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EFFECTS OF AGRICULTURAL AND FOREST PRACTICES ON BIODIVERSITY IN NORTH-WEST SPAIN

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[Effects of agricultural and forest practices on biodiversity in North-West Spain]

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To all the people who have dedicated their lives to defend nature, both the ones that saw the fruits of their dedication and the ones who did not.

And, very especially, to the children and young people who, in the future, will fight to conserve the forests of the world, I hope they have strength and persistence. I hope they learn from our mistakes.


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“Rather than love, than money, than faith,

than fame, than fairness… give me truth.”

Henry D. Thoreau

“It's up to us to save the world for tomorrow:

it's up to you and me.”

Jane Goodall

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ABSTRACT

Agricultural and forest practices affect biodiversity. In North-West Spain, the main land-use changes that have ocurred during the past 50 years are agricultural intensification and plantations of exotic tree species. This thesis focused on how agricultural and forest management practices, reflecting these changes, affect plants, butterflies and birds that depend on the agro-forestry environments of inland Galicia. The aims of the thesis were (i) to evaluate if and how birds benefited from organic farming, (ii) to evaluate if multiple aspects of butterflies and plants diversity benefited from organic farming, and (iii) to evaluate if and how *Eucalyptus* plantations affect biodiversity by comparing plant and bird species and diversity richness between native forest patches and exotic *Eucalyptus* plantations. Ultimately, the aim of the thesis was to propose ways to improve management of agro-forestry systems, in order to unite social interests and biodiversity conservation.

The effects of farming and forest practices on biodiversity were analysed during three years by means of transects in paired organic and conventional farms, and native forests and *Eucalyptus* patches. Bird, butterflies and plant species richness, diversity and abundance were compared. Birds were shown to benefit from organic farming, as both species richness and abundance were higher in organic than in conventional farms. In addition, birds were also benefited by the presence of native forests surrounding organic farms. Butterfly species richness was higher in organic than in conventional farms. Furthermore, organic farming resulted in a higher functional diversity of butterflies. Finally, both plant and bird species richness and diversity were higher in native forests than in *Eucalyptus* plantations. Therefore, the results of this thesis suggest that both organic agriculture and native forests have a key role in biodiversity conservation, and that policies aiming for sustainable agricultural practices and conservation of native forests should be prioritized and promoted.

Keywords: biodiversity; organic farming; native Atlantic forests; *Eucalyptus* plantations; North-West Spain.

RESUMEN

Las prácticas agrícolas y forestales afectan a la biodiversidad. En el Noroeste Español, las principales prácticas de los últimos 50 años son la intensificación agrícola y las plantaciones forestales con especies exóticas. Esta tesis se enfocó en cómo dichas prácticas afectan a las plantas, mariposas y aves en medio agro-forestal gallego. Los objetivos de la tesis fueron (i) evaluar si las aves se benefician de la agricultura ecológica, (ii) evaluar si las mariposas y plantas se benefician de la agricultura ecológica mediante índices de diversidad funcional, y (iii) evaluar si las plantaciones de *Eucalyptus* afectan a la biodiversidad. El objetivo principal de la tesis era proporcionar información para un mejor manejo de los sistemas rurales, para unir los intereses sociales y la conservación de la biodiversidad.

Los efectos de las prácticas agrícolas y forestales fueron analizados durante tres años mediante transectos en granjas ecológicas y convencionales, y parches de bosque autóctono y plantaciones de *Eucalyptus*. La riqueza, abundancia y diversidad de especies de aves, mariposas y plantas fueron comparadas. Se mostró que las aves se benefician de la agricultura ecológica, con una mayor riqueza y abundancia de especies en granjas ecológicas que convencionales. Asimismo, las aves se benefician de la presencia de bosques autóctonos rodeando las granjas ecológicas. Dichas granjas tienen una mayor riqueza de especies de mariposas, además de una mayor riqueza funcional. Finalmente, tanto las plantas como las aves tienen mayor riqueza y diversidad de especies en bosques autóctonos que en plantaciones de *Eucalyptus*. Por lo tanto, los resultados de esta tesis sugieren que tanto la agricultura ecológica como los bosques autóctonos tienen un papel fundamental para la conservación de la biodiversidad, por lo que se sugiere que las políticas destinadas a las prácticas agrícolas sostenibles y la conservación de los bosques autóctonos sean priorizadas.

Palabras clave: biodiversidad; agricultura ecológica; bosques atlánticos autóctonos; plantaciones de *Eucalyptus*; Noroeste Español.

RESUMO

As prácticas agrícolas e forestais afectan a biodiversidade. No Noroeste español, as principais prácticas dos últimos 50 anos son a intensificación agrícola e as plantacións forestais con especies exóticas. Esta tese centróuse en como as devanditas prácticas afectan a biodversidade, en concreto aos grupos de plantas, bolboretas e aves no medio agroforestal galego. Os obxectivos da tese foron (i) avaliar se as aves beneficianse da agricultura ecolóxica, (ii) avaliar se as bolboretas e as plantas beneficianse da agricultura ecolóxica a través dos índices de diversidade funcional, e (iii) avaliar se as plantacións de eucalipto afectan a biodiversidade. O obxectivo principal da tese foi proporcionar información para unha mellor xestión dos sistemas rurais, para unir os intereses sociais e a conservación da biodiversidade.

Os efectos das prácticas agrícolas e forestais foron analizados ao longo de tres anos a través de transectos en granxas ecolóxicas e convencionais, e en parches de plantacións de eucaliptos e en bosques nativos; neles comparouse a riqueza, abundancia e diversidade de especies de aves, bolboretas e plantas. Mostrouse que as aves beneficianse da agricultura ecolóxica, cunha maior riqueza e abundancia de especies en granxas ecolóxicas que nas convencionais. Ademais, as aves beneficianse da presenza de bosques nativos que rodean ás granxas ecolóxicas. Éstas teñen unha maior riqueza de especies de bolboretas, así como unha maior riqueza funcional. Finalmente, as plantas e as aves teñen maior riqueza e diversidade de especies nos bosques nativos que nas plantacións de eucalipto. Por conseguinte, os resultados desta tese indican que tanto a agricultura ecolóxica como os bosques nativos teñen un papel fundamental na conservación da biodiversidade, polo que se suxire priorizar as políticas dirixidas a prácticas agrícolas sostibles e á conservación dos bosques autóctonos.

Palabras chave: biodiversidade; agricultura ecolóxica; bosques nativos; plantacións de *Eucalyptus*; Noroeste español.


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II. Goded, S., Ekroos, J., Domínguez, J., Azcárate, J.G., Guitián, J.A., Smith, H.G., 2018. Effects of organic farming on plant and butterfly functional diversity in mosaic landscapes. (Manuscript).

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RESUMEN


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RESUMEN

La biodiversidad del planeta ha disminuido más rápidamente en el último medio siglo que en toda la historia de la humanidad. Las principales causas de esta rápida pérdida de biodiversidad son: la degradación del hábitat, la introducción de especies exóticas invasoras, la sobreexplotación y la contaminación. En todos los países del planeta, varios o todos estos procesos globales están teniendo lugar por separado o en conjunto, lo que está resultando en una grave pérdida de biodiversidad. Aunque hay muchos estudios que reflejan cómo estos procesos afectan a la biodiversidad, frenar la pérdida de biodiversidad todavía no es una prioridad para la mayoría de los gobiernos. Además, aunque la mayoría de los países del mundo han acordado proteger la biodiversidad en varias plataformas, directrices y reuniones internacionales, como el Convenio sobre la Diversidad Biológica (CDB) o la Estrategia Europea de Biodiversidad, ésta sigue disminuyendo.

En Europa, milenios de agricultura tradicional han dado forma al paisaje e influenciado los ecosistemas y la biodiversidad que vive en él, siendo la agricultura hoy en día el uso de suelo más dominante en Europa. Sin embargo, los sistemas agroforestales de Europa están sufriendo una grave pérdida de biodiversidad desde la Segunda Guerra Mundial a mediados del siglo XX, causada por la intensificación agrícola, la destrucción de bosques nativos y la introducción de especies de árboles exóticos de rápido crecimiento. Estos cambios en los usos agrícolas y forestales son en parte debidos a la alta población humana que vive en Europa, pero mayoritariamente a la combinación de procesos como la expansión de prácticas agrícolas dirigidas a la maximización de beneficios, mediadas por factores institucionales; la transición de una sociedad rural a urbana; y la globalización de los mercados agrícolas y forestales. Para lograr la maximización de beneficios, muchos productos comenzaron a estar disponibles, como los fertilizantes inorgánicos para la agricultura y las especies de árboles exóticos de rápido crecimiento para usos forestales. La expansión de estos productos conllevó a que los agricultores y los propietarios de tierras pudieran aumentar sus ganancias rápidamente, pero las consecuencias en forma general de externalidades ambientales (como la eutrofización, la pérdida de biodiversidad, la contaminación o la degradación del suelo, entre otras) fueran pagadas por la sociedad en general.

En España, como en muchos otros países, la agricultura ha sido intensa desde mediados del siglo XX. La intensificación agrícola se produjo tanto a nivel local como a nivel de paisaje. A nivel local, el uso de pesticidas y fertilizantes sintéticos, junto con la corta y simplificada rotación de cultivos, ha estado aumentando continuamente. A nivel de paisaje, la especialización regional de los cultivos y la racionalización estructural han producido la simplificación del paisaje que se puede observar en la mayoría de los paisajes agroforestales europeos. Como consecuencia de esta intensificación, la biodiversidad agrícola de la Península Ibérica ha disminuido considerablemente en los últimos 50 años. Esta disminución ha afectado a todos los grupos de taxones que viven

o dependen del paisaje agrícola, incluidos mamíferos, aves, artrópodos o plantas, y varios de ellos contienen especies que actualmente están clasificadas como vulnerables, amenazados o altamente amenazados por la Unión Internacional de Conservación de la Naturaleza (UICN).

En contraposición a este declive, desde principios del siglo XXI en España, comenzó a extenderse un tipo de agricultura menos intensa y más sostenible, la agricultura ecológica. Aunque más tarde que en otros países del norte y centro de Europa, la agricultura ecológica se estableció definitivamente en España alrededor de 2005 y ha ido en aumento desde entonces, siendo hoy en día el país con la mayor extensión de tierras destinadas a la agricultura orgánica de todos los países de la Unión Europea (UE). La agricultura ecológica tiene requisitos comunes para todos los países de la UE: la prohibición en el uso de pesticidas sintéticos, fertilizantes o antibióticos, la prohibición del uso de organismos modificados genéticamente, o la necesidad de criar los animales en libertad. Sin embargo, hay diferentes detalles sobre los requisitos para la agricultura ecológica según el país y la región, que son en gran medida una forma de adaptarse a la no utilización de pesticidas o fertilizantes sintéticos. En España, hay prácticas que se utilizan comúnmente en la agricultura ecológica, como la larga rotación de cultivos. El potencial de la agricultura orgánica es restaurar tanto la heterogeneidad en las fincas como la complejidad del paisaje que ha provocado la agricultura intensiva. Dentro de España, la región noroccidental, que corresponde a la provincia de Galicia, es una de las regiones donde más se ha desarrollado la agricultura ecológica, con un aumento del 33% durante los últimos 18 años.

Aunque ha habido muchos estudios que muestran cómo la agricultura ecológica puede beneficiar la biodiversidad, principalmente en el Norte y Centro de Europa, hay muy pocos estudios realizados en la región mediterránea, y solamente uno en España. Estudios anteriores han indicado que la agricultura ecológica aumenta la diversidad de invertebrados y aves en paisajes homogéneos, y que dichos efectos disminuyen a medida que aumenta la complejidad del paisaje. Pero no hay estudios que hayan analizado si este efecto ocurre en un paisaje de mosaico heterogéneo de un país mediterráneo. Además, muchos estudios han investigado cómo la agricultura ecológica puede beneficiar la biodiversidad durante la temporada de reproducción, o durante el invierno. Sin embargo, ningún estudio previo ha analizado cómo podría cambiar el efecto de la agricultura ecológica en la biodiversidad durante todo un año. Finalmente, hay un interés creciente en analizar los índices de diversidad funcional en la biodiversidad, es decir, la diversidad de rasgos en una comunidad dada que afecta la supervivencia de especies individuales, cómo interactúan las especies entre sí, o la contribución de cada especie al funcionamiento del ecosistema. Una comunidad con mayor diversidad funcional sería más resistente a los cambios ambientales o de uso del suelo. Sin embargo, está muy poco estudiado si la agricultura ecológica no sólo puede conducir a una biodiversidad más rica y más abundante, sino a comunidades más funcionalmente diversas.

Sumado a la intensificación agrícola, desde mediados del siglo XX, el paisaje de mosaico tradicional gallego también se ha reducido debido a las plantaciones de especies de árboles exóticos, principalmente del género *Eucalyptus*, que han reemplazado áreas agrícolas o de matorral e, incluso, parches de bosque autóctono directamente. Además, las plantaciones de *Eucalyptus* a menudo perturban este proceso de sucesión natural por el cual el abandono de la agricultura produciría un futuro bosque autóctono si no se interviniera. Debido a su rápido crecimiento y rentabilidad para la producción de papel, las especies de eucalipto son actualmente una de las especies de árboles plantados más importantes del mundo, con un estimación de 2,5 millones de hectáreas plantadas en todo el mundo en el 2004, principalmente en la Península Ibérica. En España, las plantaciones de eucalipto cubren 633.000 ha, teniendo sus densidades más altas en la región noroeste, en las que ahora cubren un área más grande que los bosques autóctonos. Este aumento en las plantaciones de eucalipto es una consecuencia tanto del abandono rural como de los intereses gubernamentales. Más del 70% de los propietarios de tierras que poseen plantaciones de eucalipto no viven en áreas rurales y, muy a menudo, no utilizan sus tierras como forma de vida, ya que trabajan en áreas urbanas. Como consecuencia, el abandono rural ha producido un aumento en las plantaciones de eucalipto, que a menudo no se gestionan hasta casi 12-15 años después de la plantación. Además, aunque los gobiernos locales y nacionales no han otorgado incentivos directos para la plantación de eucalipto, tampoco han priorizado la conservación y el uso de los bosques autóctonos o las plantaciones de especies nativas, ni han informado del valor económico que puede proporcionar el uso de los bosques autóctonos. Además, se ha demostrado que los eucaliptos tienen un potencial invasivo, que junto con el abandono de la agricultura ha permitido un aumento extremo en el área cubierta por esta especie exótica en Galicia.

Sin embargo, aunque se ha demostrado que las plantaciones de eucalipto afectan la biodiversidad, hay sorprendentemente pocos estudios a escala global que hayan analizado los efectos de estas plantaciones en la biodiversidad, aunque todos han demostrado cómo las plantaciones de eucalipto albergan una biodiversidad mucho más pobre que los bosques autóctonos. Además, casi no se ha estudiado si estas plantaciones afectan más a especies raras o especialistas que a especies comunes o generalistas. Dado que las plantaciones de eucalipto siguen aumentando debido al continuo abandono rural y la ausencia de acciones gubernamentales para detener su propagación, es crucial comprender cómo este cambio en el paisaje está afectando a la biodiversidad de cara a proporcionar información y herramientas contrastadas para paliar o detener su efecto negativo.

