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A review of wildfires effects across the Gran Chaco region

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A B S T R A C T

Fire is a natural element of some tropical dry ecosystems. However, during the last decades, fire occurrence has become more frequent and intense due, in part, to climate change and land use transformation. This is the case in the Gran Chaco Americano, one of the largest dry forests all over the world that extends across Argentina, Paraguay, Bolivia and Brazil. Fire has shaped the Gran Chaco landscape since ancient times, but today, as in many other regions, the pattern, frequency, severity and intensity are being dramatically altered. Based on information collected mainly over the last two decades, this paper presents a detailed review of the available literature on the fire regime across the Gran Chaco region. Here, we present a multi- disciplinary understanding considering fire behavior and dynamics in the study ecosystem within a very specific ecological, administrative and historical framework.

A noteworthy aspect of this review indicates the clear imbalance between regions in terms of available literature; while information about the Argentine Chaco is abundant, the literature for the Paraguayan or Bolivian Chaco is practically non-existent. The rainfall gradient and drought periods are key climatic drivers of fire ignitions while cattle ranching is the main socioeconomic activity of this region and key precursor of forest fires. In general, a substantial part of the available information focused on ecological aspects of the fire regime as the effect of fires on plant functional traits such as bark thickness, resprouting ability and flammability patterns. Other post fire effects on soil, invasive species, herbivory and soil seed banks have been also explored in detail to understand ecosystem recovery and research needs. We finally highlight current necessities and future prospects, mainly related to soil burn severity (SBS), invasive species and wildlife impact. Although our study specifically focused on changes in the fire regime of the Gran Chaco, some generalities were further discussed about fire regimes that could be relevant for diverse fire-sensitive ecosystems in the tropics.

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. O_2 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

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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 synthetize 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 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.

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 hervibory	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.

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 km^2(Fig. 1), representing the second largest forested region in South America -after the Amazon rainforest- and the third largest ecoregion (Rodriguez & 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).

