing critical insights into the factors driving fire activity and intensity in these fire-prone areas, as well as the response of forest to these factors.
2. At regional scale, spatiotemporal analysis highlights the significant influence of temperature, aridity, vegetation type, and land use on fire dynamics. The Humid Chaco and Pantanal ecoregions are characterized by frequent, large, but less intense fires, primarily of anthropogenic origin and sustained by continuous fine fuels. In contrast, the Dry Chaco experiences fewer but more intense fires, with higher temperatures, extended dry seasons, and increasing ignition sources from land-use changes amplifying fire activity.
3. Despite a relatively constant fire occurrence over the past two decades, future conditions are likely to promote larger and more intense fires. This includes continued intentional burns for pasture management, limited management controls, and projected changes in precipitation and temperatures. These alterations in climate and fuel composition could significantly increase the probability and intensity of fires.
4. At sub regional scales, cluster analysis has proven to be a valuable tool in understanding the spatial and temporal patterns of fire, especially in complex and diverse regions like the Paraguayan Chaco. The results facilitate the identification of high-risk areas, guiding the development of targeted fire management strategies. These strategies may include increased surveillance, prescribed burns in high-risk areas, and the promotion of fire-adapted vegetation in lower-risk regions.
5. At local scale, this thesis provides a comprehensive analysis of fire regimes and species composition within the Humid Chaco forest of Paraguay, revealing significant patterns in fire adaptation and ecosystem resilience. The findings confirm that fire incidence is relatively low in these forested areas, largely due to the dense canopy cover and humidity, which limit the spread of fires primarily to the edges of forest patches. This characteristic, suggests that this forest is a fire-influenced ecosystem, playing a crucial role in fire prevention, and highlighting the importance of further research into the flammability of its constituent species.
6. The study also identified key fire-adaptive traits, particularly the resprouting capacity of species, which is vital for post-fire recovery and maintaining biodiversity. While traits such as bark thickness and spine presence did not show significant variation across different fire regimes, the ability to resprout emerged as a crucial adaptation, particularly in fire-prone areas. This aligns with global research indicating the importance of resprouting in fire-affected ecosystems.
7. Despite the low variability in functional traits observed, the study found that functional dispersion differed significantly along the fire gradient, suggesting a more homogeneous trait assemblage in non-fire-prone zones compared to those affected by fire. The absence of a high

fire gradient within the forest underscores the need for further investigations into how other environmental factors, such as the flood pulse, interact with fire regimes to influence species composition and forest structure.

8. The limitations of this study, particularly the inability to identify a contrasting fire gradient and the high similarity in species composition across fire regimes, point to the need for future research to include more diverse ecosystems such as savannas, which are more frequently affected by fire. Additionally, exploring the interactions between fire and other environmental variables, such as precipitation, relative humidity, and the flood pulse, will be crucial for a deeper understanding of ecosystem dynamics and resilience in the Gran Chaco.

7. BIBLIOGRAPHY

- Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., and Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, 5(1), 170191. <https://doi.org/10.1038/sdata.2017.191>
- Adamoli, J., Sennhauser, E. B., Steel, J. M., and Rescia, A. (1990). Stress and disturbance: Vegetation dynamics in the dry Chaco region of Argentina. *Journal of Biogeography*, 17(5), 491–500.
- Alonso-González, E., and Fernández-García, V. (2021). MOSEV: A global burn severity database from MODIS (2000–2020). *Earth System Science Data*, 13(5), 1925–1938. <https://doi.org/10.5194/essd-13-1925-2021>
- Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., DeFries, R. S., Collatz, G. J., Hantson, S., and Kloster, S. (2017). A human-driven decline in global burned area. *Science*, 356(6345), 1356–1362. <https://doi.org/10.1126/science.aal4108>
- Andela, N., Morton, D. C., Giglio, L., Paugam, R., Chen, Y., Hantson, S., ... Randerson, J. T. (2019). The Global Fire Atlas of individual fire size, duration, speed and direction. *Earth System Science Data*, 11, 529552. <https://doi.org/10.5194/essd-11-529-2019>
- Archibald, S., Lehmann, C., Gomez-Dans, J., and Bradstock, R. (2013). Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America*, 110. <https://doi.org/10.1073/pnas.1211466110>
- Archibald, S., Lehmann, C., Belcher, C., Bond, W., Bradstock, R., Daniou, A.-L., Dexter, K., Forrester, E., Greve, M., He, T., Higgins, S., Hoffmann, W., Lamont, B., McGlenn, D., Moncrieff, G., Osborne, C., Pausas, J., Price, O., Ripley, B., and Zanne, A. (2018). Biological and geophysical feedbacks with fire in the Earth System. *Environmental Research Letters*, 13. <https://doi.org/10.1088/1748-9326/aa9ead>
- Argañaraz, J. P., Gavier Pizarro, G., Zak, M., et al. (2015a). Fire regime, climate, and vegetation in the Sierras de Córdoba, Argentina. *Fire Ecology*, 11(1), 55–73. <https://doi.org/10.4996/fireecology.1101055>
- Argañaraz, J. P., Gavier, P. G., Zak, M., Landi, M. A., and Bellis, L. M. (2015b). Human and biophysical drivers of fires in semiarid Chaco mountains of central Argentina. *Science of The Total Environment*, 520, 1–12. <https://doi.org/10.1016/j.scitotenv.2015.02.081>
- Argañaraz, J., Cingolani, A., Bellis, L., and Giorgis, M. (2020). Fire incidence along an elevation gradient in the mountains of central Argentina. *Ecologia Austral*, 30, 268–281. <https://doi.org/10.25260/EA.20.30.2.0.1054>
- Armenteras, D., González, T. M., Vargas Ríos, O., Meza Elizalde, M. C., and Oliveras, I. (2020). Incendios en ecosistemas del norte de Suramérica: Avances en la ecología del fuego tropical en Colombia, Ecuador y Perú. *Caldasia*, 42(1), 1–16. <https://doi.org/10.15446/caldasia.v42n1.77353>
- Armesto, J. J., and Gutiérrez, J. R. (1978). El efecto del fuego en la estructura de la vegetación de Chile central. *Anales del Museo de Historia Natural*, 11, 43–48.
- Bacciu, V., Sirca, C., and Spano, D. (2022). Towards a systemic approach to fire risk management. *Environmental Science and Policy*, 129, 37–44. <https://doi.org/10.1016/j.envsci.2021.12.015>
- Balao F., Paun O., Alonso C. (2018). Uncovering the contribution of epigenetics to plant phenotypic variation in Mediterranean ecosystems. *Plant Biology* 20, 38-49. <https://doi.org/10.1111/plb.12594>
- Barbero, R., Abatzoglou, J., Kolden, C., Hegewisch, K., Larkin, N., and Podschwit, H. (2014). Multi-scalar influence of weather and climate on very large-fires in the Eastern United States. *International Journal of Climatology*, 35. <https://doi.org/10.1002/joc.4090>
- Barbosa, M. L., Haddad, I., Nascimento, A. L., da Silva, G., Veiga, R., Hoffmann, T. B., Souza, A., Silva, R., Streher, A., Pereira, F., Aragão, L., and Anderson, L. (2022). Compound impact of land use and extreme climate on the 2020 fire record of the Brazilian Pantanal. *Global Ecology and Biogeography*, 31. <https://doi.org/10.1111/geb.13563>
- Baumann, M., Piquer-Rodríguez, M., Fehlenberg, V., Gavier-Pizarro, G., and Kuemmerle, T. (2016). Land-Use Competition in the South American Chaco: (pp. 215–229). https://doi.org/10.1007/978-3-319-33628-2_13