Mientras se producen todos estos cambios en el paisaje y el uso del suelo, esta tesis se ha desarrollado para analizar si estos cambios en las prácticas agrícolas y forestales en el noroeste de España están afectando la biodiversidad. Para ello, se analizó si la agricultura ecológica puede paliar la pérdida de biodiversidad que la intensificación agrícola ha producido. Asimismo, se analizaron los efectos que la expansión de plantaciones de *Eucalyptus* y la reducción de bosques autóctonos tienen sobre la biodiversidad. Además, esta tesis tuvo como objetivo comprender cómo se podrían manejar las áreas agrícolas y forestales para paliar la pérdida de biodiversidad al mismo tiempo que se promueven alternativas para que las personas vivan en áreas rurales y usen los recursos naturales de manera sostenible.

Para analizar todo esto, la presente tesis tesis se dividió en tres capítulos que se desarrollaron de la siguiente manera: en el primer capítulo, se analizó el efecto de la agricultura ecológica en las comunidades de aves durante un año entero, mediante un estudio comparativo de la riqueza y la abundancia de especies de aves entre pares de granjas ecológicas y convencionales en un paisaje heterogéneo. Además, se analizó el posible efecto de características del paisaje, como la cobertura de terreno agrícola o la presencia de bosques nativos o plantaciones de eucalipto alrededor de las fincas estudiadas. En el segundo capítulo, se estudió el efecto de la agricultura ecológica en mariposas y plantas mediante un análisis comparativo entre granjas ecológicas y convencionales en un paisaje heterogéneo. En este capítulo, se analizó el efecto sobre las mariposas y las plantas a través de los índices de riqueza funcional y de diversidad de especies. Finalmente, en el tercer capítulo se estudió el efecto de las plantaciones de eucalipto en plantas y aves. Para este fin, se comparó la riqueza de especies y diversidad de plantas y aves en parches de eucaliptos y bosques nativos.

El área de estudio consistió en un área representativa del centro de Galicia (comarca de A Ulloa y alrededores), en el noroeste peninsular. Dicho área consiste en un paisaje heterogéneo agro-forestal que contiene un gran número de granjas ecológicas (16 granjas que suman un total aproximado de 350 Ha). Además, posee buenos parches de bosque autóctono y de masas de repoblación con eucalipto. Así, la heterogeneidad ambiental de la comarca fue un escenario ideal para efectuar las comparaciones aquí planteadas.

En el primer capítulo se analizó la hipótesis de que en las granjas ecológicas habría una mayor riqueza, abundancia y distinta composición de especies de aves que en granjas convencionales, pero que los efectos dependieran de las características del paisaje. Dicha diferencia se esperaba que fuera debida al efecto de prácticas agrícolas utilizadas en agricultura ecológica tales como la falta de uso de herbicidas, fertilizantes y pesticidas sintéticos y una larga rotación de cultivos. Para ello, se realizaron muestreos en una selección de 16 pares de granjas. Cada par de granjas consistió en una con agricultura ecológica y otra con agricultura convencional, que se emparejaron acorde con un tamaño similar, mismos tipos de cultivos y un ambiente alrededor similar. Las granjas de cada par nunca estaban separadas más de 20 Km entre ellos. La biodiversidad de cada granja fue analizada en función del tipo de agricultura utilizada, el tamaño del parche, y el ambiente alrededor. Los censos fueron realizados durante todo el año para tener en cuenta tanto especies migratorias como residentes. Cada par de granjas fue visitada dos veces en cada estación.

En este estudio, se demostró que las aves se ven afectadas por la intensificación agrícola en los paisajes heterogéneos, ya que había una mayor riqueza de especies de aves en las granjas ecológicas, y que este efecto fue más importante durante el período de invierno. La mayor riqueza de especies de aves en las granjas ecológicas en el invierno es probablemente el resultado de una mayor disponibilidad de alimento en dichas granjas como resultado de las largas rotaciones de cultivos y el uso de pastos permanentes. Además, se demostró que una combinación de granjas manejadas ecológicamente rodeadas de parches de bosque autóctono, resultó en una abundancia particularmente alta de aves, probablemente debido a que el mosaico agroforestal ofrece a las aves hábitats idóneos tanto para alimentación como para refugio. Finalmente, los resultados mostraron que las aves se concentran más en granjas ecológicas en áreas muy heterogéneas, donde hay una pequeña proporción de tierras agrícolas en general, y que, por lo tanto, las granjas manejadas ecológicamente podrían funcionar como puntos de atracción, aportando parches ricos en recursos en áreas pobres para las aves agrícolas.

En el segundo capítulo, se analizó la hipótesis de que la agricultura ecológica tiene una mayor riqueza de especies y diversidad funcional de plantas y mariposas que la agricultura convencional. Para ello, utilizamos cuatro índices de diversidad funcional de uso común (riqueza funcional, uniformidad funcional, divergencia funcional y dispersión funcional), calculados en función de ciertos rasgos de respuesta funcional relacionados con la dispersión de especies, la competencia y la persistencia de la población, que reflejan la distribución de especies en paisajes dominados por el hombre.

Se esperaba que las granjas convencionales tuvieran una diversidad funcional generalmente más baja que las granjas ecológicas, pero siendo éstos efectos dependientes de los grupos taxonómicos y de las características del paisaje. Para este análisis, se utilizaron los mismos 16 pares de granjas que en el capítulo anterior. En este caso, los datos se tomaron durante la primavera y verano. El muestreo de plantas se realizó mediante la identificación de riqueza y abundancia de especies (medida como cobertura) en 4 cuadrículas de 3x3 m distribuidas uniformemente a lo largo de la mayor finca de cada granja y separadas 10 m de las demás y del borde de la finca. El muestreo de mariposas se realizó mediante transectos de 300 m para tomar datos de la riqueza, abundancia y composición de especies.

En este estudio, se demostró que la intensificación agrícola afecta negativamente a las mariposas, ya que se encontró una mayor riqueza de especies en granjas ecológicas que convencionales. Asimismo, la diversidad funcional de las mariposas es afectada, es decir, las comunidades de mariposas son más ricas en términos de diversidad funcional en granjas ecológicas que convencionales. Este resultado sugiere que la agricultura ecológica puede posiblemente aumentar la efectividad con la que la comunidad de mariposas pueden usar los recursos que están disponibles en hábitats agrícolas y, por lo tanto, ayudar a que las comunidades de mariposas sean más resilientes a cambios tanto ambientales como de usos de suelo. Además de esto, aunque no se encontraron efectos de la agricultura ecológica sobre la riqueza de especies o diversidad funcional de plantas, se demostró que algunas especies de plantas, sobre todo especies típicas de pastizales, eran más abundantes en granjas ecológicas que convencionales, realzando así el efecto positivo de las granjas manejadas ecológicamente para devolver la heterogeneidad que la intensificación agrícola ha mermado.

Finalmente, en el tercer capítulo, se analizó la hipótesis de que los bosques autóctonos tienen una mayor biodiversidad que las repoblaciones exóticas con *Eucalyptus spp*. De cara a analizar esta hipótesis, se realizó un estudio de riqueza, y diversidad de plantas herbáceas y aves 14 pares de parches. Cada par de parches consistió en un parche de bosque autóctono y otro de una plantación de *Eucalyptus*, siempre mayores de 10 ha y separados un máximo de 10 Km entre ellos. La características vegetacionales de todos los parches fueron analizada en función de ocho variables principales: riqueza de especies de árboles, densidad, altura y diámetro de los árboles, riqueza de especies y altura de sotobosque, y cobertura del sotobosque y de copas. Todas estas variables se midieron en tres cuadrículas de 20x20 m cada 250m dentro del parche. El muestreo de plantas se realizó mediante la identificación de riqueza y abundancia de especies en esas mismas tres cuadrículas. El censo de aves consistió en contar la riqueza y abundancia de especies observadas u oídas a lo largo de transectos de 500 m dentro del parche. Con todo ello, se estudió si la sustitución tanto directa como indirecta de bosques autóctonos por plantaciones de eucalipto conlleva a una disminución de la biodiversidad y, además, si lleva a disimilitudes en las comunidades, afectando más a especies raras o especialistas.

En este estudio, se demostró que tanto la riqueza como la diversidad de especies de plantas y aves era mucho menor en plantaciones de eucalipto que en bosques autóctonos. Además, se demostró que las comunidades eran muy diferentes entre estos dos tipos de parche, respondiendo ambos grupos taxonómicos a distintos procesos. Las plantas estaban caracterizadas por el proceso de “rotación de especies”, mediante el cual las especies presentes en bosques autóctonos eran especies típicas de hábitats agrícolas

y forestales, mientras que las especies presentes en plantaciones de eucalipto eran típicas de ambientes de matorral. Sin embargo, las aves sufrían el proceso de “anidación de especies”, con mucha menor riqueza y abundancia de especies tanto de generalistas como de especialistas forestales en las plantaciones de eucalipto que en los bosques autóctonos. Por todo ello, estos resultados muestran que las plantaciones de eucalipto no pueden reemplazar la biodiversidad de los bosques autóctonos, ya que albergan una muy reducida comunidad de plantas y aves, además de diferentes especies de plantas. Considerando la tasa de incremento actual de estas plantaciones exóticas y la fragmentación y pérdida de bosques autóctonos en Galicia, la pérdida de biodiversidad en general, y de especies forestales en particular, podría aumentar y ser irreparable en el futuro si la conservación de los bosques autóctonos no es priorizada y promovida.

GENERAL INTRODUCTION


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GENERAL INTRODUCTION

VALUE OF BIODIVERSITY

Biodiversity on Earth has declined faster during the past half century than at any time during the previous human history, with current extinction rates being 1,000 times higher than background rates (Pimm *et al*., 2014). The main causes of this rapid loss of biodiversity are habitat degradation, introduction of invasive exotic species, overexploitation and pollution (Millennium Ecosystem Assessment, 2005). In countries all over the planet several or all of these drivers independently or in concert cause biodiversity loss (Butchart *et al*., 2010). Although there are many studies demonstrating how these drivers affect biodiversity across the globe, mitigating loss of biodiversity is still not a priority for most governments. Moreover, even though most countries in the world have agreed to protect biodiversity in several international conventions and agreements, such as the Convention on Biological Diversity (CBD) or the European Biodiversity Strategy, biodiversity continues to decline (Butchart *et al*., 2010; Pe´er *et al*., 2014).

The intrinsic value of biodiversity, such as the ethical appreciation of nature for its own sake, is a fundamental and sufficient argument for nature conservation (Noss and Cooperrinder, 1994; CBD, 2006). The loss of biodiversity is, however, not only of ethical concern. We, humans, depend on biodiversity for our survival and welfare (Haines-Young and Potschin, 2010; Isbell *et al*., 2017). We, for example, directly and indirectly depend on plants and animals for food, provision of wood, fibre and medicines - so called provisioning ecosystem services (Millennium Ecosystem Assessment, 2005). In addition to these obvious examples, both wild and managed ecosystems contribute to ecosystem processes that benefit humanity in a variety of ways (Hooper *et al*., 2005). As an example, we depend on ecosystem functions that regulate water, retain nutrients in the soil, and regulate temperature - so called regulating ecosystem services. In addition, nature contributes to our spiritual well-being, through cultural, religious, recreational or enjoyment of nature – so called cultural ecosystem services (Millennium Ecosystem Assessment, 2005). Human modification of the intricate ecological web that all living beings are part of will inevitably have a consequence for these services. Thus, loss of biological diversity can contribute to the erosion of these services (Hooper *et al.*, 2005; Isbell *et al.*, 2017). Sometimes, we are conscious of the consequences of human actions disturbing the ecological web and can replace natural ecosystem processes lost with external inputs (e.g. in agriculture), but this may sometimes result in environmental pollution. Such consequences are not immediately obvious and therefore underestimated or ignored. However, when biodiversity loss has reached critical thresholds, the damage to ecosystem services may be difficult or impossible to reverse (Diaz *et al*., 2006; Rockström *et al*., 2009).

EUROPEAN AGROFOREST SYSTEMS AND BIODIVERSITY

The agro-forest systems of Europe have been experiencing severe biodiversity loss since the mid-20th Century, caused by a combination of agricultural intensification and concomitant landscape simplification (Henle *et al*., 2008; Concepción and Díaz, 2010); as well as habitat degradation as a result of native forest destruction (Hannah *et al*., 1995) and introduction of fast-growing exotic tree species (Barlow *et al*., 2007). These changes in the use of farmland and forests have been driven by a combination of several processes such as the high human population in Europe, the spread of farming practices aimed to increase production per unit area, the transition from a rural to urban society, and the globalisation of agricultural and forest markets (Lambin *et al.*, 2001; van Vliet *et al*., 2015). In order to increase profitability, farmers and land owners took the opportunity to use new products which became available, such as inorganic fertilizers in agriculture and fast-growing exotic tree species in forestry. However, that entailed costs in the form of environmental externalities (such as eutrophication, loss of biodiversity, pollution or soil degradation) which were mostly paid by the society at large.

In Europe, millennia of traditional agriculture has shaped the landscape and influenced the ecosystems and their biodiversity, such as that agriculture is nowadays the dominant land use in Europe (Stoate *et al*., 2009). However, since the expansion of the use of synthetic pesticides and fertilisers after the Second World War in mid-20th Century, agricultural practices have changed such that intensive agriculture has replaced the traditional, often more sustainable, agriculture (Donald *et al*., 2006; Stoate *et al*., 2009). As a consequence of this increase in farming intensity, ecological heterogeneity has decreased (Benton *et al*., 2003), with a resulting loss in biodiversity (Donald *et al*., 2006; Stoate *et al*., 2009). After more than 50 years of agricultural intensification, based on habitat conversion, use of synthetic pesticides and inorganic fertilizers, we are now experiencing its negative consequences for the environment and particularly for biodiversity.

AGRO-FOREST SYSTEMS AND BIODIVERSITY IN SPAIN

In Spain, as in the rest of Europe, agriculture has been intense for over 50 years (Guzmán *et al*., 2017). Agricultural intensification has occurred at two levels: both at a field and at a landscape level (Concepción and Díaz, 2010). At a field level, the use of synthetic pesticides and fertilisers has increased, associated with shorter and simplified crop rotations. At a landscape level, the regional specialisation of crops and the structural rationalisation have produced the simplified landscapes that can be observed in most European agro-forest landscapes (Concepción and Díaz, 2010). As a consequence of this agricultural intensification, farmland biodiversity has declined steeply (Concepción *et al*., 2008; Concepción and Díaz, 2010). This decline has affected multiple taxon that live or depend on farmland, such as mammals, birds, arthropods and plants, so that several species now are classified as vulnerable, threatened or highly threatened by the International Union of Conservation of Nature (IUCN, 2018). In addition, agricultural intensification has been shown to result in a loss in functional diversity of a given community (Flynn *et al*., 2009), i.e. the diversity of traits in a given community that affect the survival of individual species, how species interact with each other, or the contribution of each species to ecosystem functioning (Lavorel and Garnier, 2002; Cadotte *et al*., 2011). Therefore, the loss in functional diversity of a community would result on a loss of resilience to environmental or land use changes (Chillo *et al*., 2011).