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*

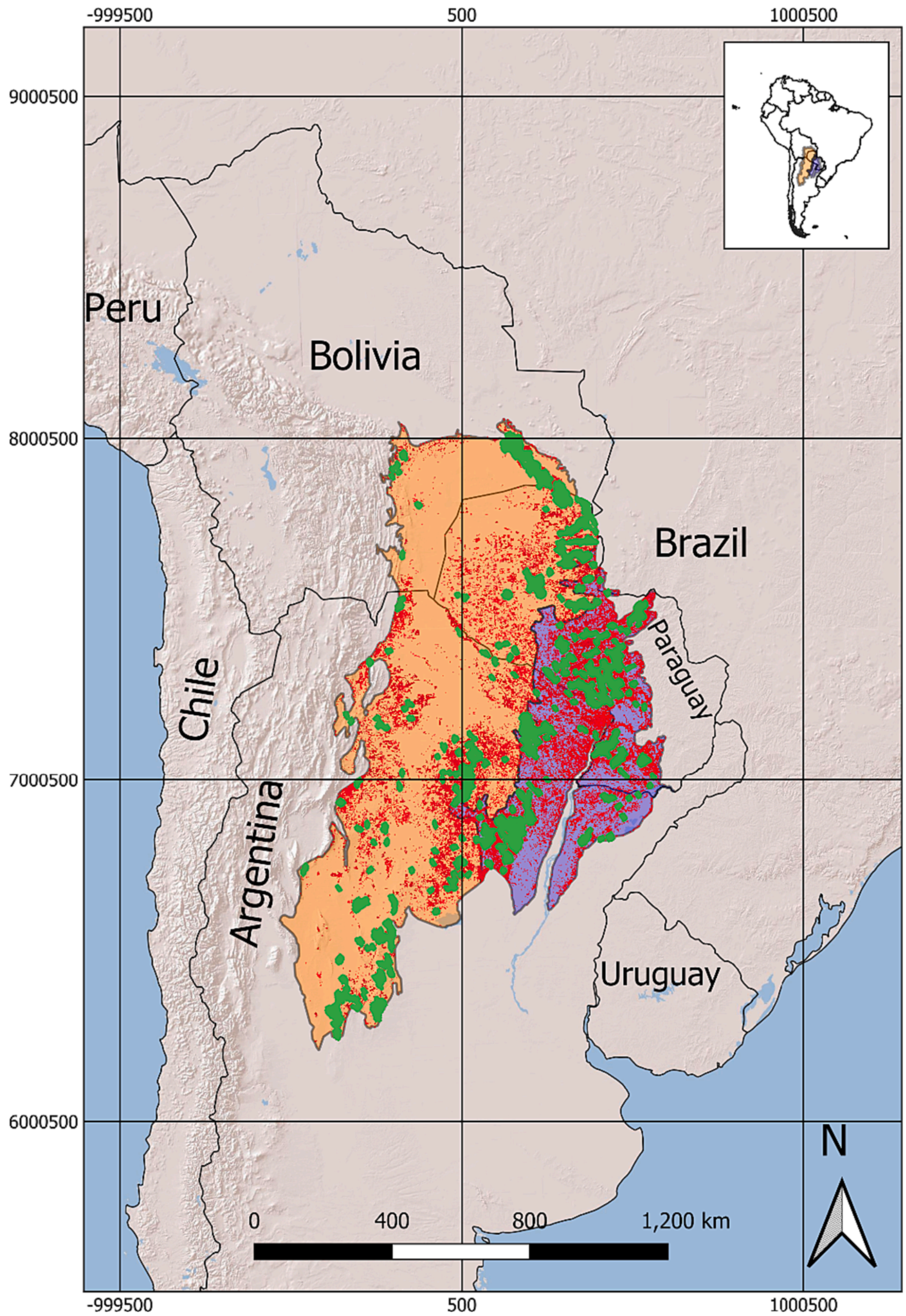

Fig. 1. Simplified map of the Gran Chaco (in colour) on a map of South America. The Gran Chaco consists of two large ecoregions: the Dry Chaco (orange area) and the Humid Chaco (purple area). Red dots represent burnt area during the last two decades detected by MODIS Version 6.1. Characterization of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

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

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).

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/km^2 (DGEEC, 2020). The late colonization of both of these countries by Mennonite 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/km^2, 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 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 (*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, 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 understory 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 CO_2 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

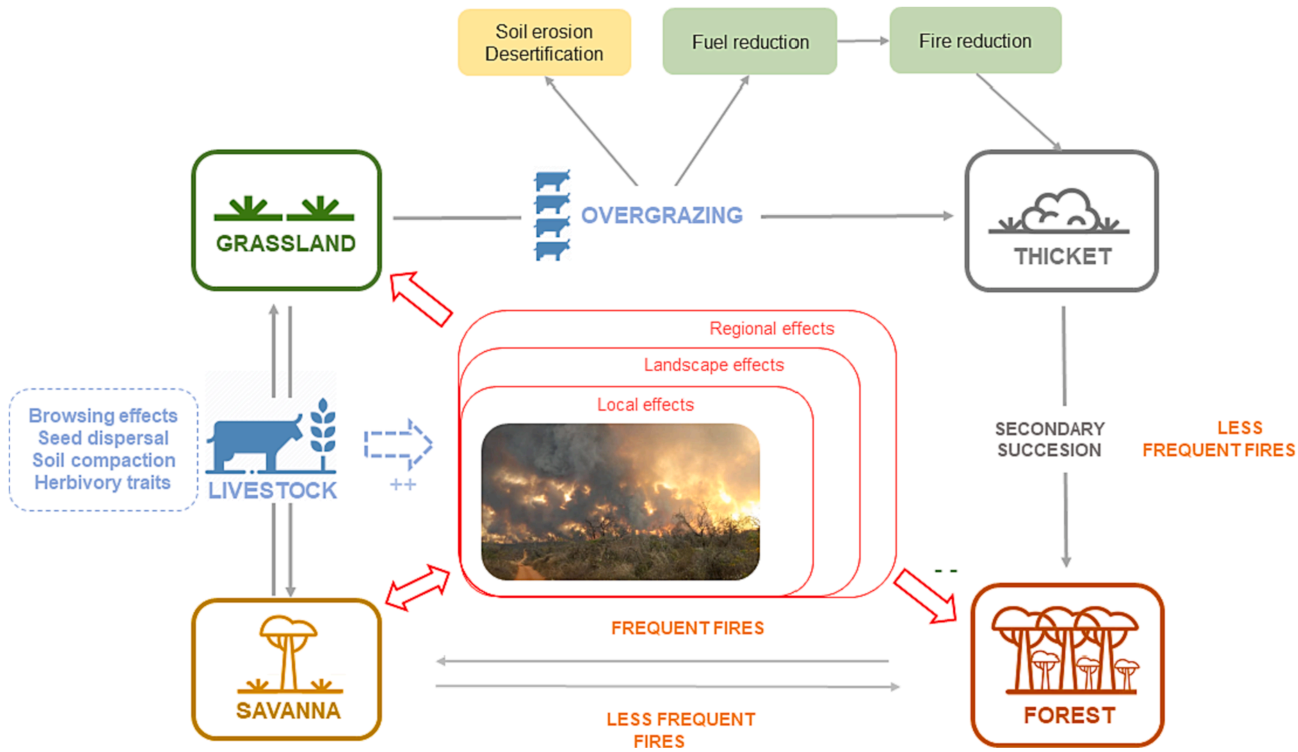

Fig. 3. Conceptual model showing the potential interactions between fire, livestock and vegetation that can theoretically result in stable mosaics of forest, savanna, grassland and thicket. Frequent fires are fires recurring at intervals of 2–5 yr. Less frequent fires are fires recurring once within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

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 (Rejžek et al., 2017). Silvopastoral 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 (Rejžek 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 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 species 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 attribute 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 perturbance. 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 (Ferreras 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, serotine) 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; Cóbar 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

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.

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 contributes little to characterizing these attributes in a particular timeframe. 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.

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Data availability

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

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