- Baumann, M., Levers, C., Macchi, L., Bluhm, H., Waske, B., Gasparri, N. I., and Kuemmerle, T. (2018). Mapping continuous fields of tree and shrub cover across the Gran Chaco using Landsat 8 and Sentinel-1 data. *Remote Sensing of Environment*, 216, 201–211. <https://doi.org/10.1016/j.rse.2018.06.044>
- Bergier, I., Silva, A., Abreu, U., Oliveira, L., Tomazi, M., Dias, F., Urbanetz, C., Nogueira, É., and Borges-Silva, J. (2019). Could bovine livestock intensification in Pantanal be neutral regarding enteric methane emissions? *Science of The Total Environment*, 655, 463–472. <https://doi.org/10.1016/j.scitotenv.2018.11.178>
- Berlinck, C. N., and Batista, E. K. L. (2020). Good fire, bad fire: It depends on who burns. *Flora*, 268, 151610. <https://doi.org/10.1016/j.flora.2020.151610>
- Bernardi, R., Staal, A., Xu, C., Scheffer, M., and Holmgren, M. (2019). Livestock Herbivory Shapes Fire Regimes and Vegetation Structure Across the Global Tropics. *Ecosystems*, 22. <https://doi.org/10.1007/s10021-019-00349-x>
- Bernardino, P. N., Dantas, V. L., Hirota, M., Pausas, J. G., and Oliveira, R. S. (2021). Savanna–Forest Coexistence Across a Fire Gradient. *Ecosystems*. <https://doi.org/10.1007/s10021-021-00654-4>
- Berry, P. E. (2002). Diversidad y endemismo en los bosques neotropicales de bajura. In M. R. Guariguata and G. H. Kattan (Eds.), *Ecología y conservación de bosques neotropicales* (pp. 83–96). Cartago, Costa Rica: LUR.
- Bilbao, B., Steil, L., Urbietta, I. R., Anderson, L., Pinto, C., González, M. E., Millán, A., Falleiro, R. M., Morici, E., Ibarregaray, V., Pérez-Salicrup, D. R., Pereira, J. M., and Moreno, J. M. (2020). Wildfires (pp. 435–496). In J. M. Moreno, C. Laguna-Defi, V. Barros, E. Calvo-Buendía, J. A. Marengo, and U. Oswald-Spring (Eds.), *Adaptation to climate change risks in Ibero-American countries—RIOCCADAPT Report* (online). McGraw Hill. Retrieved July 10, 2024, from https://www.researchgate.net/publication/346487629_Wildfires_Adaptation_to_Climate_Change_Risks_in_Ibero-American_Countries-RIOCCADAPT
- Boschetti, L., Roy, D. P., Justice, C. O., & Humber, M. L. (2015). MODIS–Landsat fusion for large area 30 m burned area mapping. *Remote Sensing of Environment*, 161, 27–42. <https://doi.org/10.1016/j.rse.2015.01.022>
- Bourgeron, P. S. (1983). Spatial aspects of vegetation structure. In F. B. Golley (Ed.), *Tropical rain forest ecosystems: Structure and function* (pp. 29–47). Elsevier.
- Bowman, D. M. J. S. (2023). Detecting, Monitoring and Foreseeing Wildland Fire Requires Similar Multiscale Viewpoints as Meteorology and Climatology. *Fire*, 6(4), Article 4. <https://doi.org/10.3390/fire6040160>
- Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D’Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., ... Pyne, S. J. (2009). Fire in the Earth System. *Science*, 324(5926), 481–484. <https://doi.org/10.1126/science.1163886>
- Bowman, D. M. J. S., Kolden, C. A., Abatzoglou, J. T., Johnston, F. H., van der Werf, G. R., and Flannigan, M. (2020). Vegetation fires in the Anthropocene. *Nature Reviews Earth and Environment*, 1(10), 500–515. <https://doi.org/10.1038/s43017-020-0085-3>
- Bowman, D. M. J. S., Murphy, B. P., Williamson, G. J., and Cochrane, M. A. (2014). Pyrogeographic models, feedbacks and the future of global fire regimes. *Global Ecology and Biogeography*, 23(7), 821–824. <https://doi.org/10.1111/geb.12180>
- Bowman, D.M.J.S., G.J. Williamson, J.T. Abatzoglou, C.A. Kolden, M.A. Cochrane, and A.M.S. Smith. 2017. Human exposure and sensitivity to globally extreme wildfire events. *Nature Ecology and Evolution* 1 (3): 1–6. <https://doi.org/10.1038/s41559-016-0058>
- Bradstock, R. A. (2010). A biogeographic model of fire regimes in Australia: Contemporary and future implications. *Global Ecology and Biogeography*, 19(2), 145–158. <https://doi.org/10.1111/j.1466-8238.2009.00512.x>
- Brando, P. M., Silvério, D., Maracahipes, L., Benzi, R., Paolucci, L., Maracahipes-Santos, L., Rattis, L., Macedo, M. N., and Balch, J. K. (2024). Legacies of multiple disturbances on fruit and seed patterns in Amazonia: Implications for forest functional traits. *Ecosphere*, 15(2), e4780. <https://doi.org/10.1002/ecs2.4780>
- Bravo, S., Abdala, N., and Ibáñez Moro, A. (2022). Soil seed banks of dry tropical forests under different land management. *Forests*, 14(1), 1–11. <https://doi.org/10.3390/f14010003>

- Bravo, S., Kunst, C., Gimenez A., B., and Moglia A., G. (2001). Fire regime of a *Elionorus muticus* Spreng. Savanna, Western Chaco region, Argentina. *International Journal of Wildland Fire*, 10. <https://doi.org/10.1071/WF01014>
- Bravo, S., Kunst, C., Leiva, M., and Ledesma, R. (2014). Response of hardwood tree regeneration to surface fires, western Chaco region, Argentina. *Forest Ecology and Management*, 326, 36–45. <https://doi.org/10.1016/j.foreco.2014.04.009>
- Bucher, E. (1987). Herbivory in arid and semi-arid regions of Argentina. *Revista Chilena de Historia Natural*, 60, 265–273.
- Bucher, E. (1998). Sustainable land use management in the South American Chaco. *Advances in GeoEcology*, 31, 905–910.
- Bustamante, M. M. C., Roitman, I., Aide, T. M., Alencar, A., Anderson, L. O., Aragão, L., Asner, G. P., Barlow, J., Berenguer, E., Chambers, J., Costa, M. H., Fanin, T., Ferreira, L. G., Ferreira, J., Keller, M., Magnusson, W. E., Morales-Barquero, L., Morton, D., Ometto, J. P. H. B., Palace, M., Peres, C. A., Silvério, D., Trumbore, S., and Vieira, I. C. G. (2016). Toward an integrated monitoring framework to assess the effects of tropical forest degradation and recovery on carbon stocks and biodiversity. *Global Change Biology*, 22(1), 92–109. <https://doi.org/10.1111/gcb.13087>
- Caldas, M. M., Goodin, D., Sherwood, S., Campos Krauer, J. M., and Wisely, S. M. (2015). Land-cover change in the Paraguayan Chaco: 2000–2011. *Journal of Land Use Science*, 10(1), 1–18. <https://doi.org/10.1080/1747423X.2013.807314>
- Calim Costa, M., Marengo, J. A., Alves, L. M., et al. (2024). Multiscale analysis of drought, heatwaves, and compound events in the Brazilian Pantanal in 2019–2021. *Theoretical and Applied Climatology*, 155(3), 661–677. <https://doi.org/10.1007/s00704-023-04655-2>
- Certini, G., Moya, D., Lucas-Borja, M., and Mastrodonardo, G. (2021). El impacto del fuego en la biota que habita en el suelo: Una revisión. *Ecología y gestión de los bosques*, 488, 118989. <https://doi.org/10.1016/J.FORECO.2021.118989>
- Chen, Y., Morton, D. C., Jin, Y., Collatz, G. J., Kasibhatla, P. S., van der Werf, G. R., DeFries, R. S., and Randerson, J. T. (2013). Long-term trends and interannual variability of forest, savanna and agricultural fires in South America. *Carbon Management*, 4(6), 617–638. <https://doi.org/10.4155/cmt.13.61>
- Chia, E. K., Bassett, M., Leonard, S. W. J., Holland, G. J., Ritchie, E. G., Clarke, M. F., and Bennett, A. F. (2016). Effects of the fire regime on mammal occurrence after wildfire: Site effects vs landscape context in fire-prone forests. *Forest Ecology and Management*, 363, 130–139. <https://doi.org/10.1016/j.foreco.2015.12.008>
- Chuvieco, E., Roteta, E., Sali, M., Stroppiana, D., Boettcher, M., Kirches, G., Storm, T., Khairoun, A., Pettinari, M. L., Franquesa, M., and Albergel, C. (2022). Building a small fire database for Sub-Saharan Africa from Sentinel-2 high-resolution images. *Science of The Total Environment*, 845, 157139. <https://doi.org/10.1016/j.scitotenv.2022.157139>
- Clark, D. B. (2000). Los factores edáficos y la distribución de las plantas. In M. R. Guariguata and G. H. Kattan (Eds.), *Ecología y conservación de bosques neotropicales* (pp. 193–221). LUR.
- Clarke, P. J., Lawes, M. J., Murphy, B. P., Russell-Smith, J., Nano, C. E. M., Bradstock, R., Enright, N. J., Fontaine, J. B., Gosper, C. R., Radford, I., Midgley, J. J., and Gunton, R. M. (2015). A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of The Total Environment*, 534, 31–42. <https://doi.org/10.1016/j.scitotenv.2015.04.002>
- Cochrane, M. A. (2001). Synergistic interactions between habitat fragmentation and fire in tropical forests. *Conservation Biology*, 15(6), 1515–1521.
- Cochrane, M. A., and Laurance, W. F. (2002). Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*, 18(3), 311–325
- Cochrane, M.A., Ryan, K.C. (2009). Fire and fire ecology: Concepts and principles. In: *Tropical Fire Ecology*. Springer Praxis Books. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-77381-8_2
- Coria, R. D., Bravo, S., and Kunst, C. (2021). Un aporte al entendimiento de la lignificación de los pastizales/sabanas del Chaco Semiárido sudamericano. *Ecología Austral*, 31, 390–574. <https://doi.org/10.25260/EA.21.31.3.0.1615>