In addition, since mid-20th Century, the traditional mosaic landscape in North-West Spain has been modified as plantations of exotic tree species, firstly *Pinus radiata*, but later mainly *Eucalyptus* spp., have been replacing agricultural areas, scrubland and, native forest patches (Teixido *et al.*, 2010). Without these, abandoned agriculture land would if left unmanaged ultimately become native forest, but plantations of exotic *Eucalyptus* species often disrupt this natural succession (Calviño-Cancela *et al*., 2012). Due to their fast growth and high profitability for paper and biofuel production (Turnbull, 1999), *Eucalyptus* species are currently one of the most important planted tree species in the world, with an estimated 2.5 million ha being planted worldwide by 2004, mainly in the Iberian Peninsula (Potts *et al*., 2004). In Spain, *Eucalyptus* plantations cover 633,000 ha (Montero and Serrada, 2013). Furthermore, *Eucalyptus* plantations have their highest densities in the North-West region, where they now cover a larger area than native forests (IFN, 2017).

This increase in *Eucalyptus* plantations is a consequence of both rural abandonment and governmental interests (Calviño-Cancela *et al*., 2012). More than 70% of the land owners that own *Eucalyptus* plantations, are not living in rural areas (IGE, 2017) and, very commonly, not using their lands as a way of living since they work in urban areas (Marey-Pérez *et al*., 2006). The rural abandonment has produced an increase in *Eucalyptus* plantations, which are very often non-managed until clear-cutting around 12-15 years after plantation, although undergrowth cutting is required by the national law for fire prevention. In addition, although both the local and national governments have not directly given incentives for plantation of *Eucalyptus spp.*, they have neither prioritised the conservation and use of native forests or native species plantations, nor informed the economic, environmental, social and landscape values that native forest conservation and management can provide. In addition, *Eucalyptus* spp. have been shown to have an invasive potential (Sanz Elorza *et al*., 2001; Calviño-Cancela and Rubido-Bará, 2013), which together with the abandonment of agriculture has allowed an increase in the cover area of this exotic species.

MITIGATION OF CHANGE

To counteract the continuing decline of farmland biodiversity, a less intense and more sustainable type of farming – organic farming - started to spread across the globe, being established in Europe around the end of the 20th Century (European Environment Agency, 2005). Organic farming has some common requirements in all European Union countries: the prohibition of use of synthetic pesticides, inorganic fertilisers, antibiotics (for stimulating animal growth), and genetically modified organisms, as well as regulations concerning animal welfare (European Environment Agency, 2005). Nevertheless, the ways to accommodate the non-use of synthetic pesticides or inorganic fertilisers are partly different in each country, and include long crop rotations and dependence on manure, compost or nitrogen-fixing crops, amongst other practices. All these measures combined mean that organic farming has the potential to restore the field heterogeneity and landscape complexity that intensive agriculture has eroded (Benton *et al*., 2003).

In Spain, although later than in other Northern and Central European countries, organic farming was definitely established around 2005 and has been increasing ever since then, being nowadays the European country with the highest share of farmland managed organically out of all EU-countries (European Environment Agency, 2005). Within Spain, the province of Galicia, is one of the regions where organic farming has been mostly developed. There has been a 33% increase in organic farming during the last 18 years (CRAEGA, 2015). This increase in the Northwestern region of Spain might have occurred for one or several of the following reasons: the characteristic temperate-humid climate of the region favouring the production of a big variety of crops (Martínez-Cortizas and Pérez-Alberti, 1999), the traditional small field sizes and mosaic landscape of the area leading to a more economically viable conversion to organic farming by local farmers, or the relative value of economical incentives given to organic farmers through the Common Agricultural Policy (CAP).

In addition, the conservation of the traditional use and management of native forests in Galicia have implied the conservation of the few remnant patches of these increasingly rare habitats, together with the biodiversity associated to them. The only areas where patches of Atlantic native forests are still conserved in Galicia are either those in which traditional uses, such as chestnut collection or sustainable oak wood exploitation, are maintained, or those corresponding to very remote and inaccessible areas (Guitián *et al.*, 2004). Therefore, the promotion of traditional native forest uses, with the help of new technologies, could lead to an implementation of sustainable rural practices, in order to keep rural inhabitants and, as a consequence, conserve mature native forests and their associated biodiversity.

THE STUDY AREA

The Northwestern Iberian Peninsula constitutes an important region in terms of biodiversity, due to both geographical features and landscape characteristics. It is the southwestern border of the Eurosiberian biogeographical region (Rivas-Martínez *et al.*, 2014), limiting with the Mediterranean region, present in the rest of the Iberian Peninsula. Because of this, many species typical to the Atlantic-European Province have their southernmost limit here, and species typical to the West Iberian Mediterranean Province have their northernmost populations here. In addition, the province constitutes both a wintering ground for migratory bird species breeding in Northern Europe (SEO/BirdLife, 2012), and a breeding ground to many European-African species (Martí and Del Moral, 2003). Concerning the landscape, North-West Spain is one of the few Western European territories which still conserves a traditional agro-forestry mosaic landscape in some areas. The traditional small-sized fields of the area, together with the ancient use of agriculture, scrubland and forest resources have resulted in a typical mosaic landscape in which patches of pastures and grasslands are embedded within patches of native forest, mainly comprised of oaks (*Quercus robur and Q. pyrenaica*), chestnut (*Castanea sativa*) and birch (*Betula alba)*, amongst many other tree species. Some of these forest patches contain trees older than 500 years, combined with young trees that grew after farmland abandonment (Corbelle and Crecente, 2014). This long-existing mosaic landscape harbours many plant, bird, mammal, and insect species which depend on it for their existence.

However, the traditional landscape of North-western Iberian Peninsula, corresponding to the province of Galicia, have experienced structural changes including rural abandonment, agricultural intensification and changes in forest practices, with consequences for biodiversity.

In most of the rural areas of Galicia, the population has decreased by more than 72% since 1986 (IGE, 2017). The decrease of rural inhabitants is a consequence of both the movement of young people to the cities, which started in 1950s and still occurs nowadays, and the resulting ageing of the rural population with a third of the population being older than 65 years in most rural areas of Galicia (IGE, 2017). Due to this, most of agricultural land has either been abandoned (from 1962 to 2009 the number of agricultural exploitations in Galicia decreased by 82%; IGE, 2017), or intensified (from 1985 to 1996 the production of milk products increased by 36%; Sau *et al.,* 1999). In addition to this, rural abandonment has been also associated with a loss of traditional forest practices. As an example, the traditional consumption and trade of chestnuts and oak wood, which contributed to the conservation of the remnants of mature forest patches in Galicia, has been highly abandoned, with only less than 20% of the mature chestnut forests are in use in Galicia nowadays (IGE, 2017). This loss of management of the natural and semi-natural habitats can lead to a loss of cultural knowledge and value of these habitats, which in turn has an effect on biodiversity conservation (Gadgil *et al*., 1993). One result of these changes is that the once big patches of mature native oak forests have been highly fragmented and reduced due to overexploitation and exotic tree plantations (Teixido *et al.*, 2010), and, thus, the mature deciduous Atlantic forest now constitutes an extraordinary rare habitat (Guitián *et al.*, 2004).

THE FOCUS OF THIS THESIS

Although there have been many studies that showed how organic farming can benefit biodiversity in many other regions, mainly Northern and Central Europe, there are very few studies on the Mediterranean basin (Tuck *et al.*, 2014), and only one in Spain (Concepción and Díaz, 2010). Previous studies have indicated that organic farming increases diversity of invertebrates and birds in homogeneous landscapes, and that such effects decrease as the complexity of the landscape increases (Rundlöf *et al.*, 2008; Batáry *et al.*, 2010; Geiger *et al.*, 2010; Smith *et al.*, 2010). However, there are no studies that have analysed if this effect occurs in a heterogeneous mosaic landscape of a Mediterranean country. In addition, many studies have investigated how organic farming can benefit biodiversity during breeding season (Kleijn *et al.*, 2006), and a few during winter (Geiger *et al*., 2010; Chamberlain *et al*., 2010). Nevertheless, no previous studies have analysed how the effect of organic farming on biodiversity might change during an entire year. In addition, it is very much understudied if organic farming not only leads to a richer and more abundant biodiversity, but also to more functionally diverse communities.

In addition, although *Eucalyptus* plantations have been shown to affect biodiversity, there are surprisingly few studies at a global scale that have analysed the effects of these plantations on biodiversity (Calviño-Cancela *et al.*, 2012). However, all of the few studies done in the Iberian Peninsula have shown how *Eucalyptus* plantations harbour a much poorer biodiversity than native forests (Bongiorno, 1982; Pina, 1989; Proença *et al*., 2010; Calviño-Cancela, 2013). Even fewer studies have analysed if these plantations predominantly affect rare species or specialists more than common species or generalists. As *Eucalyptus* plantations are still increasing due to both the continuing rural abandonment and the absence of governmental actions to stop their spread, it is crucial to understand how this change in land-use affects biodiversity.

With this as a background, the present thesis was developed in order to analyse if organic farming can mitigate the biodiversity loss caused by agricultural intensification in a heterogeneous landscape of North-West Spain. In addition, the present thesis analysed the impacts that the spread of *Eucalyptus* plantations and the reduction of native Atlantic forests have on biodiversity. By increasing the knowledge on these issues, this thesis also aimed to promote alternatives for people to live in rural areas and use the natural resources sustainably. The thesis was divided into three chapters as follows:

In Chapter I, the effect of organic farming on bird communities was analysed during an entire year, by means of a comparative study of bird species richness and abundance between organic and conventional paired farms in a heterogeneous landscape. In addition, the possible effects of landscape features such as land openness or presence of native forest or *Eucalyptus* plantations around the studied farms were analysed. This chapter is directly transcribed from the published paper: Goded, S., Ekroos, J., Domínguez, J., Guitián, J.A., Smith, H.G., 2018. Effects of organic farming on bird diversity in North-West Spain. *Agriculture*, *Ecosystems & Environment*, *257*, 60-67. The original paper is included as an appendix.

In Chapter II, the effect of organic farming on butterflies and plants was studied by means of a comparative analysis between organic and conventional farms in a heterogeneous landscape. In this chapter, the effect on butterflies and plants was analysed both by means of species richness and functional diversity indices. This chapter is based on the manuscript: Goded, S., Ekroos, J., Domínguez, J., Azcárate, J.G., Guitián, J.A., Smith, H.G., 2018. Effects of organic farming on plant and butterfly functional diversity in mosaic landscapes.

Finally, in Chapter III the effect of *Eucalyptus* plantations on plants and birds was studied. To this end, the species and diversity richness of both plants and birds in *Eucalyptus* and native forest patches were compared. This chapter is based on the manuscript: Goded, S., Ekroos, J., Domínguez, J., Azcárate, J.G., Guitián, J.A., Smith, H.G., 2018. Effects of *Eucalyptus* plantations on biodiversity in North-West Spain.

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The main aim of this thesis was to measure the effects of contemporary agricultural and forest practices on biodiversity in North-West Spain. The effects of agricultural practices were measured by analysing if organic farming can mitigate the loss of biodiversity that agricultural intensification has caused. The effects of forest practices were measured by analysing if the conversion of native Atlantic forests to *Eucalyptus* plantations leads to biodiversity loss. In order to achieve these aims, several specific aims were divided as follows:

Chapter I: Effects of organic farming on bird diversity in North-West Spain

(1) Investigate if organic farming has an effect on bird species richness and abundance by comparing matched organic and conventional farms.
(2) Analyse if the effect of organic farming on bird species richness and abundance is affected by the amount of land under organic management.
(3) Analyse if the effect of organic farming on farmland bird assemblages is modified by landscape structure.
(4) Analyse if the effects of organic farming on birds differ between seasons.

Chapter II: Effects of organic farming on plant and butterfly functional diversity in mosaic landscapes

(1) Investigate if organic farming has an effect on plant and butterfly diversity by comparing matched organic and conventional farms.
(2) Analyse if organic farming affects both taxonomic and functional diversity of plants and butterflies.
(3) Analyse if the effects of organic farming on the taxonomic and functional diversity of plants and butterflies are modified by landscape structure.

Chapter III: Effects of *Eucalyptus* plantations on biodiversity in North-West Spain

(4) Analyse if patches of native forest have a higher species richness and diversity of birds and plants than patches of *Eucalyptus* plantation.
(5) Analyse if *Eucalyptus* plantations lead to biotic homogenization driven by a systematic loss of rare or specialist bird or plant species or species turnover, compared to native forests.


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CHAPTER I

Effects of organic farming on bird diversity in North-West Spain


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1.1 INTRODUCTION

The ongoing decline of European farmland biodiversity is generally attributed to the intensification of European agriculture during the past half century (Donald *et al.*, 2001; Stoate *et al.*, 2001). Agricultural intensification can occur both at field and at landscape scales (Benton *et al.*, 2003, Concepción *et al.*, 2008). At field scales, intensification involves e.g. increased use of inorganic fertilisers and pesticides and simplified crop rotations. At landscape scales, structural rationalisation and regional specialisation of agriculture drive landscape simplification. Both processes have detrimental consequences for farmland biodiversity. Organic farming has been suggested to be a way of counteracting the decline of farmland biodiversity (Hole *et al.*, 2005). Organic farming benefits biodiversity mainly because of the restricted use of agro-chemicals, choice of crop type and crop rotations (Smith *et al.*, 2010). Ultimately, organic farming is thought to counteract the decline of farmland biodiversity because it has the potential to restore the loss of heterogeneity that agricultural intensification has produced (Benton *et al.,* 2003).

Several studies have analysed the potential of organic farming as a tool to enhance farmland biodiversity in Europe, with results varying mainly because of the moderating effect of landscape complexity (Tuck *et al*., 2014). Most studies have shown that organic farming increases diversity of invertebrates and birds in homogeneous landscapes (intensively-farmed plains), and that effects level off as the complexity of the landscape increases (Rundlöf & Smith, 2006; Rundlöf *et al.*, 2008; Batáry *et al.*, 2010; Tuck *et al*., 2014). However, relatively few studies have analysed if organic farming affects biodiversity in Mediterranean countries (Tuck *et al.*, 2014). Since agriculture in Mediterranean countries differs from that in the more well-studied Central and Northern Europe, it is important to address if the effect of organic farming on biodiversity generalizes also to these countries, resulting in a more general understanding of how organic farming affects biodiversity in different biogeographic regions.

Birds have been a prominent group in studies of the biodiversity consequences of organic farming, both because of the public interest in birds and the relative ease by which they can be studied. Still many aspects are understudied also for this group. First, most studies on the effect of organic farming on farmland birds have been done during the breeding season (Kleijn *et al.*, 2006; Concepción & Díaz, 2010), and only a few during the migration season (Dänhardt *et al.*, 2010), or in winter (Geiger *et al.*, 2010; Chamberlain *et al*., 2010; Morales *et al*., 2015). Since birds are more strongly central-place foragers in spring and summer compared to autumn and winter (see e.g. Smith *et al*., 2014), and availability of food resources in winter might be a key limiting factor for some bird species, mainly granivorous (Chamberlain *et al*., 2010), we can also expect birds to differ in their responses to organic farming between seasons, which may provide different resources in different times of the year. No study has analysed effects of farming regime on farmland birds across an entire year. Second, while it is known that organic farming differentially affect species with different ecological traits (Birkhofer *et al*., 2014), few studies on birds have investigated differential effects of organic farming on functional groups (but see Filippi-Codaccioni *et al*., 2009; Dänhardt et al. 2010). In particular, because organic farming benefits plants and some arthropod groups (Tuck *et al*., 2014; Lichtenberg *et al*., 2017), organic farming can be expected to have contrasting effects on bird feeding guilds (cf. Kragten & de Snoo, 2007). Third, while it is known that the extent of organic farming can affect biodiversity (Rundlöf *et al*., 2010), only one study has investigated this for birds (Gabriel et al., 2010).

In this study we investigate if organic farming affects the abundance and diversity of farmland birds in central Galicia (North West Spain) during an entire year. In this region, the extent of organic farming has increased with more than 33% during the last 18 years, but the intended positive consequences for biodiversity (CRAEGA, 2014, 2015) remain unknown. The agricultural landscapes in Northwestern Spain are generally heterogeneous, with small agricultural fields embedded within patches of forest, but experience some intensification at field and landscape scales (Sau *et al.*, 1999). Hence, it is not evident that the positive effects of organic farming on biodiversity that has been found in simplified landscapes in Central and Northern Europe would occur in these landscapes. Furthermore, because Northwestern Spain is an important wintering ground for some Northern European species (SEO/BirdLife, 2012), and a breeding ground for many Southern species, our study not only has local implication, but may inform about the value of organic farming in creating high-quality winter habitat both for local residents and migrants from more northerly areas.

We tested the hypothesis that the abundance and species richness of birds that at least partly utilise farmland benefit from organic farming. We did this through an entire year by (1) comparing organic and conventional farms and by (2) comparing areas with different amounts of land under organic management. We furthermore analysed if the benefits of organic farming on farmland bird assemblages depended on landscape context, since previous studies have shown different effects of open patches of agricultural land on farmland biodiversity depending on landscape complexity. In complex (mixed forest-farmland) landscapes, open agricultural patches benefit farmland bird diversity (Zakkak *et al.*, 2014; Salaverri, 2015). We analysed the effect of landscape context by studying the effects of landscape features, and the joint effects of farming management and landscape context. Whilst accounting for effects of overall land-use as farmland and forest, we expected a positive effect of the amount of farmland in the landscape on farmland bird diversity. We tested if insect and seed-eating species benefited more from organic farming compared to vertebrate-eaters and omnivorous birds (cf. Kragten & de Snoo, 2007), in particular if any such effect was stronger in winter when insects and seeds are naturally scarce, due to the lack of use of pesticides and other management practices common in organic farming (Chamberlain *et al*., 2010).

1.2 MATERIALS AND METHODS

1.2.1 Study area

We performed the study in the centre of Galicia (Ulloa Shire and surroundings), in the North West of Spain. The study area consisted of a heterogeneous landscape of farmland-forest, of 421 km^2, 550 m over sea level, with 46% of the land being forests and 35% consisting of farmland, with an average field size of 4.7 ha (IGE, 2012). Forests consisted of big patches of native deciduous forest, mainly comprised of oak (*Quercus robur*), chestnut (*Castanea sativa*) and birch (*Betula alba),* all of which are increasingly replaced by exotic tree plantations of eucalyptus (*Eucalyptus globulus* and *E. nitens).*

We selected 16 pairs of organic and conventional farms, matched to as far as possible minimise differences not related to farming practice within pairs (cf. Rundlöf & Smith, 2006). We identified organic farms based on whether they were registered in the Galician Regulating Board of Organic Agriculture (CRAEGA). We matched farms to pairs based on proximity (max 20 km apart), and land use (14 pairs of farms with grasslands used both for grazing and mowing, and 2 pairs of wheat farms). The majority (n = 13) of organic farms were mixed with animal husbandry and arable production (including fodder), while only two conventional farms were mixed. To minimise variability in landscape structure within pairs, we selected farms so that both farms in a pair had a similar percentage of agricultural land surrounding the centre of the farm (using 500 m radii).

Both organic and conventional farms used liquid manure to fertilize fields, and three organic farms fertilised with composted manure, which is recommended but not mandatory for organic farming in the area (CRAEGA, 2014). Conventional farms typically use synthetic insecticides every spring to control for the crane fly (*Tipula* spp.), irrespectively of the actual densities of crane flies. Six conventional farms rotated grassland and maize annually, ploughing and planting grass after the maize was harvested in late summer, while eight conventional farms had permanent grasslands all year round. In ten of the studied organic farms, farmers kept grasslands for five years approximately, after which they ploughed them, whereas four farms had permanent pastures (Appendix A).

We divided the entire 421 km^2 study area into 500 x 500 m squares in order to obtain study sites containing both organic and conventional fields, as both conventional and organic farms in the study region consisted of several fields interspersed amongst other farms and landscape features. We thereafter chose two study squares to represent each of the 16 organic farms. Because of the farm structure, the squares often contained some conventional managed land; we therefore selected the squares containing the highest and lowest possible percentage of organic land on each organic farm. We chose one study square to represent each of the 16 conventional farms which was as similar as possible in terms of percentage of agriculture than the matched organic squares of its pair. Thus, the total data consisted of 32 organic study squares and 16 conventional study squares. For each study square, we calculated the percentages of agricultural land, shrubs, native forests, exotic plantations and urban areas based on a GIS-vector layer, digitalised based on aerial photographs and field visits, using ArcGIS 9.3 (ESRI, 2006).

1.2.2 Bird censuses

We monitored birds by counting all birds seen and heard, identified to the species level, along 500-m transects situated within each study square, following, as far as possible the diagonal of the square, and walking within the studied fields when possible. We separated transects on the same organic farm with at least 200 m, as it was taken to be the detection radius for birds. The same observer visited the single conventional and the two organic study squares within a pair on the same day to minimise bias (cf. Kleijn *et al*., 2006), while systematically switching the order in which the three squares were visited to reduce effects of time of day (cf. Dänhardt *et al.*, 2010). We made all observations from sunrise and during the following four hours, but not during days with rain or strong wind. We visited each pair of farms twice during spring (April-June), summer (July-September), and autumn (October-December), but because of weather constraints only once during winter (January-March).

1.2.3 Quantification of landscape variables and bird feeding groups

We quantified the percentage cover of agricultural land, shrub area, native forest area, exotic plantation area and urban area in our study squares. Since the landscape variables in each study square were correlated, we used principal components analysis (PCA) to create a set of uncorrelated landscape descriptors (Concepción *et al.*, 2008). From the five original landscape variables introduced in the PCA, we selected the three first principal components, which together explained 91.8% of the total variation. PC1 was positively correlated with the percentage of agricultural land in the study square ($r_P = 0.852$), and thus it was interpreted as a measure of land openness. PC2 was positively correlated with the percentage of shrub area ($r_P = 0.861$), characterising the prevailing habitat type on abandoned agricultural land, whereas PC3 was positively correlated with the percentage of native forest ($r_P = 0.786$) and negatively correlated with the amount of exotic plantations ($r_P = -0.598$), and was therefore interpreted as a measure of forest composition. None of the PC-variables were related to farming practice or to proportion of organic land ($|t| \leq 1.39$, $P \geq 0.17$ in all cases), i.e. all three PC-variables could be included together in the analyses together with farming practice or proportion of organic land.

To test if birds with different feeding preferences were differently affected by organic farming, we classified all observed bird species into six feeding guilds based on diet: vertebrate-feeders, invertebrate-feeders, seed-eaters, omnivores, grazers and invertebrate-feeders switching to berries in autumn (Appendix C). This information was extracted from Dänhardt et al. (2010), with additional information for species not covered (Cramp and Simmons, 1980). However, in contrast to Dänhardt et al. (2010), we classified the Common Starling *(Sturnus vulgaris*) as an insect-berry eater assuming it to have the same diet as the Spotless Starling (*S. unicolor*) in winter (unpublished data). Birds corresponding to the vertebrate-feeder and grazer classes were omitted from analyses because of low sample sizes.

1.2.4 Statistical analyses

1.2.4.1 Organic versus conventional squares

To investigate the effect of organic versus conventional farming on birds, we compared data collected on transects performed in the conventional study squares and one of the organic squares per matched organic farm, by taking each conventional study square with the most similar organic study square in terms of percentage of agricultural land from the two organic squares in its matched pair. We analysed species richness using general linear mixed-effects models (using library nlme; Pinheiro *et al.*, 2011) since assumptions of normally distributed residuals were met. For abundance residuals did not meet the assumptions of normality, so we used generalised linear mixed-effects models (library lme4; Bates *et al.*, 2014) with Poisson error distributions. For the latter models, we added an observation level random effect (Harrison, 2014) to handle overdispersion when needed. In each model, we entered farming practice (organic or conventional), season (factorial with four levels) and the three continuous principal components, as fixed terms. We also entered two-way interactions between farming practice and season, farming practice and the three principal components and season and the three principal components. We pooled data collected within the same season at each farm, and thus obtained a total sample with 128 observations (i.e. four observations per farm in 32 farms). We used farm identity nested within pair identity as random factors to account for non-independent observations within each farm and within each pair. In addition, to correct for the lower study effort taken during the winter, we entered an offset in the abundance model. We defined species richness as the total number of species observed on the two visits of each season, and bird abundance as the sum of all birds observed on both visits during each season. We simplified the full model by deleting non-significant interactions one at a time, evaluated using likelihood ratio tests. To interpret significant main terms and interactive effects between predictors, we used effects plots derived using package Effects (Fox, 2003), showing estimated marginal mean values and 95% confidence intervals. In addition, we assessed the interactive effects of continuous variables by extracting individual slope estimates and significance levels for the levels in the respective design variables.

We analysed if the abundance of birds in each feeding groups (invertebrate-feeders, seed-eaters, omnivores and invertebrate-feeders switching to berries in autumn) were affected by farming practice separately using generalised linear mixed models as above, assuming an overdispersed Poisson error distributions. In addition, to analyse whether bird abundance in different feeding groups differed statistically significantly from each other and between farming practices, we combined all feeding groups in one joint analysis, including feeding group identity, season, farming practice, and PCA variables as fixed terms, and the offset described above to control for seasonal differences in the study effort. We additionally included pair, farm identity and the interaction between farm identity and feeding group as random intercept-terms in the joint model. We included only the significant interactions from the individual feeding group analyses presented above to reduce model complexity. The significance of each factor was tested with likelihood ratio tests. All statistical analyses were done using R 3.2.3 (R Core Team, 2018).

1.2.4.2. High and low organic squares

We analysed bird responses to increasing proportions of organic land by comparing study squares containing the highest and lowest possible percentage of organic land on each organic farm (ranging from 2 to 72%). We defined bird species richness and abundances following the same procedure as in the organic versus conventional square design. We created the same linear mixed effects model for number of species and generalised linear mixed effects model for abundance as above, except for replacing the fixed factor farming practice (organic versus conventional) with the level of organic land in the study square (i.e. high versus low). We finally specified models for independent and joint analyses of bird abundance belonging to the four feeding groups as described above, but replacing the fixed factor organic versus conventional with the fixed factor low versus high proportions of organic land in the study squares.

1.3 RESULTS

1.3.1 Effects of organic versus conventional farming

In total, we found 84 bird species and 9,359 individuals in conventional squares and 75 species and 8,542 individuals in the matching organic study squares (Table 1; Appendix B).

Table 1: Mean species richness and abundance per transect for organic and conventional squares, and for organic squares with high and low proportion of organic land, separately for each season. Standard deviation is given in parentheses.

Organic vs conventional					
		Spring	Summer	Autumn	Winter
Species richness	Conv	29.31 (2.94)	29.44 (4.21)	23.88 (3.79)	15.75 (3.57)
	Org	28.81 (3.10)	27.06 (3.39)	22.00 (3.12)	18.31 (2.98)
Abundance	Conv	147.69 (37.18)	180.50 (54.81)	180.75 (92.94)	76.00 (49.12)
	Org	135.12 (37.71)	148.44 (37.90)	177.12 (80.11)	77.25 (29.67)
High vs. low proportions of organic farming					
Species richness	High	28.81 (2.71)	28.19 (3.23)	20.94 (4.34)	19.06 (4.14)
	Low	29.19 (3.06)	26.38 (3.56)	21.50 (4.18)	17.38 (3.10)
Abundance	High	136.56 (38.30)	193.75 (71.86)	166.37 (65.99)	90.06 (29.42)
	Low	130.69 (36.12)	149.56 (45.97)	172.00 (93.40)	66.81 (23.38)

Species richness increased with increasing proportions of agricultural land in the study squares (Table 2A). Species richness was also affected by an interaction between the season and farming practice, being higher in organic than conventional farms in winter (contrast, $F_{1,12} = 10.93$, $P = 0.0063$; Table 1; Fig. 1).

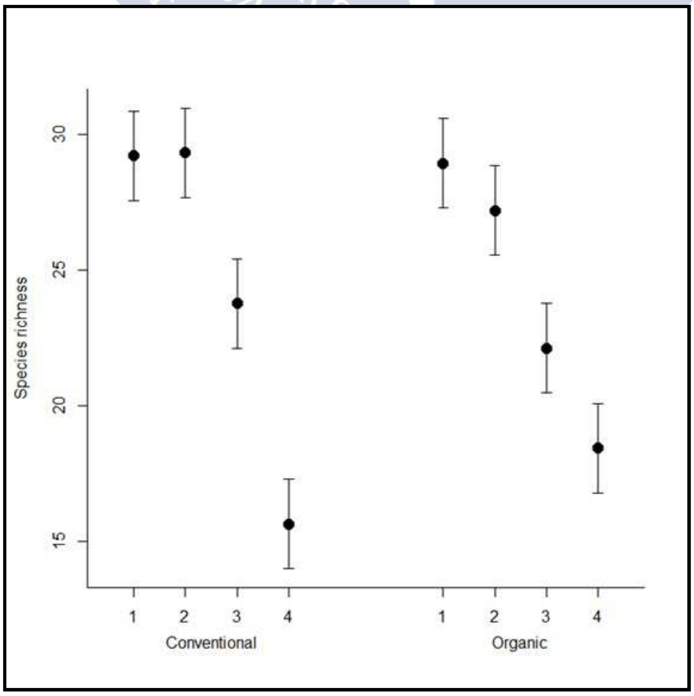

Fig. 1. Bird species richness during each season: spring (1), summer (2), autumn (3) and winter (4), for conventional and organic squares. Mean and standard error for data pooled over visits shown.

As expected, bird abundance was significantly related to the season, being higher in summer and autumn compared to spring and winter (Table 2A). Lastly, bird abundance was significantly affected by the interaction between the composition of forest (PC3) and farming practice (Table 2A). Based on individually extracted slopes, the interaction was explained by increasing bird abundance in organic squares with increasing amounts of native forest (z = 2.08, P = 0.0372), whereas bird abundance did not significantly change with forest composition in conventional study squares (z = -1.72, P = 0.0857; Fig. 2A).