- Correa, D., Alcantara, E., Libonati, R., Massi, K., and Park, E. (2022). Increased burned area in the Pantanal over the past two decades. *Science of The Total Environment*, 835, 155386. <https://doi.org/10.1016/j.scitotenv.2022.155386>
- Coughlan, R., Di Giuseppe, F., Vitolo, C., Barnard, C., Lopez, P., and Drusch, M. (2021). Using machine learning to predict fire-ignition occurrences from lightning forecasts. *Meteorological Applications*, 28(1), e1973.
- Cristofanelli, P., Trisolino, P., Calzolari, F., Busetto, M., Calidonna, C. R., Amendola, S., Arduini, J., Fratticioli, C., Hundal, R. A., Maione, M., Marcucci, F., Marinoni, A., Montaguti, S., Renzi, L., Roccato, F., Bonasoni, P., and Putero, D. (2024). Influence of wildfire emissions to carbon dioxide (CO₂) observed at the Mt. Cimone station (Italy, 2165 m asl): A multi-year investigation. *Atmospheric Environment*, 330, 120577. <https://doi.org/10.1016/j.atmosenv.2024.120577>
- Crotteau J.S., Morgan Varner J., Ritchie M.W. (2013). Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management* 287, 103–112. <https://doi.org/10.1016/j.foreco.2012.09.022>.
- Cruz, M. S. (2000). Estructura y aprovechamiento de vegetación secundaria en X'hazil Sur y Anexos, ejido de la zona maya de Quintana Roo (Tesis profesional). Instituto Tecnológico de Chetumal, Chetumal, Quintana Roo.
- D'Antonio, C. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23, 63–87.
- Da Ponte, E., García-Calabrese, M., Kriese, J., Cabral, N., Perez de Molas, L., Alvarenga, M., Caceres, A., Gali, A., García, V., Morinigo, L., Ríos, M., and Salinas, A. (2022). Understanding 34 years of forest cover dynamics across the Paraguayan Chaco: Characterizing annual changes and forest fragmentation levels between 1987 and 2020. *Forests*, 13(1), Article 1. <https://doi.org/10.3390/f13010025>
- da Silva Junior, C. A., Teodoro, P. E., Delgado, R. C., Teodoro, L. P. R., Lima, M., de Andréa Pantaleão, A., Baio, F. H. R., de Azevedo, G. B., de Oliveira Sousa Azevedo, G. T., Capristo-Silva, G. F., Arvor, D., and Facco, C. U. (2020). Persistent fire foci in all biomes undermine the Paris Agreement in Brazil. *Scientific Reports*, 10(1), Article 1. <https://doi.org/10.1038/s41598-020-72571-w>
- Daldegan, G. A., De Carvalho, O. A., Guimarães, R. F., Gomes, R. A. T., Ribeiro, F. D. F., and McManus, C. (2014). Spatial Patterns of Fire Recurrence Using Remote Sensing and GIS in the Brazilian Savanna: Serra do Tombador Nature Reserve, Brazil. *Remote Sensing*, 6(10), Article 10. <https://doi.org/10.3390/rs6109873>
- Dantas, V. L., Batalha, M. A., França, H., and Pausas, J. G. (2015). Resource availability shapes fire-filtered savannas. *Journal of Vegetation Science*, 26, 395–403. <https://www.jstor.org/stable/43912856>
- Dantas, V. L., Oliveira, L. C. S., Marcati, C. R., and Sonsin-Oliveira, J. (2024). Coordination of bark and wood traits underlies forest-to-savanna evolutionary transitions. *Journal of Biogeography*, 51(9), 1801–1813. <https://doi.org/10.1111/jbi.14850>
- Dantas, V., and Pausas, J. (2022). The legacy of the extinct neotropical megafauna on plants and biomes. *Nature Communications*, 13. <https://doi.org/10.1038/s41467-021-27749-9>
- Datta, A., and Krishnamoorti, R. (2022). Understanding the Greenhouse Gas Impact of Deforestation Fires in Indonesia and Brazil in 2019 and 2020. *Frontiers in Climate*, 4. <https://doi.org/10.3389/fclim.2022.799632>
- De Faria, B. L., Staal, A., Silva, C. A., Martin, P. A., Panday, P. K., and Dantas, V. L. (2021). Climate change and deforestation increase the vulnerability of Amazonian forests to post-fire grass invasion. *Global Ecology and Biogeography*, 30(12), 2368–2381. <https://doi.org/10.1111/geb.13388>
- De La Sancha, N., Boyle, S., McIntyre, N., Brooks, D., Yanosky, A., Soto, E., Mereles, M., Camino, M., and Stevens, R. (2021). The disappearing Dry Chaco, one of the last dry forest systems on earth. *Landscape Ecology*, 36. <https://doi.org/10.1007/s10980-021-01291-x>
- de Souza, E. B., Bao, F., Damasceno Junior, G. A., and Pott, A. (2021). Differences between species in seed bank and vegetation helps to hold functional diversity in a floodable Neotropical savanna. *Journal of Plant Ecology*, 14(4), 605–615. <https://doi.org/10.1093/jpe/rtab014>
- Delgado, D., Finegan, B., Zamora, N., and Meir, P. (1997). Efectos del aprovechamiento forestal y el tratamiento silvicultural en un bosque húmedo del noreste de Costa Rica: Cambios en la riqueza y composición de la vegetación (Serie Técnica, Informe Técnico No. 298). CATIE.
- Devisscher, T., Malhi, Y., and Boyd, E. (2018). Deliberation for wildfire risk management: Addressing conflicting views in the Chiquitania, Bolivia. *The Geographical Journal*, 185. <https://doi.org/10.1111/geoj.12261>

- Díaz, S., Fargione, J., Chapin, S., and Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biology*, 4(8), e277. <https://doi.org/10.1371/journal.pbio.0040277>
- Ellis, T. M., Bowman, D. M. J. S., Jain, P., Flannigan, M. D., and Williamson, G. J. (2022). Global increase in wildfire risk due to climate-driven declines in fuel moisture. *Global Change Biology*, 28(4), 1544–1559. <https://doi.org/10.1111/gcb.16006>
- Fernández, P. D., Matthias, B., Germán, B., Natalia, B. R., Sandra, B., Ignacio, G. N., Mauro, L., Sofia, M., Sofia, N. A., Nasca, J. A., Torcuato, T., and Ricardo, G. H. (2020). In *Encyclopedia of the World's Biomes* (pp. 562–576). Elsevier.
- Fernández-García V., Marcos E., Fulé P.Z., Reyes O., Santana V.M., Calvo L. (2020). Fire regimes shape diversity and traits of vegetation under different climatic conditions. *Science of The Total Environment* 716, 137137. <https://doi.org/10.1016/j.scitotenv.2020.137137>.
- Feron, S., Cordero, R.R., Damiani, A. et al. South America is becoming warmer, drier, and more flammable. *Commun Earth Environ* 5, 501 (2024). <https://doi.org/10.1038/s43247-024-01654-7>
- Ferreira, C. M., Finegan, B., Kanninen, M., Delgado, L. D., and Segura, M. (2002). Composición florística y estructura de bosques secundarios en el municipio de San Carlos, Nicaragua. *Revista Forestal Centroamericana*, 38, 44-50.
- Fidelis, A., and Zironi, H. L. (2021). And after fire, the Cerrado flowers: A review of post-fire flowering in a tropical savanna. *Flora*, 280, 151849. <https://doi.org/10.1016/j.flora.2021.151849>
- Flannigan, M. D., Wotton, B. M., Marshall, G. A., de Groot, W. J., Johnston, J., Jurko, N., and Cantin, A. S. (2016). Fuel moisture sensitivity to temperature and precipitation: Climate change implications. *Climate Change*, 134(1), 59–71. <https://doi.org/10.1007/s10584-015-1521-0>
- Flannigan, M., Stocks, B., Turetsky, M., and Wotton, M. (2008). Impacts of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology*, 15, 549–560. <https://doi.org/10.1111/j.1365-2486.2008.01660.x>
- Furquim, F. F., Scasta, J. D., and Overbeck, G. E. (2024). Interactive effects of fire and grazing on vegetation structure and plant species composition in subtropical grasslands. *Applied Vegetation Science*, 27(3), e12800. <https://doi.org/10.1111/avsc.12800>
- Gallo, V., Avilla, L. S., Pereira, R. C. L., and Absolon, B. A. (2013). Distributional patterns of herbivore megamammals during the late Pleistocene of South America. *Anais da Academia Brasileira de Ciências*, 85(2), 533–546.
- Giglio, L., Boschetti, L., Roy, D. P., Humber, M. L., and Justice, C. O. (2018). The Collection 6 MODIS burned area mapping algorithm and product. *Remote Sensing of Environment*, 217, 72–85. <https://doi.org/10.1016/j.rse.2018.08.005>
- Giglio, L., Csiszar, I., and Justice, C. O. (2006). Global distribution and seasonality of active fires as observed with the terra and aqua moderate resolution imaging spectroradiometer (MODIS) sensors. *Journal of Geophysical Research-Biogeosciences*, 111. <https://doi.org/10.1029/2005JG000142>
- Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T. P., Vanwambeke, S. O., Wint, G. R. W., and Robinson, T. P. (2018). Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Scientific Data*, 5(1), 180227. <https://doi.org/10.1038/sdata.2018.227>
- Grassi, D. (2020). Estado del Clima en Paraguay 2019. Secretaría Técnica de Planificación del Desarrollo Económico y Social. Retrieved from https://www.stp.gov.py/v1/wp-content/uploads/2020/11/Presentacio%CC%81n-Estado-del-Clima-Paraguay-2019_compressed.pdf
- Grau, H., Torres, R., Gasparri, N., Blendinger, P., Marinaro, S., and Macchi, L. (2014). Natural grasslands in the Chaco: A neglected ecosystem under threat by agricultural expansion and forest-oriented conservation policies. *Journal of Arid Environments*, 123, 40–46. <https://doi.org/10.1016/j.jaridenv.2014.01.006>
- Grau-Andrés, R., Moreira, B., and Pausas, J. G. (2024). Global plant responses to intensified fire regimes. *Global Ecology and Biogeography*, 33(8), e13858. <https://doi.org/10.1111/geb.13858>
- Grime JP, Thompson K, et al. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos* 79, 259–281. doi:10.2307/3546011
- Laliberté, E., Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*. *Ecology* 91(1): 299-305.