When analysing feeding guilds separately, only the abundance of seedeaters and omnivores were significantly related to an interaction involving farming practice. The abundance of seedeaters was significantly related to an interaction between farming practice and the composition of forest (PC3; Table 2A), being the net effect of PC3 marginally positive in organic study squares (z = 1.87, P = 0.0621), and marginally negative in conventional squares (z = -1.65, P = 0.0987) (Fig. 2B). In addition, the abundance of seedeaters significantly decreased with an increasing percentage of shrubs (PC2; Table 2A). Omnivore abundance was also related to an interaction between farming practice and the composition of forest (PC3; Table 2A), with a significantly positive net effect of PC3 in organic study squares, (z = 2.09, P = 0.0366) and a marginally non-significant negative net effect in conventional study squares (z = -1.76, P = 0.0781). The abundances of invertebrate-feeders, omnivores and invertebrate-berry eaters all significantly differed between seasons (Table 2A), with lower abundances in spring and winter for invertebrate-feeders and omnivores, and in summer and winter for invertebrate-berry eaters.

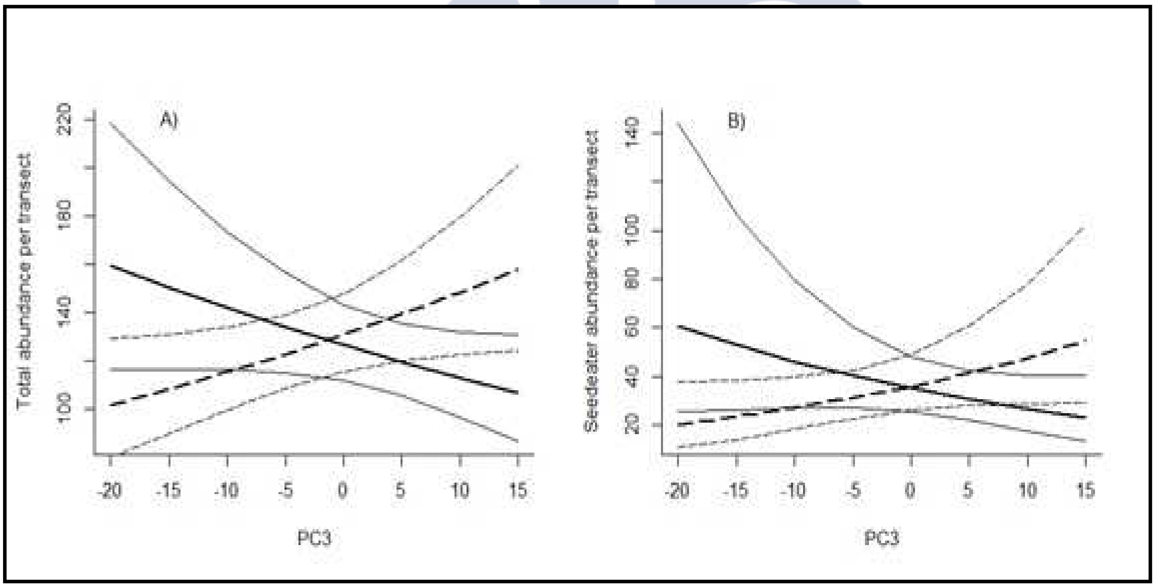

Fig. 2. Total abundance observed per transect with confidence intervals for all species (A) and seedeaters (B) in relation to PC3 (composition of forest) for organic squares (dashed lines), and conventional squares (solid lines). Increasing values of PC3 indicates decreasing proportions of exotic plantations and increasing proportions of native deciduous forest.

However, a joint analysis combining all feeding guilds showed that only the effect of season was significantly different between the feeding guilds (χ^2_9 = 29.01, P = 0.0006), as the relative abundance in spring was higher for invertebrate-berry eaters compared to the other feeding guilds. Thus, although the separate analyses for each feeding guild suggested different effects of landscape or farming effects on birds belonging to a different feeding guild, these differences were not significantly different between feeding guilds.

1.3.2 Effects of increasing proportions of organic land

A total of 78 species and 9,699 individuals were found on study squares with high proportion of organic land, in contrast to the 77 species and 8,293 individuals, in squares with low proportion of organic land (Table 1; Appendix C).

Species richness was not significantly related to the proportion of organic land (Table 2B), but was significantly related to season, with highest species richness in spring and lowest in winter (Table 1). In addition, species richness increased with increasing amounts of agricultural land (PC1; Table 2B).

When the proportion of agricultural land was low, bird abundance tended to increase with the proportion of land that was organic (Table 2B). Abundance was also related to the interaction between the amount of agricultural land (PC1) and season, which was most likely due to disproportionately high summer abundances in study squares with low compared to high proportions of agricultural land, where abundances were equally high across all seasons.

For seed-eaters, the interaction between the amount of agricultural land (PC1) and the proportion of organic land was significantly affected by abundance (Fig. 3, Table 2B), with significant increases in abundance with increasing agricultural land in study squares with low proportion of organic land (z = 3.63, P = 0.0003), but no relationship in study squares with high proportion of organic land (z = -0.29, P = 0.772). For invertebrate feeders, the interaction between PC1 and proportion of organic land was marginally non-significantly related to abundance (Table 2B). Abundance increased with increasing agricultural land in study squares with low proportion of organic land (z = 2.54, P = 0.0111), whereas it did not so in squares with high proportion of organic land (z = 0.45, P = 0.655). Furthermore, omnivore abundance also increased as the amount of agricultural land (PC1) increased (Table 2B). Finally, the abundance of invertebrate-berry eaters increased as the amount of agricultural land (PC1) increased (Table 2B). These analyses were partially supported by a joint analysis, in which the three-way interaction between food class, amount of agricultural land (PC1) and proportion of organic land marginally significantly influenced bird abundances (χ^2_3 = 7.84, P = 0.049). Seed-eater abundances increased with increasing amount of agricultural land in study squares with low proportion of organic land, whereas no such effects were evident for the other feeding groups or in study squares with high proportions of organic land.

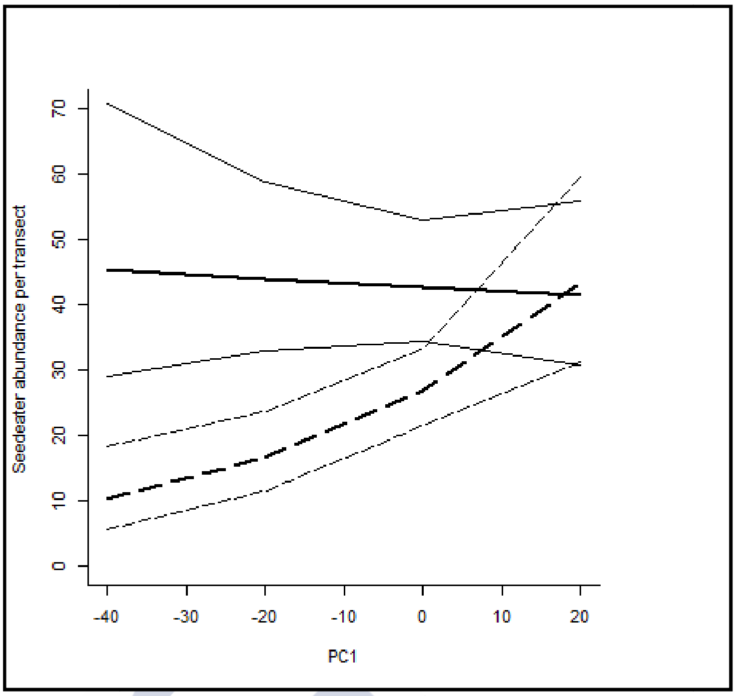

Fig. 3. Abundance of seed eating bird species ± 95% confidence intervals in relation to the amount of surrounding agricultural land (PC1) in squares with low (dashed lines) and high (solid lines) proportion of organic land. Increasing values of PC1 indicates increasing proportions of total agricultural land in the study squares.

1.4 DISCUSSION

In our study, organic farming affected species richness and abundance of birds but its effects varied between seasons, and were modified by the amount of agricultural land and the composition of forests in the landscapes. Whereas organic farming benefited species richness compared to conventional farming in some contexts, only bird abundance was affected by increasing proportions of organic farming. The paucity of direct effects of organic farming was most likely because of the highly heterogeneous landscapes in our study area, which may make the marginal effects of organic farming on birds smaller compared to what is the case in more homogeneous landscapes dominated by intensive agriculture (Geiger *et al*., 2010; Smith *et al.*, 2010; Concepción *et al.*, 2012). In particular, we found the highest effect of organic farming on bird species richness in winter, whereas the highest effect of organic farming on bird abundance was found in heterogeneous landscapes with organic fields embedded within patches of native deciduous forest. In contrast, in areas with large patches of open landscape, the effect of organic farming was lowest. Our results suggest that organic farming may benefit farmland birds in heterogeneous farmland mosaics by promoting complementary resources under specific seasonal and landscape contexts, as it has been observed before (Chamberlain *et al.*, 2010; Gabriel *et al.*, 2010).

When comparing organic and conventional squares, bird abundance in organic farms increased with increasing proportions of native deciduous forests and decreasing proportions of exotic plantations. In contrast, bird abundance did not respond to forest composition in conventional farms. Separate analyses suggest that this effect was mainly driven by seedeaters and omnivores, the latter all belonging to the family

Corvidae which has earlier been shown to benefit from organic farming (Birkhofer *et al.*, 2014). Organic farming may benefit seedeaters and omnivores given a high share of native forests, if the combination offers complementary resources for foraging and roosting (cf. Smith *et al*., 2014). Exotic plantations are known to be poor habitats for these birds in the North of the Iberian Peninsula (Proença *et al.*, 2010; Calviño-Cancela, 2013). Although our results suggest that mosaic landscapes consisting of organic lands and native forest could enhance bird numbers, we also note that high corvid abundances may have negative effects on some other farmland birds in the breeding season because of nest predation (Gabriel *et al.*, 2010; but see Madden *et al*., 2015).

In addition, we found higher bird species richness in organic farms in winter compared to conventional farms. Some other studies have also observed a higher species richness in winter in organic than conventional farms (Chamberlain *et al.*, 2010; Geiger *et al.*, 2010), but not in complex landscapes, similar to the ones studied here. Our results could partly be due to organic farms using grasslands for grazing during winter, whereas some conventional farms in our data (6 out of 16) ploughed the land every year after harvesting maize in late summer. As ploughing drastically reduces long-term food supply for farmland birds (Wilson *et al.*, 1996), a higher number of plant seeds would be accessible for farmland birds in organic farms in winter. Although long crop rotation is not a requisite of organic farming in the study region (CRAEGA, 2014), it is much more common for organic grasslands than for conventional, and our results suggest that long rotations can have an important benefit on the biodiversity of birds. The availability of food resources in winter may be a key limiting factor for seed-eating species, and high-quality foraging habitats may be more important for birds in winter than the farming type *per se* (Chamberlain *et al.*, 2010). However, the benefits of organic farming to bird species richness in winter could also partly relate to mixed farming, which has been previously shown to benefit farmland birds (Hole *et al.*, 2005). Whatever the cause, our results show that organic farming has the potential to benefit farmland bird conservation by restoring high-quality winter habitat conditions in Southern Europe, which may be particularly important in key wintering grounds such as the Iberian Peninsula. Therefore, organic farming may be beneficial for both northern migrants and southern resident bird species in important Mediterranean wintering areas and, thus, could play a more important role in overall bird conservation than expected.

Whereas bird species richness did not increase with increasing proportions of organic farming (measured as ‘low’ and ‘high’ levels of organic land within a pair of study sites with organic land), bird abundance increased with increasing amounts of organic land. However, this effect was modulated by the proportion of agricultural land, such that high proportions of organic farming increased bird abundance when the proportions of agricultural land were low. This interactive effect was significantly stronger in seedeaters, which may accumulate in food-rich organic fields when the proportion of non-crop habitats is high, offering habitats used for predator avoidance or shelter (Robinson & Sutherland, 1999). Concentration effects in farmland have been suggested to take place mainly in structurally simple landscapes, where mobile organisms may aggregate in a single resource-rich patch (Kleijn *et al.*, 2011). In our study, abundance was high in big patches of agricultural land regardless of whether agricultural practices to a higher or lower extent consisted of organic farming. Our results suggest that big patches of agriculture benefit farmland birds in heterogeneous landscapes characterized by small individual fields, as has been previously shown (Fahrig *et al.*, 2011; Salaverri, 2015).

Notably, the number of bird species increased as the proportion of agricultural land in each study square increased, independently of management contrast (i.e. organic vs. conventional farming, or ‘low’ vs. ‘high’ proportions of organic land). Our results agree with other studies in heterogeneous landscapes of Mediterranean countries (Zakkak *et al.*, 2014; Salaverri, 2015) and elsewhere (Vepsäläinen *et al*., 2010), showing increasing species richness of birds with increasing patch size of open land (but see Concepción & Díaz, 2011). As individual fields were rarely larger than 15 ha in our study area, larger patches of open agricultural lands can benefit a broad suit of bird species by providing larger feeding areas in combination with sufficient amounts of non-crop areas to provide complementary resources (Smith *et al*., 2014). Therefore, maintaining open agricultural lands can help maintaining high bird species richness in heterogeneous landscapes, although whether large, organically managed open farmland could be more beneficial than agricultural lands in general for bird species richness remains an open question.

Finally, when comparing organic and conventional farming, total bird abundance decreased as the proportion of shrub area increased. This effect was also observed in three out of the four studied bird food guilds (invertebrate feeders, seed-eaters and invertebrate feeders changing to berries in autumn). In our study area, shrubs develop quickly after farmland abandonment (Corbelle-Rico *et al*., 2012), and consist mainly of species belonging to the genera *Ulex* and *Cytisus* which often form very think and dense vegetation. Similar negative effects of shrub encroachment on bird diversity and abundance have been observed in other studies in heterogeneous landscapes (Suárez-Seoane *et* al., 2002; Zakkak *et al.*, 2014; Salaverri, 2015), in contrast to cropland-dominated landscapes, where shrubs may benefit biodiversity (Concepción and Díaz, 2011). Land abandonment in economically marginal areas is a major threat to European farmland biodiversity, which to some extent has been driven by former CAP policies throughout Europe (Donald *et al.*, 2002; Corbelle-Rico *et al*., 2012). In our study area, 74% of the agricultural land of the area was abandoned during the past 30 years (IGE, 2012), because of non-favourable rural development. However, during the last 18 years, organic farming has increased markedly in our study area (CRAEGA, 2015), and in our study, 14 out of the 16 organic farmers converted to organic farming mainly because it was the only economically viable option given current incentives favouring organic farming. In this context, future research may reveal whether agri-environment schemes such as organic farming or High Nature Value farming incentives within the Common Agricultural Policy can counteract farmland abandonment in structurally heterogeneous landscapes and thus protect remaining biodiversity-rich habitats on marginal land.

1.5 CONCLUSIONS

Organic farming has the potential to benefit bird species richness and abundance in heterogeneous farmland, especially as it comes to seed-eating species, but such beneficial effects depend on landscape context. According to our study, the combination of organic farming and forests consisting of native deciduous tree species benefits farmland birds. Bird abundance increases with increasing proportions of agricultural land in mosaic landscapes given the presence of organic farming, a relatively low proportion of agricultural land (less than 64% of the total area) and small field size (less than 5ha on average). Organic farming is based on restricted use of synthetic fertilizers and pesticides, but to manage without these many other aspects of the farming systems differ. Future research needs to establish what aspects of organic farming (arable or mixed farming, long rotations, use of composted manure, etc.) contribute to positive biodiversity effects and if some of these can be implemented in conventional farming.

Our study also suggests that larger areas of organic farming have the potential to benefit farmland birds in very heterogeneous areas, with low proportions of agricultural land, probably by providing resource-rich patches embedded within resource-poor areas, and therefore, concentrate some bird species, such as seedeaters, which may benefit from high food availability in organic farms.

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Table 2: Total species richness and abundances (total and for each feeding guild) in relation to season, farm type (A) or level of organic (B) and land-use descriptors (PC1, PC2, PC3) analysed using general linear mixed-effects models with F-tests (species richness) or generalized linear mixed models with LR-tests (abundances). PC1 was a measure of land openness, PC2 a measure of land abandonment and PC3 a measure of composition of forest in each studied square. Significant and marginally non- significant values in bold. Sign of effects for continuous variables shown as (+) or (-).

A) Organic vs. conventional squares								
Terms	**Total Species Richness**		**Total Abundance**					
Season	**$F_{3,90} = 61.07$**	**P < 0.0001**	**$\chi^2_3 = 8.32$**	**P = 0.0399**				
Farm type	$F_{1,12} = 0.05$	P = 0.8269	$\chi^2_1 = 4.38$	P = 0.112				
PC1	**$F_{1,12} = 11.35$ (+)**	**P = 0.0056**	$\chi^2_1 = 2.002$	P = 0.1571				
PC2	$F_{1,12} = 0.02$	P = 0.8868	**$\chi^2_1 = 7.04$ (–)**	**P = 0.0079**				
PC3	$F_{1,12} = 0.21$	P = 0.6550	$\chi^2_1 = 4.35$	P = 0.1134				
Season × Farm type	**$F_{3,90} = 3.62$**	**P = 0.016**						
Farm type × PC3			**$\chi^2_1 = 4.32$**	**P = 0.0377**				
	Invertebrate eaters		**Seedeaters**		**Omnivores**		**Invertebrate berry-eaters**	
Season	**$\chi^2_3 = 20.67$**	**P < 0.0001**	$\chi^2_3 = 2.86$	P = 0.4128	**$\chi^2_3 = 26.68$**	**P < 0.0001**	**$\chi^2_3 = 8.34$**	**P = 0.0395**
Farm type	$\chi^2_1 = 0.43$	P = 0.5129	$\chi^2_1 = 3.81$	P = 0.149	**$\chi^2_1 = 5.97$**	**P = 0.0504**	$\chi^2_1 = 1.48$	P = 0.2233
PC1	$\chi^2_1 = 1.41$	P = 0.235	$\chi^2_1 = 0.502$	P = 0.4783	$\chi^2_1 = 2.51$	P = 0.1132	**$\chi^2_1 = 8.74$ (+)**	**P = 0.0031**
PC2	**$\chi^2_1 = 3.38$ (–)**	**P = 0.0658**	**$\chi^2_1 = 4.66$ (–)**	**P = 0.0309**	$\chi^2_1 = 2.601$	P = 0.1068	**$\chi^2_1 = 4.99$ (–)**	**P = 0.0254**
PC3	$\chi^2_1 = 0.01$	P = 0.9273	$\chi^2_1 = 3.85$	P = 0.1456	**$\chi^2_1 = 5.48$ (–)**	**P = 0.0645**	$\chi^2_1 = 0.11$	P = 0.741
Farm type × PC3	$\chi^2_1 = 0.04$	P = 0.8424	**$\chi^2_1 = 4.38$**	**P = 0.0363**	**$\chi^2_1 = 5.38$**	**P = 0.0203**	$\chi^2_1 = 0.18$	P = 0.6733
B) High-low org squares								
Terms	**Total Species Richness**		**Total Abundance**					
Season	**$F_{3,93} = 83.62$**	**P < 0.0001**	**$\chi^2_3 = 19.22$**	**P = 0.0038**				
Level organic	$F_{1,12} = 1.25$	P = 0.2846	**$\chi^2_1 = 8.52$**	**P = 0.0141**				
PC1	**$F_{1,12} = 9.83$ (+)**	**P = 0.0086**	**$\chi^2_1 = 22.97$ (+)**	**P = 0.0003**				

PC2	$F_{1,12} = 0.01$	P = 0.9328	$\chi^2_1 = 0.63$	P = 0.4272				
PC3	$F_{1,12} = 0.46$	P = 0.5113	$\chi^2_1 = 0.14$	P = 0.7048				
Season × PC1			**$\chi^2_3 = 8.61$**	**P = 0.035**				
PC1 × Level organic			**$\chi^2_1 = 3.78$**	**P = 0.052**				
	Invertebrate eaters		**Seedeaters**		**Omnivores**		**Invertebrate berry-eaters**	
Season	**$\chi^2_3 = 22.15$**	**P < 0.0001**	$\chi^2_3 = 4.73$	P = 0.1929	**$\chi^2_3 = 52.85$**	**P < 0.0001**	$\chi^2_3 = 1.44$	P = 0.6971
Level organic	$\chi^2_1 = 0.81$	P = 0.3667	**$\chi^2_1 = 11.65$**	**P = 0.0011**	$\chi^2_1 = 2.55$	P = 0.1104	$\chi^2_1 = 1.25$	P = 0.2627
PC1	$\chi^2_1 = 2.54$	P = 0.1112	**$\chi^2_1 = 11.08$ (+)**	**P = 0.0039**	**$\chi^2_1 = 4.67$ (+)**	**P = 0.0375**	**$\chi^2_1 = 8.13$ (+)**	**P = 0.0043**
PC2	**$\chi^2_1 = 4.37$ (–)**	**P = 0.0365**	$\chi^2_1 = 0.35$	P = 0.5557	$\chi^2_1 = 0.43$	P = 0.5591	$\chi^2_1 = 0.79$	P = 0.3742
PC3	$\chi^2_1 = 0.07$	P = 0.7908	$\chi^2_1 = 2.82$	P = 0.0929	$\chi^2_1 = 0.21$	P = 0.6494	$\chi^2_1 = 0.13$	P = 0.7158
PC1 × Level organic	**$\chi^2_1 = 3.44$**	**P = 0.0633**	**$\chi^2_1 = 7.96$**	**P = 0.0048**	$\chi^2_1 = 0.47$	P = 0.4906	$\chi^2_1 = 0.43$	P = 0.2312

1.7. APPENDICES

APPENDIX A

Data on studied farms, showing their identity (FarmID), pair number (Pair), Total area (in Ha), time since organic (Org. time, in years, until year of study), type of crop (Crop), crop on rotations (Rot), rotation time (Rot. time: annual (A), permanent (P) or number of years), type of use of fields (Type: arable or mixed arable and animal husbandry), number of transect (Trans.), level of organic (Level org: high, low or none), and percentage of organic land (P.org), agriculture (P.agr), native forest (P.for), exotic plantations (P.pla), shrub (P.shr) and urban areas (P.urb) in the studied square.

FarmID	Pair	Farmtype	Total area	Org. Time	Crop	Rot	Rot. Time	Type	Trans.	Level org	P. org	P. agr	P. for	P. pla	P. shr	P. urb
									1	low	7.13	70.76	13.17	5.35	1.9	1.64
Laxe	1	Org	12	11	Wheat	Rye	A	Arable	2	high	31.95	45.22	4.31	31.87	12.45	1.63
Vilapequena	1	Conv	9	NA	Wheat	Rye	A	Arable	1	none	0.00	25.36	15.39	0.78	3.79	0.66
									1	low	24.01	36.64	32.26	0.00	24.24	0.00
Cernada	2	Org	50	13	Pasture	Maize	5	Mixed	2	high	41.36	45.87	14.65	5.98	18.25	4.57
Bouzachás	2	Conv	40	NA	Pasture	Maize	3	Arable	1	none	0.00	57.78	8.89	3.36	13.5	0.00
									1	low	72.21	91.13	4.9	3.19	0.00	7.51
Burgo	3	Org	33	12	Pasture	Pasture	P	Mixed	2	high	45.67	80.79	12.5	2.07	0.00	0.74
Vilamaior	3	Conv	14	NA	Pasture	Pasture	2	Arable	1	none	0.00	70.43	12.95	12.17	0.00	0.06
									1	low	9.69	64.34	15.76	11.64	6.77	0.94
Arqueixal	4	Org	30	13	Pasture	Pasture	7	Mixed	2	high	31.58	76.21	6.99	6.64	1.69	3.53
Ulloa	4	Conv	15	NA	Pasture	Maize	A	Arable	1	none	0.00	61.02	35.72	5.69	5.00	0.82
									1	low	29.44	63.17	22.11	5.37	0.00	5.37
Friol	5	Org	45	12	Pasture	Maize	5	Mixed	2	high	31.73	44.31	23.01	24.26	0.99	1.69
Ferreira	5	Conv	25.4	NA	Pasture	Pasture	1	Arable	1	none	0.00	63.35	28.37	0.00	2.64	0.17
									1	high	41.23	63.84	20.5	1.77	2.00	4.46
Maruxa	6	Org	22	9	Pasture	Pasture	5	Mixed	2	low	27.23	54.34	5.00	16.77	5.92	1.43
Outeiro	6	Conv	27	NA	Pasture	Pasture	3	Arable	1	none	0.00	57.36	25.00	12.93	0.00	0.94
									1	low	17.02	72.65	15.3	0.00	0.00	4.48
Vilance	7	Org	20	11	Pasture	Pasture	5	Mixed	2	high	19.46	70.01	18.38	0.00	0.00	4.11

Peibás	7	Conv	40	NA	Pasture	Maize	1	Arable	1	none	0.00	79.15	9.21	11.95	0.00	3.02
									1	high	48.99	53.75	3.38	19.65	17.08	0.11
Chotoiba	8	Org	45	14	Pasture	Pasture	P	Mixed	2	low	46.39	68.17	7.84	11.39	4.12	1.23
Soengas	8	Conv	40	NA	Pasture	Maize	A	Mixed	1	none	0.00	69.99	14.97	4.33	6.04	0.00
									1	high	39.86	70.00	19.16	0.00	2.64	4.15
Pasión	9	Org	32	13	Pasture	Pasture	P	Mixed	2	low	9.87	64.03	10.41	6.42	16.00	1.66
Gulfar	9	Conv	9	NA	Pasture	Pasture	P	Mixed	1	none	0.00	77.19	4.74	0.00	13.74	0.00
									1	low	12.81	84.66	2.99	1.05	3.98	3.14
Olveda	10	Org	13	1	Pasture	Pasture	4	Mixed	2	high	34.37	70.00	20.62	0.00	6.32	0.00
Artelac	10	Conv	20	NA	Pasture	Maize	3	Arable	1	none	0.00	72.94	19.65	6.88	3.28	0.00
									1	low	2.32	53.44	20.03	4.42	16.59	0.2
Güimil	11	Org	7	11	Pasture	Pasture	5	Mixed	2	high	16.04	63.7	20.68	2.41	6.45	0.00
Chorente	11	Conv	13	NA	Pasture	Pasture	3	Arable	1	none	0.00	49.8	24.41	7.11	7.42	0.5
									1	low	9.04	67.84	20.32	0.00	59.11	2.51
Rodeiro	12	Org	33	8	Pasture	Pasture	5	Mixed	2	high	9.79	51.24	20.73	0.00	25.12	0.00
Barbeitos	12	Conv	25	NA	Pasture	Pasture	5	Arable	1	none	0.00	60.68	7.86	2.14	23.52	0.37
									1	low	9.65	70.00	11.15	0.00	5.12	10.59
Sabadelle	13	Org	20	13	Pasture	Pasture	P	Arable	2	high	24.89	73.14	7.64	0.00	0.00	6.04
Lois	13	Conv		NA	Pasture			Arable	1	none	0.00	79.28	11.09	1.63	0.00	0.95
									1	low	4.73	86.18	10.00	0.00	0.00	1.15
Antonio	14	Org	30	11	Pasture	Maize	5	Mixed	2	high	10.3	87.4	7.39	0.00	0.00	5.21
Lalín	14	Conv		NA	Pasture	Maize	A	Arable	1	none	0.00	61.94	19.14	0.74	0.00	11.91
									1	low	1.18	55.27	0.00	1.35	37.69	0.00
Trigo	15	Org	19	14	Wheat	Rye	A	Arable	2	high	19.01	29.45	0.00	0.86	62.14	0.00
Val	15	Conv		NA	Wheat	Rye	A	Arable	1	none	0.00	86.11	3.68	4.3	0.00	5.91
									1	low	3.65	36.34	7.96	20.83	11.78	12.3
Milhulloa	16	Org	9.2	15	Pasture	Pasture	5	Mixed	2	high	24.91	37.47	4.13	34.85	14.09	5.95
Mariñao	16	Conv	8	NA	Pasture	Pasture	A	Arable	1	none	0.00	47.29	26.29	5.64	3.62	9.77

APPENDIX B

List of species and their abundances observed during each season and total in one organic (Org) and its matched conventional (Conv) square. Represented are also the food preferences for each species (0 _ vertebrate-feeders, 1 _ invertebrate-feeders, 2 _ seedeaters, 3 _ grazers, 4 _ omnivores, 5 _ invertebrate-feeders switching to berries in autumn).