Guerra, C., Berdugo, M., Eldridge, D., Eisenhauer, N., Singh, B., Cui, H., Abades, S., Alfaro, F., Bamigboye, A., Bastida, F., Blanco-Pastor, J., De los Ríos, A., Durán, J., Grebenc, T., G. Illan, J., Liu, Y.-R., Makhalyane, T., Mamet, S., Molina-Montenegro, M., and Delgado-Baquerizo, M. (2022). Global hotspots for soil nature conservation. *Nature*, 610. <https://doi.org/10.1038/s41586-022-05292-x>

Guyra Paraguay. (2019). Informe de incendios en el área del Pantanal Paraguayo 2019. https://guyra.org.py/wp-content/uploads/2019/11/Informe-de-Incendios-en-el-Pantanal-Paraguayo-2019_.pdf

Halofsky, J. E., Peterson, D. L., and Harvey, B. J. (2020). Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology*, 16(1), 4. <https://doi.org/10.1186/s42408-019-0062-8>

Hantson, S., Arneeth, A., Harrison, S. P., Kelley, D. I., Prentice, I. C., Rabin, S. S., Archibald, S., Mouillot, F., Arnold, S. R., Artaxo, P., Bachelet, D., Ciais, P., Forrest, M., Friedlingstein, P., Hickler, T., Kaplan, J. O., Kloster, S., Knorr, W., Lasslop, G., Li, F., Mangeon, S., Melton, J. R., Meyn, A., Sitch, S., Spessa, A., van der Werf, G. R., Voulgarakis, A., & Yue, C. (2016). The status and challenge of global fire modelling. *Biogeosciences*, 13(13), 3359–3375. <https://doi.org/10.5194/bg-13-3359-2016>

Hardesty, J., Myers, R., and Fulks, W. (2005). Fire, ecosystems, and people: A preliminary assessment of fire as a global conservation issue. *The George Wright Forum*, 22(4), 78–86.

Hempson, G. P., Midgley, J. J., Lawes, M. J., Vickers, K. J., and Kruger, L. M. (2014). Comparing bark thickness: Testing methods with bark–stem data from two South African fire-prone biomes. *Journal of Vegetation Science*, 25(5), 1247–1256. <https://doi.org/10.1111/jvs.12171>

Herrero, M. L., Torres, R., and Renison, D. (2016). Do Wildfires Promote Woody Species Invasion in a Fire-Adapted Ecosystem? Post-fire Resprouting of Native and Non-native Woody Plants in Central Argentina. *Environmental Management*, 57. <https://doi.org/10.1007/s00267-015-0616-8>

Hoffmann, W. A., Jaconis, S., McKinley, K. L., Geiger, E. L., Gotsch, S. G., and Franco, A. C. (2012). Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries. *Austral Ecology*, 37(6), 634–643. <https://doi.org/10.1111/j.1442-9993.2011.02324.x>

Hoffmann, W. A., Adasme, R., Haridasan, M., de Carvalho, M. T., Geiger, E. L., Pereira, M. A. B., Gotsch, S. G., and Franco, A. C. (2009). Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology*, 90(5), 1326–1337. <https://doi.org/10.1890/08-0741.1>

Huerta S., Calvo L., Fernández-García V., Marcos E. (2021). Efectos de las medidas de restauración después de incendios forestales en comunidades de matorral propensas al fuego. En: Almendro M.B., Jordán M.M. (Eds.), *El Suelo: Clave para una Gestión Ambiental Sostenible en un Escenario de Cambio Global*. 407-410.

Ibáñez Moro, A.V., Bravo, S.J., Abdala, N.R., Borghetti, F., Chaib, A.M., Galetto, L., 2021. Heat shock effects on germination and seed survival of five woody species from the chaco region. *Flora* 275, 151751. <https://doi.org/10.1016/j.flora.2020.151751>.

INE::Instituto Nacional de Estadística. (n.d.). Retrieved November 14, 2024, from <https://www.ine.gov.py/publicacion/2/poblacion>

Intergovernmental Panel On Climate Change (IPCC). (2023). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. <https://doi.org/10.1017/9781009157896>

Jacobs, D. B., and Cramer, L. A. (2017). Applying information network analysis to fire-prone landscapes: Implications for community resilience. *Ecology and Society*, 22(1), art52. <https://doi.org/10.5751/ES-09119-220152>

Jones, M., Abatzoglou, J., Veraverbeke, S., Andela, N., Lasslop, G., Forkel, M., Smith, A., Burton, C., Betts, R., Werf, G., Sitch, S., Canadell, J., Santín, C., Kolden, C., Doerr, S., and Le Quéré, C. (2022). Global and Regional Trends and Drivers of Fire Under Climate Change. *Reviews of Geophysics*, 60. <https://doi.org/10.1029/2020RG000726>

Junk, W. J., and Nunes da Cunha, C. (2012). Pasture clearing from invasive woody plants in the Pantanal: A tool for sustainable management or environmental destruction? *Wetlands Ecology and Management*, 20, 111–122. <https://doi.org/10.1007/s11273-011-9246-y>