		Spring		**Summer**		**Autumn**		**Winter**		**Total Abundance**	
Species	**Food class**	**Org**	**Conv**	**Org**	**Conv**	**Org**	**Conv**	**Org**	**Conv**	**Org**	**Conv**
Accipiter gentilis	0	0	1	1	0	0	0	0	0	1	1
Accipiter nisus	0	0	0	1	1	1	1	0	0	2	2
Aegithalos caudatus	1	66	45	46	77	120	118	6	17	238	257
Alauda arvensis	2	6	46	12	22	7	146	1	28	26	242
Alectoris rufa	2	1	1	0	13	0	0	0	0	1	14
Anas platyrhynchos	3	0	0	0	0	0	1	0	0	0	1
Anthus pratensis	1	0	0	10	14	97	223	11	89	118	326
Anthus trivialis	1	14	16	15	27	0	0	1	0	30	43
Apus apus	1	26	36	22	14	0	0	3	0	51	50
Ardea cinerea	0	0	0	0	0	1	2	1	1	2	3
Buteo buteo	0	10	12	12	12	13	19	8	5	43	48
Carduelis cannabina	2	47	72	135	164	37	35	11	12	230	283
Carduelis carduelis	2	0	13	0	13	16	43	0	7	16	76
Carduelis chloris	2	94	104	44	64	61	55	24	86	223	309
Certhia brachydactyla	1	4	4	0	2	2	1	4	2	10	9
Ciconia ciconia	0	1	3	0	1	0	0	2	0	3	4
Circus cyaneus	0	0	0	0	1	0	0	0	0	0	1
Circus pygargus	0	0	4	0	0	0	0	0	0	0	4
Cisticola juncidis	1	7	1	2	0	0	0	0	0	9	1
Columba livia	2	0	21	10	107	0	97	0	101	10	326
Columba palumbus	2	84	64	114	87	63	58	20	6	281	215
Corvus corax	4	0	0	2	0	4	0	1	1	7	1
Corvus corone	4	127	190	178	223	214	159	86	84	605	656
Coturnix coturnix	2	1	11	0	2	0	0	2	0	3	13
Cuculus canorus	1	20	19	2	0	0	0	0	0	22	19
Cyanistes caeruleus	1	89	62	119	121	60	54	40	25	308	262
Delichon urbicum	1	3	2	9	5	0	3	0	2	12	12
Dendrocopus major	1	1	2	7	7	9	4	2	1	19	14
Emberiza calandra	2	5	14	0	10	0	0	0	1	5	25
Emberiza cia	2	0	2	0	3	0	0	12	0	12	5
Emberiza cirlus	2	50	45	52	49	38	67	26	22	166	183
Emberiza citrinella	2	0	7	0	3	0	0	0	0	0	10
Erithacus rubecula	1	94	97	211	224	210	179	111	89	626	589
Falco tinnunculus	0	0	0	17	12	0	0	0	0	17	12
Ficedula hypoleuca	1	0	0	23	40	0	0	0	0	23	40
Fringilla coelebs	2	131	156	62	53	193	490	169	135	555	834
Fringilla montifringilla	2	0	0	0	0	123	17	6	2	129	19
Gallinago gallinago	1	0	0	0	0	0	10	0	0	0	10
Garrulus glandarius	4	26	14	52	59	70	72	22	8	170	153

Hieraaetus pennatus	0	0	1	0	1	0	0	0	0	0	2
Hippolais polyglotta	1	22	9	10	4	0	0	1	0	33	13
Hirundo rustica	1	50	17	29	45	0	0	7	0	86	62
Lanius collurio	0	2	5	0	1	0	0	0	0	2	6
Lanius meridionalis	0	0	0	0	0	0	1	0	0	0	1
Lophophanes cristatus	1	0	10	1	2	5	4	0	0	6	16
Lullula arborea	2	3	4	15	22	8	3	8	8	34	37
Luscinia megarhynchos	5	2	4	0	0	0	0	0	0	2	4
Milvus migrans	0	0	3	1	2	0	0	1	0	2	5
Milvus milvus	0	0	6	0	5	0	8	0	3	0	22
Motacilla alba	1	12	13	46	21	108	60	16	11	182	105
Motacilla cinerea	1	0	1	0	0	4	2	1	0	5	3
Motacilla flava	1	0	0	8	28	0	0	0	0	8	28
Muscicapa striata	1	0	0	1	0	0	1	0	0	1	1
Oriolus oriolus	5	11	10	6	2	0	0	0	0	17	12
Parus major	1	33	25	36	24	37	26	29	25	135	100
Passer domesticus	2	140	141	164	282	133	106	156	67	593	596
Passer montanus	2	0	0	0	0	0	0	4	0	4	0
Periparus ater	1	19	2	38	59	99	73	42	36	198	170
Phalacrocorax carbo	0	0	0	0	0	1	0	0	1	1	1
Phoenicurus ochrurus	1	1	14	6	8	3	9	0	8	10	39
Phylloscopus collybita	1	7	0	0	0	1	1	10	4	18	5
Phylloscopus ibericus	1	54	68	24	30	14	10	3	0	95	108
Pica pica	4	17	10	33	23	30	17	11	10	91	60
Picus viridis	1	22	22	17	19	16	8	12	6	67	55
Prunella modularis	1	23	30	27	33	41	40	12	24	103	127
Pyrrhula pyrrhula	2	3	7	6	21	7	4	3	1	19	33
Regulus ignicapillus	1	44	28	62	46	26	37	15	3	147	114
Saxicola torquata	1	34	55	74	54	14	22	7	14	129	145
Serinus serinus	2	83	114	84	153	21	6	21	12	209	285
Sitta europaea	1	0	3	7	18	12	29	1	6	20	56
Streptopelia decaocto	2	0	0	0	0	0	1	0	0	0	1
Streptopelia turtur	2	44	26	32	29	0	0	2	0	78	55
Strix aluco	0	1	1	0	0	0	0	2	0	3	1
Sturnus unicolor	5	192	282	179	221	574	214	78	120	1023	837
Sturnus vulgaris	5	0	0	0	0	15	2	10	0	25	2
Sylvia atricapilla	5	68	60	56	39	1	1	13	0	138	100
Sylvia communis	5	5	5	1	1	0	0	1	0	7	6
Sylvia melanocephala	5	0	0	0	0	0	1	0	0	0	1
Sylvia undata	5	1	9	3	17	2	21	0	9	6	56
Troglodythes troglodythes	1	87	84	92	74	107	87	84	53	370	298
Turdus iliacus	5	0	0	0	0	0	26	6	0	6	26
Turdus merula	5	145	161	119	127	163	141	68	36	495	465
Turdus philomelos	5	38	44	14	14	4	9	18	14	74	81
Turdus viscivorus	5	20	15	21	33	49	68	25	21	115	137
Upupa epops	1	7	10	5	0	0	0	0	0	12	10

APPENDIX C

List of species and their abundances observed during each season and total in both organic with high proportion of organic land (High) and squares with low proportion of organic land (Low). Represented are also the food preferences for each species (0 _ vertebrate-feeders, 1 _ invertebrate-feeders, 2 _ seedeaters, 3 _ grazers, 4 _ omnivores, 5 _ invertebrate-feeders switching to berries in autumn).

		Spring		**Summer**		**Autumn**		**Winter**		**Total Abundance**	
Species	**Food class**	**High**	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**	**High**	**Low**
Accipiter gentilis	0	0	0	2	1	0	0	0	0	2	1
Accipiter nisus	0	0	1	1	2	2	1	1	0	4	4
Aegithalos caudatus	1	43	70	36	46	82	119	18	6	179	241
Alauda arvensis	2	22	13	16	17	32	19	7	3	77	52
Alectoris rufa	2	1	3	2	0	7	5	0	1	10	9
Anas platyrhynchos	3	0	0	0	0	1	0	0	0	1	0
Anthus pratensis	1	0	0	0	10	147	135	21	36	168	181
Anthus trivialis	1	13	19	5	16	1	0	0	1	19	36
Apus apus	1	32	35	14	11	2	0	0	3	48	49
Ardea cinerea	0	0	0	0	0	0	1	2	0	2	1
Buteo buteo	0	9	8	16	13	13	12	5	8	43	41
Carduelis cannabina	2	55	45	285	155	75	59	64	13	479	272
Carduelis carduelis	2	2	6	0	0	4	16	0	0	6	22
Carduelis chloris	2	115	103	33	47	88	49	59	13	295	212
Certhia brachydactyla	1	2	5	3	0	3	2	0	4	8	11
Ciconia ciconia	0	2	1	0	0	0	0	4	0	6	1
Circus cyaneus	0	0	0	0	0	0	0	0	0	0	0
Circus pygargus	0	0	2	0	1	0	0	1	0	1	3
Cisticola juncidis	1	7	0	2	2	0	0	0	0	9	2
Columba livia	2	7	0	48	71	0	0	0	0	55	71
Columba palumbus	2	99	58	133	98	171	92	68	11	471	259
Corvus corax	4	0	0	2	1	4	1	1	1	7	3
Corvus corone	4	122	126	201	179	220	232	112	81	655	618
Coturnix coturnix	2	2	5	0	2	0	0	0	2	2	9
Cuculus canorus	1	26	23	0	2	4	0	0	0	30	25
Cyanistes caeruleus	1	71	97	142	135	67	69	25	44	305	345
Delichon urbicum	1	3	0	11	0	0	0	0	0	14	0
Dendrocopus major	1	2	1	11	6	8	7	7	2	28	16
Emberiza calandra	2	19	16	0	0	0	0	0	0	19	16
Emberiza cia	2	2	4	2	2	0	0	11	1	15	7
Emberiza cirlus	2	40	52	54	66	57	41	30	21	181	180
Emberiza citrinella	2	3	3	0	3	0	0	0	0	3	6
Erithacus rubecula	1	116	99	257	188	244	211	106	99	723	597
Falco tinnunculus	0	0	0	20	4	0	0	0	0	20	4
Ficedula hypoleuca	1	0	0	29	17	0	0	0	0	29	17
Fringilla coelebs	2	124	114	50	36	209	172	138	117	521	439
Fringilla montifringilla	2	0	0	0	0	95	28	0	6	95	34
Gallinago gallinago	1	0	0	0	0	0	0	0	0	0	0
Garrulus glandarius	4	19	16	69	49	58	86	20	19	166	170

Hieraaetus pennatus	0	0	2	0	1	0	0	0	0	0	3
Hippolais polyglotta	1	22	14	3	9	0	0	0	1	25	24
Hirundo rustica	1	40	35	49	52	15	0	2	7	106	94
Lanius collurio	0	1	3	7	3	0	0	0	0	8	6
Lanius meridionalis	0	0	0	0	0	0	0	2	0	2	0
Lophophanes cristatus	1	5	0	5	1	4	3	0	0	14	4
Lullula arborea	2	5	3	10	14	7	10	9	12	31	39
Luscinia megarhynchos	5	2	1	0	0	0	0	0	0	2	1
Milvus migrans	0	0	2	1	0	0	0	0	1	1	3
Milvus milvus	0	0	0	0	0	1	0	0	0	1	0
Motacilla alba	1	16	11	46	33	74	98	17	12	153	154
Motacilla cinerea	1	0	0	0	0	2	2	1	0	3	2
Motacilla flava	1	0	0	0	8	0	0	0	0	0	8
Muscicapa striata	1	0	0	1	0	0	0	0	0	1	0
Oriolus oriolus	5	8	11	9	3	1	0	0	0	18	14
Parus major	1	30	35	33	27	42	33	40	29	145	124
Passer domesticus	2	116	152	232	136	199	90	149	93	696	471
Passer montanus	2	0	20	2	41	2	36	4	17	8	114
Periparus ater	1	22	19	43	34	116	103	30	25	211	181
Phalacrocorax carbo	0	0	0	0	0	0	1	0	0	0	1
Phoenicurus ochrurus	1	5	2	12	7	6	3	2	2	25	14
Phylloscopus collybita	1	0	7	0	0	2	1	15	7	17	15
Phylloscopus ibericus	1	62	49	12	26	16	15	1	3	91	93
Pica pica	4	25	14	43	22	55	29	22	11	145	76
Picus viridis	1	23	18	20	16	25	8	16	7	84	49
Prunella modularis	1	17	24	34	24	52	38	19	23	122	109
Pyrrhula pyrrhula	2	5	8	13	2	12	3	3	3	33	16
Regulus ignicapillus	1	28	50	53	63	28	27	10	22	119	162
Saxicola torquata	1	41	43	77	60	18	15	10	4	146	122
Serinus serinus	2	110	91	222	79	16	21	19	19	367	210
Sitta europaea	1	1	0	21	5	16	14	2	1	40	20
Streptopelia decaocto	2	0	0	1	0	0	0	0	0	1	0
Streptopelia turtur	2	46	42	11	42	1	0	1	2	59	86
Strix aluco	0	0	1	0	0	0	0	2	0	2	1
Sturnus unicolor	5	216	163	343	208	318	548	103	73	980	992
Sturnus vulgaris	5	0	0	0	0	0	15	35	0	35	15
Sylvia atricapilla	5	60	59	46	53	4	2	7	10	117	124
Sylvia communis	5	4	3	0	1	0	0	1	2	5	6
Sylvia melanocephala	5	0	0	0	0	0	1	0	0	0	1
Sylvia undata	5	3	2	19	4	10	2	6	0	38	8
Troglodythes troglodythes	1	93	82	104	97	114	101	79	81	390	361
Turdus iliacus	5	0	0	0	0	0	0	0	6	0	6
Turdus merula	5	177	137	164	103	155	136	81	72	577	448
Turdus philomelos	5	29	39	4	16	14	2	17	15	64	72
Turdus viscivorus	5	8	16	13	19	53	38	35	17	109	90
Upupa epops	1	8	3	4	0	0	1	0	5	12	9


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CHAPTER II:

Effects of organic farming on plant and butterfly functional diversity in mosaic landscapes


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2.1. INTRODUCTION

In much of Europe, agricultural intensification during more than half a century has resulted in widespread loss of farmland biodiversity (Donald *et al.*, 2001; Storkey et al., 2012). Organic farming is thought to be a way of counteracting these declines of farmland biodiversity, mainly because of less intensive agricultural practices including lack of use of synthetic fertilizers and pesticides and long and more varied crop rotations (Hole *et al.,* 2005). A multitude of studies have analysed the potential of organic farming to serve as a tool to enhance farmland biodiversity, with generally positive but highly variable effects on biodiversity (Tuck *et al*., 2014; Lichtenberg *et al*., 2017). This variability has to a large extent been attributed to variation in landscape structure, with most studies indicating that organic farming increases diversity of plants, invertebrates and birds in homogeneous but less so in heterogeneous landscapes (Roschewitz *et al*., 2005; Rundlöf & Smith, 2006; Rundlöf *et al.*, 2008b; Batáry *et al.*, 2010; Geiger *et al*., 2010).

Most studies that analysed the effect of organic farming on biodiversity have focused on species richness and abundance (Bengtsson *et al.*, 2005; Schneider *et al.*, 2014), and many studies also consider species richness and abundance of broad functional groups (Tuck *et al*., 2014; Lichtenberg *et al*., 2017). However, land-use changes may not only lead to species loss, but also to the loss of specific functional traits that play a role in ecosystem processes (Flynn *et al*., 2009). The diversity of traits in a community affecting the performance of individual species, i.e. functional diversity, is increasingly used as an indicator for ecosystem functioning (Diaz and Cabido 2001; Lavorel and Garnier, 2002; Cadotte *et al*., 2011). Functionally diverse communities may be more resilient to environmental change (Chillo *et al.*, 2011) and functional diversity has been shown to better relate to ecosystem functioning compared to taxonomic diversity (Gagic *et al.,* 2015). Understanding the effect of land-use change on functional diversity can therefore contribute to the overall understanding of the ecological mechanisms that drive biodiversity loss, and ultimately how these changes affect the ecosystem (Cadotte *et al*., 2011). However, only a few studies have explicitly analysed how functional rather than taxonomic diversity, or richness of functional groups, responds to organic farming (Rader *et al.,* 2014; Forrest *et al.*, 2015; also see Da Silva *et al.*, 2017). These studies suggest that components of plant functional diversity benefit from organic farming (Rader *et al.,* 2014), in contrast to insect functional diversity, which has rather suggested to benefit from the availability of non-crop habitats (Forrest *et al.,* 2015). However, comparing responses in plant and arthropod taxa to context-dependent effects of organic farming should ideally be based on a common study design. Only a few studies have explicitly analysed functional diversity across multiple taxa (e.g. Jonason *et al.*, 2017), and none of these have studied effects of organic farming on functional diversity. Studying the effects of organic farming on functional diversity of multiple taxa could reveal whether organic farming can restore the loss of functional diversity in agricultural ecosystems (Cadotte *et al*., 2011; Flynn *et al*., 2009).

In this study, we analysed how organic and conventional agriculture affected functional diversity of plants and butterflies that to a large extent rely on farmland in a previously understudied heterogeneous region, North-Western Spain (Tuck *et al.*, 2014; Goded *et al*., 2018). In this region, the extent of organic farming has increased with more than 33% during the last 18 years (CRAEGA, 2015), and maintaining biodiversity is one of the stated objectives for organic farming in Spain (CRAEGA, 2014). Studying the effect of organic farming on functional diversity in complex landscape mosaics can help understanding how farmland can be managed to maintain functional diversity in heterogeneous agricultural landscapes, which are generally at risk in Europe (Tscharntke *et al.*, 2005). We focused on plants and butterflies as biodiversity indicators (Ekroos *et al.*, 2013), as they may respond differently to local habitat characteristics because of their different mobility, and because their ecological traits are well described (see e.g. Jonason *et al.*, 2017).