- Keeley, J. E., and Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics*, 53, 203–225. <https://doi.org/10.1146/annurev-ecolsys-102320-095612>
- Keeley J.E., Fotheringham C.J., Baer-Keeley M. (2005). Factors affecting plant diversity during post-fire recovery and succession of Mediterranean-climate shrublands in California, USA. *Diversity and Distributions* 11, 525–537. <https://doi.org/10.1111/j.1366-9516.2005.00200.x>
- Kellman, M., and Meave, J. (1997). Fire in the tropical gallery forests of Belize. *Journal of biogeography*, 24(1), 23–34.
- Kelly, L. T., Fletcher, M.-S., Menor, I. O., Pellegrini, A. F. A., Plumanns-Pouton, E. S., Pons, P., Williamson, G. J., and Bowman, D. M. J. S. (2023). Understanding Fire Regimes for a Better Anthropocene. *Annual Review of Environment and Resources*, 48(Volume 48, 2023), 207–235. <https://doi.org/10.1146/annurev-environ-120220-055357>
- Kimura H., Tsuyuzaki S. (2011). Fire severity affects vegetation and seed bank in a wetland. *Applied Vegetation Science* 14, 350–357. <https://doi.org/10.1111/j.1654-109X.2011.01126.x>.
- Kreider, M., Higuera, P., Parks, S., Rice, W., White, N., and Larson, A. (2024). Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation. *Nature Communications*, 15. <https://doi.org/10.1038/s41467-024-46702-0>
- Kumar, S., Getirana, A., Libonati, R., Hain, C., Mahanama, S., and Andela, N. (2022). Changes in land use enhance the sensitivity of tropical ecosystems to fire-climate extremes. *Scientific Reports*, 12(1), Article 1. <https://doi.org/10.1038/s41598-022-05130-0>
- Kunst, C. (2011). Ecología y uso del fuego en la región chaqueña argentina: Una revisión. *CIDEU*, 10, 81–105.
- Kunst, C., Bravo, S., Monti, Cornacchione, M., and Godoy. (2003). El fuego y el manejo de pasturas naturales y cultivadas en la región chaqueña In C. Kunst, S. Bravo y J. Panigatti Editors (Ed). *Fuego en los ecosistemas argentinos* (pp 1-12).
- Laino, R., Musalem, K., Caballero-Gini, A., Bueno-Villafañe, D., and Chaparro, S. (2018). Habitat use and behavior of *Crax fasciolata* in the Paraguayan Humid Chaco. *El Hornero*, 33(2), 121–127. Retrieved November 21, 2024, from https://www.scielo.org.ar/scielo.php?script=sci_arttext&pid=S0073-34072018000200006&lng=es&dtlng=es
- Laino, R., Musalem, K., Laino, L. D., Caballero-Gini, A., Bueno-Villafañe, D., Aranda, L., Esquivel, A., Riveros, M. F., Nardelli, L. R., Cantero, N., and Irala, R. (2022). Islands of Forests Among Savannas: Key Elements for Conservation and Production in the Paraguayan Humid Chaco. In F. Montagnini (Ed.), *Biodiversity Islands: Strategies for Conservation in Human-Dominated Environments* (Vol. 20, pp. 185–205). Springer International Publishing. https://doi.org/10.1007/978-3-030-92234-4_8
- Lamont, B. B., He, T., and Yan, Z. (2019). Evolutionary history of fire stimulated resprouting, flowering, seed release and germination. *Biological Reviews*, 94(3), 903–928. <https://doi.org/10.1111/b r v.1 24 8 3>
- Landi, M. A., Di Bella, C. M., Bravo, S. J., and Bellis, L. M. (2021). Structural resistance and functional resilience of the Chaco forest to wildland fires: An approach with MODIS time series. *Austral Ecology*, 46(2), 277–289. <https://doi.org/10.1111/aec.12977>
- Lawes, M. J., and Clarke, P. J. (2011). Ecology of plant resprouting: Populations to community responses in fire-prone ecosystems. *Plant Ecology*, 212(12), 1937–1943. <https://doi.org/10.1007/s11258-011-9994-z>
- Lawes, M. J., Richards, A., Dathe, J., and Midgley, J. J. (2011). Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology*, 212(12), 2057–2069. <https://doi.org/10.1007/s11258-011-9954-7>
- Le Page, Y., Oom, D., Silva, J., Jönsson, P., and Pereira, J. (2010). Seasonality of vegetation fires as modified by human action: Observing the deviation from eco-climatic fire regimes. *Global Ecology and Biogeography*, 19, 575–588. <https://doi.org/10.1111/j.1466-8238.2010.00525.x>
- Leal Filho, W., Azeiteiro, U. M., Salvia, A. L., Fritzen, B., and Libonati, R. (2021). Fire in Paradise: Why the Pantanal is burning. *Environmental Science and Policy*, 123, 31–34. <https://doi.org/10.1016/j.envsci.2021.05.005>
- Libonati, R., Dacamara, C., Peres, L., Sander de Carvalho, L., and Garcia, L. (2020). Rescue Brazil's burning Pantanal wetlands. *Nature*, 588. <https://doi.org/10.1038/d41586-020-03464-1>

- Libonati, R., Geirinhas, J. L., Silva, P. S., Monteiro dos Santos, D., Rodrigues, J. A., Russo, A., Peres, L. F., Narcizo, L., Gomes, M. E. R., Rodrigues, A. P., DaCamara, C. C., Pereira, J. M. C., and Trigo, R. M. (2022). Drought–heatwave nexus in Brazil and related impacts on health and fires: A comprehensive review. *Annals of the New York Academy of Sciences*, 1517(1), 44–62. Scopus. <https://doi.org/10.1111/nyas.14887>
- Lindenmayer, D., Taylor, C., Blanchard, W., Zylstra, P., and Evans, M. J. (2023). What environmental and climatic factors influence multidecadal fire frequency? *Ecosphere*, 14(8), e4610. <https://doi.org/10.1002/ecs2.4610>
- Lipoma, M., Fortunato, V., Enrico, L., and Diaz, S. (2019). Where does the forest come back from? Soil and litter seed banks and the juvenile bank as sources of vegetation resilience in a semiarid Neotropical forest. *Journal of Vegetation Science*, 31. <https://doi.org/10.1111/jvs.12842>
- Lipoma, M., Gurvich, D., Urcelay, C., and Diaz, S. (2016). Plant community resilience in the face of fire: Experimental evidence from a semi-arid shrubland. *Austral Ecology*, 41. <https://doi.org/10.1111/aec.12336>
- López-Poma R., Orr B.J., Bautista S. (2014). Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape. *International Journal of Wildland Fire* 23, 1005–1015. <https://doi.org/10.1071/WF13150>.
- Loto, D., and Bravo, S. (2020). Species composition, structure, and functional traits in Argentine Chaco forests under two different disturbance histories. *Ecological Indicators*, 113, 106232. <https://doi.org/10.1016/j.ecolind.2020.106232>
- Magnani, M., Díaz-Sierra, R., Sweeney, L., Provenzale, A., and Baudena, M. (2023). Fire Responses Shape Plant Communities in a Minimal Model for Fire Ecosystems across the World. *The American Naturalist*, 202(3), E83–E103. <https://doi.org/10.1086/725391>
- Manzo-Delgado, L., Sanchez-Colon, S., and Alvarez, R. (2009). Assessment of seasonal forest fire risk using NOAA-AVHRR: A case study in central Mexico. *International Journal of Remote Sensing*, 30, 4991–5013. <https://doi.org/10.1080/01431160902852796>
- Marengo, J., and Bernasconi, M. (2014). Regional differences in aridity/drought conditions over Northeast Brazil: Present state and future projections. *Climatic Change*, 129. <https://doi.org/10.1007/s10584-014-1310-1>
- Marengo, J., Cunha, A.P., Cuartas, L., Deusdará-Leal, K., Broedel, E., Seluchi, M., Michelin, C., Baião, C., Chuchón Angulo, E., Almeida, E., Kazmierczak, M., Mateus, N., Silva, R., and Bender, F. (2021). Extreme drought in the Brazilian Pantanal in 2019–2020: Characterization, causes, and impacts. *Frontiers in Water*, 3, 639204. <https://doi.org/10.3389/frwa.2021.639204>
- Marques, J., Alves, M., Silveira, C., Amaral e Silva, A., Silva, T., Santos, V., and Calijuri, M. (2021). Fires dynamics in the Pantanal: Impacts of anthropogenic activities and climate change. *Journal of Environmental Management*, 299, 113586. <https://doi.org/10.1016/j.jenvman.2021.113586>
- Juárez-Martínez, A., and Rodríguez-Trejo, D. (2003). EFECTO DE LOS INCENDIOS FORESTALES EN LA REGENERACIÓN DE *Pinus oocarpa* var. *Ochoterena*. *Revista Chapingo. Serie Ciencias Forestales y Del Ambiente*, 9, 125–130.
- Martins, P. I., Belém, L. B. C., Peluso, L. M., Szabo, J. K., Trindade, W. C. F., Pott, A., Junior, G. A. D., Jimenez, D., Marques, R., Peterson, A. T., Libonati, R., and Garcia, L. C. (2024). Fire-sensitive and threatened plants in the Upper Paraguay River Basin, Brazil: Identifying priority areas for Integrated Fire Management and ecological restoration. *Ecological Engineering*, 209, 107411. <https://doi.org/10.1016/j.ecoleng.2024.107411>
- Martins, P. I., Belém, L. B. C., Szabo, J. K., Libonati, R., and Garcia, L. C. (2022). Prioritising areas for wildfire prevention and post-fire restoration in the Brazilian Pantanal. *Ecological Engineering*, 176, 106517. <https://doi.org/10.1016/j.ecoleng.2021.106517>
- Mason, N. W. H., Mouillot, D., Lee, W. G., and Bastow, W. J. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Mataveli, G. A. V., Pereira, G., de Oliveira, G., Seixas, H. T., Cardozo, F. da S., Shimabukuro, Y. E., Kawakubo, F. S., and Brunzell, N. A. (2021). 2020 Pantanal’s widespread fire: Short- and long-term implications for biodiversity and conservation. *Biodiversity and Conservation*, 30(11), 3299–3303. <https://doi.org/10.1007/s10531-021-02243-2>

- Maturo HM, Oakley LJ, Prado DE (2005). Vegetación y posición fitogeográfica de la Reserva El Bagual. In: Di Giacomo AG, Krapovickas SF (eds) Historia natural y paisaje de la Reserva El Bagual, Formosa, Argentina. Asociación Ornitológica de La Plata, Buenos Aires, 592pp
- McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., Tepley, A. J., Varner, J. M., Veblen, T. T., Adalsteinsson, S. A., Balch, J. K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M. L., Coen, J., Crandall, R., ... Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology*, 108(5), 2047–2069. <https://doi.org/10.1111/1365-2745.13403>
- McPherson, G. R. (1997). Ecology and management of North American savannas. The University of Arizona Press.
- McWethy, D. B., Schoennagel, T., Higuera, P. E., Krawchuk, M., Harvey, B. J., Metcalf, E. C., Schultz, C., Miller, C., Metcalf, A. L., Buma, B., Virapongse, A., Kulig, J. C., Stedman, R. C., Ratajczak, Z., Nelson, C. R., and Kolden, C. (2019). Rethinking resilience to wildfire. *Nature Sustainability*, 2(9), 797–804. <https://doi.org/10.1038/s41893-019-0353-8>
- Meave, J., Soto, M. A., Calvo, I. L. M., Paz, H. H., and Valencia, A. S. (1992). Análisis sinecológico del bosque mesófilo de montaña de Omiltemi, Guerrero. *Boletín de la Sociedad Botánica de México*, 52, 31–77
- Mendoza, M. (2006). Skulls Collected for Scalping in the Gran Chaco (pp. 113–118).
- Mereles, F. (2005). Una aproximación al conocimiento de las formaciones vegetales del Chaco paraguayo. *Rojasiana*, 6, 5-48.
- Mereles, M. (2013). Análisis cualitativo para la determinación de las ecorregiones en la región Occidental, Paraguay. *Paraquaria Natural*, 1, 12–20.
- Mereles, M., Céspedes, G., De Egea, J., and Spichiger, R. (2020). Estudios fitosociológicos en el gran Chaco: Estructura, composición florística y variabilidad del bosque de *Schinopsis balansae* en el Chaco húmedo boreal, Paraguay. *Bonplandia*, 29, 39. <https://doi.org/10.30972/bon.2914108>
- Milán, M., and González, E. (2022). Beef–cattle ranching in the Paraguayan Chaco: Typological approach to a livestock frontier. *Environment, Development and Sustainability*, 1–26. <https://doi.org/10.1007/s10668-022-02261-2>
- Montenegro, G., Ginocchio, R., Segura, A., Keeley, J. E., and Gómez, M. (2004). Fire regimes and vegetation responses in two Mediterranean-climate regions. *Revista Chilena de Historia Natural*, 77, 455–464.
- Moore, P., Hannah, B., de Vries, J., Marijn, P., Steffens, R., and Stoof, C. R. (2020). Wildland Fire Management under COVID-19 . Brief 1 , Review of Materials. 2–14.
- Mouchet, M. A., Villéger, S., Mason, N. W. H., and Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Mowat, E. J., Webb, J. K., and Crowther, M. S. (2015). Fire-mediated niche-separation between two sympatric small mammal species. *Austral Ecology*, 40(1), 50–59. <https://doi.org/10.1111/aec.12166>
- Müller, D., Suess, S., Hoffmann, A. A., and Buchholz, G. (2013). The value of satellite-based active fire data for monitoring, reporting, and verification of REDD+ in the Lao PDR. *Human Ecology*, 41(1), 7–20. <https://doi.org/10.1007/s10745-013-9565-0>
- Myers, R. (2006). Convivir con el fuego—Manteniendo los ecosistemas y los medios de subsistencia mediante el Manejo Integral del Fuego. Tallahassee, FL: The Nature Conservancy.
- Myers, R. L. (2000). Fire in tropical and subtropical ecosystems. In J. K. Brown and J. Smith (Eds.), *Wildland fire in ecosystems: Effects of fire on flora* (pp. 161–173). General USDA Forest Service Technical Report RMRS-GTR-24. Ogden, Utah, United States.
- Napier, J. D., and Chipman, M. L. (2022). Emerging palaeoecological frameworks for elucidating plant dynamics in response to fire and other disturbance. *Global Ecology and Biogeography*, 31(1), 138–154. <https://doi.org/10.1111/geb.13416>
- Naval, C., Albornoz, J., Bellis, L., Baldini, C., Arcamone, J., Silveti, L., Alvarez, M., and Arganaraz, J. (2023). Megaincendios 2020 en Córdoba: Incidencia del fuego en áreas de valor ecológico y socioeconómico. *Ecología Austral*, 33, 136–151. <https://doi.org/10.25260/EA.23.33.1.0.2120>

- Newman-Thacker, F., Castellnou, M., Bartholomeus, H., and Stoof, C. (2023). What is a fire resilient landscape? Towards an integrated definition. *Ambio*, 52. <https://doi.org/10.1007/s13280-023-01891-8>
- Nurdiati, S., Sopaheluwakan, A., Julianto, M. T., Septiawan, P., and Rohimahastuti, F. (2022). Modelling and analysis impact of El Niño and IOD on land and forest fire using polynomial and generalized logistic function: Case study in South Sumatra and Kalimantan, Indonesia. *Modeling Earth Systems and Environment*, 8(3), 3341–3356. <https://doi.org/10.1007/s40808-021-01303-4>
- Oliveira, L. O. F. de, Abreu, U. G. P. de, Dias, F. R. T., Fernandes, F. A., Nogueira, E., and Silva, J. C. B. da. (2016). Estimativa da população de bovinos no Pantanal por meio de modelos matemáticos e índices tradicionais (No. 99). <https://doi.org/10.13140/RG.2.2.21046.50242>
- Olson, D., and Dinerstein, E. (2003). The Global 200: Priority Ecoregions for Global Conservation. *Annals of the Missouri Botanical Garden*, 89. <https://doi.org/10.2307/3298564>
- Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., and Lehmann, C. E. R. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, 220(1), 1024. <https://doi.org/10.1111/nph.15236>
- Pacheco, M., Oliveira, A., Fernandes, P., and Silva, J. (2022). Effect of Fuel Management and Forest Composition on Fire Behavior. *Environmental Sciences Proceedings*, 17(1), Article 1. <https://doi.org/10.3390/envirosci2022017046>
- Pais, C., Olabarria, J., Elimbi Moudio, M. P., Garcia-Gonzalo, J., González, M., and Shen, M. (2023). Global scale coupling of pyromes and fire regimes. *Communications Earth and Environment*, 4. <https://doi.org/10.1038/s43247-023-00881-8>
- Pantanal Biosphere Reserve, Brazil | UNESCO. (n.d.). Retrieved January 12, 2023, from <https://www.unesco.org/en/man-and-biosphere/pantanal-biosphere-reserve-brazil>
- Pantoja, V. (2008). Las dos caras del fuego: Invitando a reflexionar sobre la “cara buena” y la “cara mala” del fuego (Informe Técnico del Equipo Global para el Manejo del Fuego 2008-1). The Nature Conservancy.
- Paula, S., Naulin, P. I., Arce, C., Galaz, C., and Pausas, J. G. (2016). Lignotubers in Mediterranean basin plants. *Plant Ecology*, 217(6), 661–676. <https://doi.org/10.1007/s11258-015-0538-9>
- Pausas, J. G. (2004). Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean Basin). *Climatic Change*, 63(3), 337–350. <https://doi.org/10.1023/B:CLIM.0000018508.94901.9c>
- Pausas, J. G., and Verdú, M. (2005). Plant persistence traits in fire-prone ecosystems of the Mediterranean Basin: A phylogenetic approach. *Oikos*, 109(1), 196–202. <https://doi.org/10.1111/j.0030-1299.2005.13596.x>
- Pausas, J. G., Llovet, J., Rodrigo, A., and Vallejo, R. (2008). Are wildfires a disaster in the Mediterranean Basin? A review. *International Journal of Wildland Fire*, 17(6), 713–723. <https://doi.org/10.1071/WF07151>
- Pausas, J. G., and Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience*, 59(7), 593–601. <https://doi.org/10.1525/bio.2009.59.7.10>
- Pausas, J. G., Alessio, G. A., Moreira, B., and Corcobado, G. (2012). Fires enhance flammability in *Ulex parviflorus*. *New Phytologist*, 193(1), 18–23. <https://doi.org/10.1111/j.1469-8137.2011.03945.x>
- Pausas, J. G., and Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist*, 204(1), 55–65. <https://doi.org/10.1111/nph.12921>
- Pausas, J. G. (2015). Bark thickness and fire regime. *Functional Ecology*, 29(3), 315–327. <https://doi.org/10.1111/1365-2435.12372>
- Pausas, J. G. (2017). Bark thickness and fire regime: Another twist. *New Phytologist*, 213(1), 13–15.
- Pausas, J. G., and Ribeiro, E. (2017). Fire and plant diversity at the global scale. *Global Ecology and Biogeography*, 26(8), 889–897. <https://doi.org/10.1111/geb.12596>
- Pausas, J. G., and Keeley, J. E. (2019). Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment*, 17(6), 289–295.
- Pausas, J. G., and Paula, S. (2019). Grasses and fire: The importance of hiding buds. A response to Moore et al.
- Pausas, J. G., and Keeley, J. E. (2023). Evolutionary fire ecology: An historical account and future directions. *BioScience*, 73(8), 602–608. <https://doi.org/10.1093/biosci/biad059>
- Pennington, R. T., and Hughes, C. E. (2014). The remarkable congruence of new and old World savanna origins. *New Phytologist*, 204(1), 4–6. <https://doi.org/10.1111/nph.12996>

- Pérez de Molas L (2015). Manual de familias y géneros de árboles del Paraguay. FAO, San Lorenzo, p 216.
- Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M., Cornwell, W., Craine, J., Gurvich, D., Urcelay, C., Veneklaas, E., Reich, P., Poorter, L., Wright, I., Ray, P., Enrico, L., Pausas, J., Vos, A., and Van der Heijden, M. (2013). Nuevo manual para la medición estandarizada de caracteres funcionales de plantas. *Australian Journal of Botany*, 61, 167–234.
- Petchey, O. L., and Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- Petchey, O. L., and Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9, 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Pivello, V., Guimarães Vieira, I., Christianini, A., Ribeiro, D., Menezes, L., Berlinck, C., Melo, F., Marengo, J., Tornquist, C., Tomas, W., and Overbeck, G. (2021). Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. *Perspectives in Ecology and Conservation*, 19. <https://doi.org/10.1016/j.pecon.2021.06.005>
- Pla, L; Casanoves, F; Di Rienzo, J; Fernandez, F; Finegan, B. 2008. Confidence intervals for functional diversity indices considering species abundance. XXIV International Biometric Conference, Dublin, 2008.
- Pulido, F. and Ediciones Universidad de Valladolid. (2021). Hacia los territorios inteligentes frente a incendios forestales. <https://doi.org/10.24197/ciudades.24.2021.65-78>
- Randerson, J. T., et al. (2006). The impact of boreal forest fire on climate warming. *Science*, 314(5802), 1130–1132. <https://doi.org/10.1126/science.1132075>
- Ricotta, C. (2005). A note on functional diversity measures. *Basic and Applied Ecology*, 6, 479–486. <https://doi.org/10.1016/j.baae.2005.01.001>
- Rodríguez Trejo, D. A., Martínez Muñoz, P., and Lara, P. J. M. (2019). Efectos del fuego en el arbolado de un bosque tropical de pino y en el de una selva baja caducifolia en Villaflores, Chiapas. *Ciencia Florestal*, 29(3), 1033–1047. <https://doi.org/10.5902/1980509853144>
- Roman-Cuesta, R. M., Carmona-Moreno, C., Lizcano, G., New, M., Silman, M., Knoke, T., Malhi, Y., Oliveras, I., Asbjornsen, H., and Vuille, M. (2014). Synchronous fire activity in the tropical high Andes: An indication of regional climate forcing. *Global Change Biology*, 20. <https://doi.org/10.1111/gcb.12538>
- Rundel P.W., Arroyo M.T.K., Cowling R.M., Keeley J.E., Lamont B.B., Pausas J.G., Vargas P. (2018). Fire and plant diversification in Mediterranean-climate regions. *Frontiers in Plant Science* 9: 851. <https://doi.org/10.3389/fpls.2018.00851>
- Russell-Smith, J., and Stanton, P. (2002). Fire regimes and fire management of rainforest communities across northern Australia. In R. Bradstock, J. Williams, and M. Gill (Eds.), *Flammable Australia: The fire regimes and biodiversity of a continent* (pp. 329–350). Cambridge University Press.
- Sample, M., Thode, A. E., Peterson, C., Gallagher, M. R., Flatley, W., Friggens, M., Evans, A., Loehman, R., Hedwall, S., Brandt, L., Janowiak, M., and Swanston, C. (2022). Adaptation Strategies and Approaches for Managing Fire in a Changing Climate. *Climate*, 10(4), Article 4. <https://doi.org/10.3390/cli10040058>
- Santacruz-García, A. C., Bravo, S., del Corro, F., and Ojeda, F. (2019). A comparative assessment of plant flammability through a functional approach: The case of woody species from Argentine Chaco region. *Austral Ecology*, 44(8), 1416–1429. <https://doi.org/10.1111/aec.12815>
- Schubert, A. T., Nano, C. E. M., Clarke, P. J., and Lawes, M. J. (2016). Evidence for bark thickness as a fire-resistance trait from desert to savanna in fire-prone inland Australia. *Plant Ecology*, 217(6), 683–696. <https://doi.org/10.1007/s11258-016-0611-z>
- Silvério, D., Brando, P., Balch, J., Putz, F. E., Nepstad, D., Oliveira-Santos, C., and Bustamante, M. (2013). Testing the Amazon savannization hypothesis: Fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368, 20120427. <https://doi.org/10.1098/rstb.2012.0427>
- Smith, A. M. S., Kolden, C. A., Paveglio, T. B., Cochrane, M. A., Bowman, D. M., Moritz, M. A., Kliskey, A. D., Alessa, L., Hudak, A. T., Hoffman, C. M., Lutz, J. A., Queen, L. P., Goetz, S. J., Higuera, P. E., Boschetti, L., Flannigan, M., Yedinak, K. M., Watts, A. C., Strand, E. K., ... Abatzoglou, J. T. (2016). The Science of Firescapes: Achieving Fire-Resilient Communities. *BioScience*, 66(2), 130–146. <https://doi.org/10.1093/biosci/biv182>

- Snook, L. (1993). Stand dynamics of mahogany (*Swietenia macrophylla* King) and associated species after fire and hurricanes in tropical forests of the Yucatán Peninsula (Tesis doctoral). Yale University, New Haven, CT.
- Spichiger, R., Ramella, L., Palese, R., & Mereles, F. (1991). Proposición de leyenda para la cartografía de las formaciones vegetales del Chaco paraguayo. III. *Candollea*, 46, 541-564.
- Spittler, P. (2000). Dinámica de los bosques secundarios secos de la región Chorotega, Costa Rica. En M. Quesada (Ed.), *Avances en el manejo del bosque secundario en Costa Rica: Memorias* (pp. 182–198). TEC, COSEFORMA, GTZ.
- Staver, A. C., Bond, W. J., Cramer, M. D., and Wakeling, J. L. (2012). Topdown determinants of niche structure and adaptation among African Acacias. *Ecology Letters*, 15(7), 673–679. <https://doi.org/10.1111/j.1461-0248.2012.01784.x>
- Stoof, C. R., and Kettridge, N. (2022). Living With Fire and the Need for Diversity. *Earth's Future*, 10(4), e2021EF002528. <https://doi.org/10.1029/2021EF002528>
- Syphard, A. D., Radeloff, V. C., Hawbaker, T. J., and Steward, S. I. (2009). Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology*, 23(4), 758–769. <https://doi.org/10.1111/j.1523-1739.2009.01223.x>
- Tedim, F., McCaffrey, S., Leone, V., Vazquez-Varela, C., Depietri, Y., Buergelt, P., and Lovreglio, R. (2021). Supporting a shift in wildfire management from fighting fires to thriving with fires: The need for translational wildfire science. *Forest Policy and Economics*, 131, 102565. <https://doi.org/10.1016/j.forpol.2021.102565>
- The Nature Conservancy (TNC). (2006). Fuego en Centroamérica, fuegos forestales y no forestales: Una amenaza recurrente a la biodiversidad, la salud y las economías de Centroamérica (19 pp.)
- Tilman, D. (2001). Functional diversity. En Levin, S. A. (Ed.), *Encyclopedia of Biodiversity* (Vol. 3, pp. 109–120). Academic Press.
- Torres, R. C., and Renison, D. (2017). Human-induced vegetation changes did not affect tree progeny performance in a seasonally dry forest of central Argentina. *Journal of Arid Environments*, 147, 125–132. <https://doi.org/10.1016/j.jaridenv.2017.07.016>
- Torres, R., Giorgis, M., Trillo, C., Volkmann, L., Demaio, P., Heredia, J., and Renison, D. (2013). Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina. *Austral Ecology*, 39. <https://doi.org/10.1111/aec.12084>
- Uyttewaal, K., Stoof, C., Canaleta, G., Cifre Sabater, M., Langer, E., Ludwig, F., Kroeze, C., Moran, P., Ottolini, I., and Prat-Guitart, N. (2024). Uplifting local ecological knowledge as part of adaptation pathways to wildfire risk reduction: A case study in Montseny, Catalonia (Spain). *Ambio*, 53. <https://doi.org/10.1007/s13280-024-02030-7>
- Vallejo V.R., Arianoutsou M., Moreira F. (2012). Fire ecology and post-fire restoration approaches in southern European forest types. In: Moreira F., Arianoutsou M., Corona P., De Las Heras J. (Eds.), *Post-Fire Management and Restoration of Southern European Forests*. 93–119. Springer: Dordrecht, The Netherlands.
- Veraverbeke, S., Lhermitte, S., Verstraeten, W. W., and Goossens, R. (2010). The temporal dimension of differenced Normalized Burn Ratio (dNBR) fire/burn severity studies: The case of the large 2007 Peloponnese wildfires in Greece. *Remote Sensing of Environment*, 114(11), 2548–2563. <https://doi.org/10.1016/j.rse.2010.05.029>
- Vidal-Riveros, C., Souza-Alonso, P., Bravo, S., Laino, R., and Ngo Bieng, M. A. (2023). A review of wildfires effects across the Gran Chaco region. *Forest Ecology and Management*, 549, 121432. <https://doi.org/10.1016/j.foreco.2023.121432>
- Vidal-Riveros, C., Watler Reyes, W. J., Ngo Bieng, M. A., and Souza-Alonso, P. (2024a). Assessing Fire Regimes in the Paraguayan Chaco: Implications for Ecological and Fire Management. *Fire*, 7(10), Article 10. <https://doi.org/10.3390/fire7100347>
- Vidal-Riveros, C., Currey, B., McWethy, D. B., Bieng, M. A. N., and Souza-Alonso, P. (2024b). Spatiotemporal analysis of wildfires and their relationship with climate and land use in the Gran Chaco and Pantanal ecoregions. *Science of The Total Environment*, 955, 176823. <https://doi.org/10.1016/j.scitotenv.2024.176823>
- Villalba, L., Ortiz, B., and Gengler, N. (2018). Principales mamíferos del Chaco Central (p. 68). WCS, WWF, USAID.

- Villéger, S., Mason, N. W. H., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Villéger, S., Grenouillet, G., and Brosse, S. (2013). Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages: Decomposing functional β -diversity. *Global Ecology and Biogeography*, 22(6), 671–681. <https://doi.org/10.1111/geb.12021>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Ward, D. S., Kloster, S., Mahowald, N. M., Rogers, B. M., Randerson, J. T., and Hess, P. G. (2012). The changing radiative forcing of fires: Global model estimates for past, present, and future. *Atmospheric Chemistry and Physics*, 12(22), 10857–10886. <https://doi.org/10.5194/acp-12-10857-2012>
- Withey, K., Berenguer, E., Palmeira, A. F., Espírito-Santo, F. D., Lennox, G. D., Silva, C. V., Aragao, L. E., Ferreira, J., França, F., Malhi, Y., and Rossi, L. C. (2018). Quantifying immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20170312. <https://doi.org/10.1098/rstb.2017.0312>
- Zeballos, S. R., Giorgis, M. A., Cingolani, A. M., Cabido, M., Whitworth-Hulse, J. I., and Gurvich, D. E. (2014). Do alien and native tree species from Central Argentina differ in their water transport strategy? *Austral Ecology*, 39(8), 984–991. <https://doi.org/10.1111/aec.12171>

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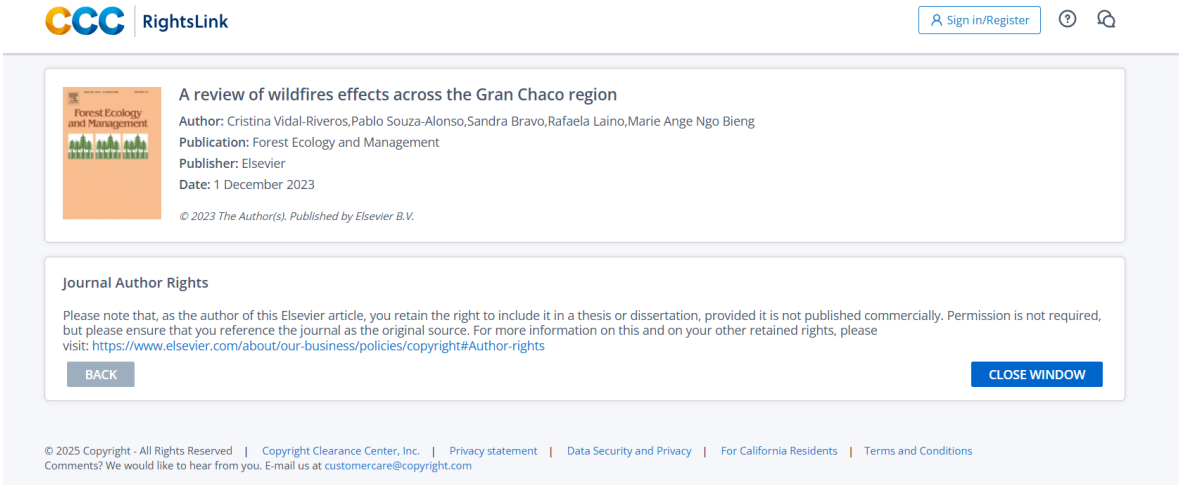
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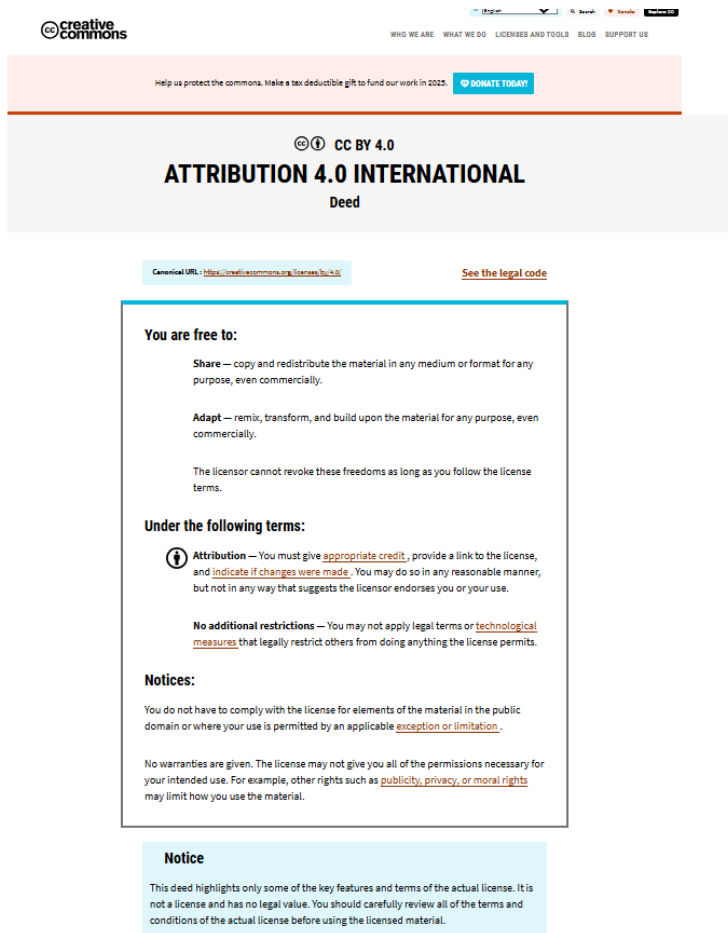
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Figure 3. Mosaic vegetation of the Humid Chaco of Paraguay comprised by forest-palm savannas and wetland. Reproduced from Mereles et al., (2020)

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Fire is a key ecological factor in many terrestrial ecosystems, with its effects shaped by human and climatic influences. South America, particularly the Gran Chaco and Pantanal, is a global fire hotspot, where land-use changes and increasing fire threaten biodiversity. This study evaluates forest responses to fire in the Paraguayan Humid Chaco, focusing on species assemblages. Results showed 2020 had the largest burned area, with maximum temperature, tree cover, and livestock density as key fire drivers. Four distinct fire regimes were identified, influencing functional traits but not significantly altering forest structure or composition. This study provides the first assessment of fire regime impacts on forests in the Paraguayan Humid Chaco, offering valuable insights into fire dynamics and forest resilience