We used four commonly used functional diversity indices (functional richness, functional evenness, functional divergence and functional dispersion; Mason *et al.*, 2005; Laliberté and Legendre 2010), calculated based on functional response traits related to species dispersal, competition and population persistence (following Jonason *et al.*, 2017), which reflect the distribution of species in human-dominated landscapes (Henle *et al.*, 2004). Similar to effects of taxonomic diversity in functional groups (Tuck *et al.*, 2014; Lichtenberg *et al.*, 2017), we expected conventional farms to have lower overall functional diversity than organic farms, but the effects being dependent on species groups and on the characteristics of the landscape.

2.2. MATERIALS AND METHODS

2.2.1. Study site

The study area was situated in the centre of Galicia (Ulloa Shire and surroundings), NW Spain. The study area consisted of a heterogeneous landscape of farmland-forest, of 421 km^2, 550 m over sea level, with 46% of the land being forests and 35% consisting of farmland, with an average field size of 4.7 ha (IGE, 2012). The remaining 19% mainly consisted of abandoned farmland and scrubland. Forests consisted of big patches of native deciduous forest, mainly comprised of oak (*Quercus robur*), chestnut (*Castanea sativa*) and birch (*Betula alba)*. These forests, together with the farmland and scrubland areas, are increasingly replaced by exotic tree plantations of Eucalyptus (*Eucalyptus globulus* and *E. nitens)*. The landscapes in NW Spain are heterogeneous, with small agricultural fields embedded within patches of forest, but agricultural intensification still occurs at field scale and across entire landscapes in some areas (Sau *et al.*, 1999).

We performed a comparative study of 16 conventional and 16 organic farms which were matched in pairs based on proximity (max 20 km apart), and land use (14 pairs of farms with grasslands used both for grazing and mowing, and 2 pairs of wheat farms), in order to as far as possible eliminate differences not related to farming practice (cf. Rundlöf & Smith, 2006). We identified organic farms based on whether they were registered in the Galician Regulating Board of Organic Agriculture (CRAEGA). The majority (n = 13) of organic farms were mixed with animal husbandry and arable production (including fodder), while only two conventional farms were mixed (see Goded *et al.*, 2018 for further description of farms). The largest field of every farm, ranging from 1 to 17 ha, was chosen for surveys of functional diversity. In order to quantify the effect of landscape heterogeneity, two different landscape features were calculated based on a GIS vector layer on land-use around 500-m of the centre of each field: the proportions of agricultural land and shrub area (Goded *et al*., 2018). The land-use layer was digitalised using ArcGIS 9.3 (ESRI, 2006) based on aerial photographs and field visits.

2.2.2. Surveys

Data were collected between mid-April and mid-August in 2015 and 2016. Data collection was always done by the same person on the same day for each pair. The order in which the surveys were carried out within the pair was systematically switched between visits, to avoid systematic effects of time of day (cf. Dänhardt *et al.*, 2010).

Plant presence and abundance were recorded in four plots of 3 x 3 m, distributed along the centre of each field and separated by at least 10 metres from each other and from the field border (Concepción and Díaz, 2010). Abundance was estimated as percentage cover on a scale between **+** and 5 (Braun-Blanquet, 1979). The survey was carried out once each year, at the maximum flowering time which in this region is between mid-May and mid-July. Butterflies were recorded along one 300-m transect across the centre of the farm field between mid-April and mid-August and only on sunny, non-windy days with temperatures above 17°C. At normal walking pace, the butterfly species richness and abundance at 3m on both sides of each transect were recorded (cf. Pollard, 1977; Ahnström, 2009). Plant and butterfly species that could not be identified in the field were photographed and later identified using handbooks (García, 2013 for plants; Tolman, 2008 for butterflies) and help from taxonomic experts. In addition, plants were classified according to their characteristic phytosociological class, which allowed to link each species with the typical habitat in which this class usually appears, following the indicators of vegetation types in Rivas-Martínez *et al*. (2002).

2.2.3. Functional trait selection

Functional response traits (Laliberté and Legendre 2010) were selected for plants and butterflies, in order to calculate functional diversity indices. These traits were chosen as they have been shown to be related to species dispersal, competition and population persistence (following Jonason *et al.*, 2017), and they determine how species respond to land use and environmental change (Henle *et al*., 2004).

For plants, pollination mode**,** leaf dry matter content (LDMC), life-span, seed mass and seed terminal velocity were the selected response traits (Jonason *et al.*, 2017). Pollination mode was a categorical variable describing whether plants were pollinated by wind or by insects. LDMC is the oven-dry mass in milligrams of a leaf divided by its water-saturated fresh-mass in grams (Cornelissen *et al.*, 2003), and has previously been shown to positively relate to greater population stability and to predict species' responses to land use changes (Garnier *et al*., 2004). The observed plants were also classified according to their life-span in annual or perennial species, which may predict species responses to habitat area and connectivity (Lindborg, 2007). Species that were classified as perennial and biennial, depending on data source, were all classified as perennial. Seed mass is the oven-dry mass of the average seed of a species in milligrams (Cornelissen *et al.*, 2003), and it measures resistance to habitat degradation and seedling competitive ability (Jonason *et al*., 2014). Finally, terminal velocity refers to the speed by which a diaspore travels through still air and it can be used as a response trait as it represents a survival strategy through wind dispersal (Jonason *et al.*, 2017). The response trait data for all observed plant species was taken from the LEDA database

(Kleyer *et al.,* 2008), from which we obtained complete data for all traits for 63 out of the observed 77 species. Therefore, those 63 species with data for all traits were used for the analyses.

For butterflies, average wing length, larval phagy type and potential egg production were selected as response traits (Jonason *et al.*, 2017). Average wing length is a proxy for dispersal ability (Sekar, 2012), which in turn is important for species persistence in fragmented landscapes (Kuussaari *et al*., 2014). Larval phagy type is a categorical value given to each species depending on the degree of larval specialisation of host plants: Specialist (S), Generalist (G) or Oligotrophic (O), based on the number of host plants in which larvae feed (Jonason *et al.,* 2017). Specialist species (whose larvae depend only on a limited number of host plants) normally require large agricultural patches and mosaic landscapes where there is higher probability of occurrence of their host plants and, thus, they are more vulnerable to habitat loss or fragmentation than generalist species (Steffan-Dewenter and Tscharntke 2000; Öckinger *et al*., 2010). Potential egg production is a proxy which measures reproductive potential (Jonason *et al.,* 2017). Species with a low reproductive rate have been suggested to decrease population persistence and lower emigration rates, which in turn can lead to increased risk of stochastic extinction (Henle *et al.,* 2004). In addition, the risk of stochastic extinctions can in turn be dependent on landscape composition (Hanski, 1999). The response trait data for all the observed butterfly species were based on Bink (1992).

2.2.4. Functional diversity indices

In order to analyse functional responses of all species groups to agricultural management and landscape effects, we calculated four functional indices based on Laliberté & Legendre (2010): functional richness, functional evenness, functional divergence and functional dispersion. Functional richness measures the total volume of functional space in a community of species, based on the presence or absence of species along the margin of functional space (i.e. the total volume of multi-dimensional trait space in a given community; Norman *et al*., 2005). Thus, functional richness does not weigh species based on their species-specific abundance. Low functional richness may indicate that there are some unused resources available to the community (Norman *et al*., 2005). Functional evenness quantifies the evenness in the distribution of abundance among all species in the functional space; thus, high functional evenness may reflect an effective use of the total available functional space (Mason *et al*., 2005). Functional evenness equals one if all species have equal abundances in the functional space, and it declines towards zero with increasing unevenness (Weiher, 2010). Functional divergence measures the amount of species with the most extreme values in functional traits; therefore, a high value of functional divergence may imply a lower overlap in functional space between the dominant species and thus lower competition between them. Finally, functional dispersion measures the abundance-weighed distance to the centroid of functional space (Laliberté & Legendre ,2010). Unlike functional richness, functional dispersion considers species relative abundances, and in contrast to functional evenness and divergence it also estimates the dispersion of species in trait space; low values of functional dispersion reflect high community specialisation (Laliberté & Legendre ,2010).

The total species richness and abundance of the two species groups (using cover for plants) were pooled together over transects and years. With these data, the four functional indices were calculated using the dbFD function (FD package; R Development Core Team). Rows in which some trait values were missing were omitted from the analyses, as functional indices are sensitive to data incompleteness. In addition, sites with less than three species had also to be taken out, as functional indices could not be calculated on those sites. Therefore, after removing sites with incomplete trait data or less than three species, the total sample consisted of 30 sites (15 organic and 15 conventional farms) for plants, and 25 sites (14 organic and 11 conventional) for butterflies. To statistically account for the secondary unbalance in the number of organic and conventional farms for butterflies, we used the Satterthwaite degree of freedom correction in the analyses when needed.

2.2.5. Statistical analyses

2.2.5.1. Interrelationships between functional traits

For plant functional traits, seed terminal velocity was moderately correlated to seed-mass ($R^2 = 0.42$, df = 65, $p = 0.0004$): Following Jonason *et al*. (2017) both values were kept in the analyses as they represent distinctly different survival strategies. In addition, there was a significant difference in LDMC ($t_{28.3} = -4.403$, $p = 0.0001$) between the two pollination modes. Finally, there was no significant difference in LDMC ($t_{53.1} = -0.68$, $p = 0.49$), seed mass ($t_{44.03} = -1.03$, $p = 0.31$) or terminal velocity ($t_{57.9} = -0.12$, $p = 0.26$), between annual and perennial species.

For butterflies, although egg production was highly correlated to wing length ($R^2 = 0.75$, df = 17, $p = 0.0001$), they were both kept in the analyses as they measure different aspects of species responses to changes (see above). Therefore we used relative egg production defined as the residuals from a regression between egg production and wing length to calculate the functional diversity indices. There was no significant difference in wing length ($t_{8.8} = 0.48$, $p = 0.64$) or egg production ($t_{7.3} = 1.03$, $p = 0.32$) between generalists and oligotrophic species.

2.2.5.2. Functional diversity analyses

Linear Mixed Models with Satterthwaite degrees of freedom corrections were used to measure the effect of farming practice and landscape variables on species richness and the four functional diversity indices. For each species group, species richness and the four different functional indices were evaluated separately, using farming practice (organic or conventional), size of fields and the proportion of agriculture and shrubs within a 500-m radius from the centre of the studied field as fixed variables, together with the two-way interactions between all fixed variables. All analyses were calculated using one single value per farm. There was no significant correlation between the fixed variables. Pair identity was included as random factor to take into account that the observations within each pair were not independent. For all models, residuals were normally distributed. The final models were obtained by removing the least significant interactions sequentially, while respecting marginality, until remaining factors were significant at $p < 0.05$. Finally, we performed a species indicator analysis to determine whether any particular plant or butterfly species were significantly more abundant in organic or conventional farms. All statistical analyses were done using R 3.2.3 (R Development Core Team, 2008), using the lmer function in library lme4 (Bates *et al*., 2014) and the multipatt function in library indicspecies (De Cáceres, 2013).

2.3. RESULTS

2.3.1. Plants

We observed 77 species of plants in total, with an average of 18.2 (± 5.5 SD) species and an abundance (cover) of 125.7 % (± 53.9) per organic farm, whereas 15.5 (± 6.3) species, with an abundance of 99.4 % (± 43.7), were observed on average at the conventional farms (Appendix A). 12 species were only observed in organic farms and 16 species only in conventional farms. Three plant species (*Anthemis arvensis*, *Cerastium glomeratum* and *Trifolium pratensis*) were significantly more abundant in organic than conventional farms (indicator value IV = 0.734, p = 0.025; IV = 0.761, p = 0.005; IV = 0.755, p = 0.013, respectively). The species richness of plants was not significantly influenced by farm type (organic vs. conventional), field size or proportion of surrounding agriculture ($F_{1,12} = 2.46$, p = 0.1425; $F_{1,12} = 0.02$, p = 0.8899 and $F_{1,12} = 0.29$, p = 0.602, respectively). In addition, plant species richness was significantly correlated to functional richness ($R^2 = 0.61$, df = 28, p = 0.0003). However, plant functional richness decreased significantly with an increasing proportion of surrounding agricultural land ($F_{1,25} = 11.61$, p = 0.0022; Fig. 1). Functional evenness was significantly related to the interaction between size of fields and proportion of agricultural land ($F_{1,22.9} = 6.45$, p = 0.0183), increasing as the size of fields increased in landscapes with low proportions of agricultural land, while the opposite occurred with high proportions of agricultural land (Fig. 2). Finally, neither farm type nor field size or proportion of surrounding agriculture or shrub significantly affected plant functional divergence ($F_{1,11.3} = 0.15$, p = 0.7089; $F_{1,24.1} = 0.77$, p = 0.3878; $F_{1,20.7} = 1.58$, p = 0.2224 and $F_{1,23.7} = 2.09$, p = 0.1616, respectively) or dispersion ($F_{1,13.8} = 0.37$, p = 0.5502; $F_{1,16.6} = 0.22$, p = 0.6435; $F_{1,23.9} = 2.16$, p = 0.1542 and $F_{1,21.2} = 0.11$, p = 0.7414, respectively).

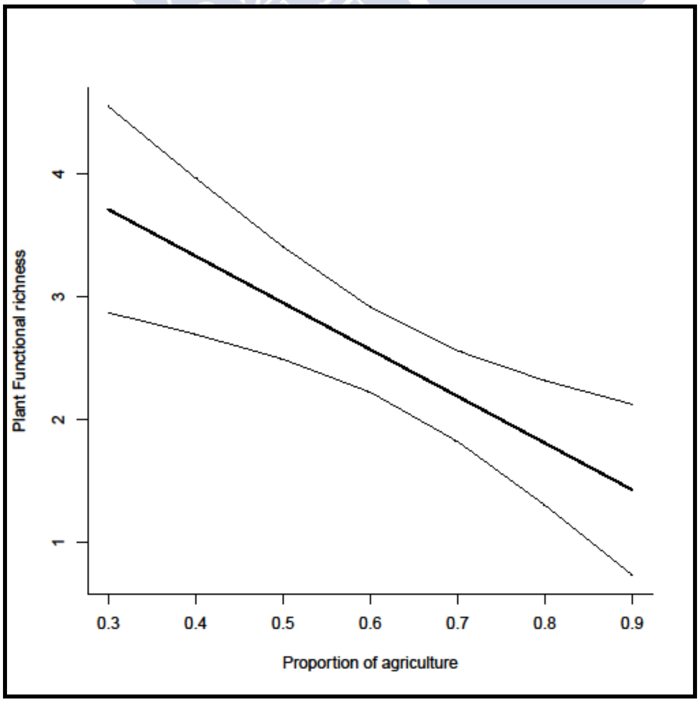

Fig. 1: Effect of the proportion of agriculture in the landscape around each studied field on plant functional richness. Predicted relationship and 95% confidence intervals shown.

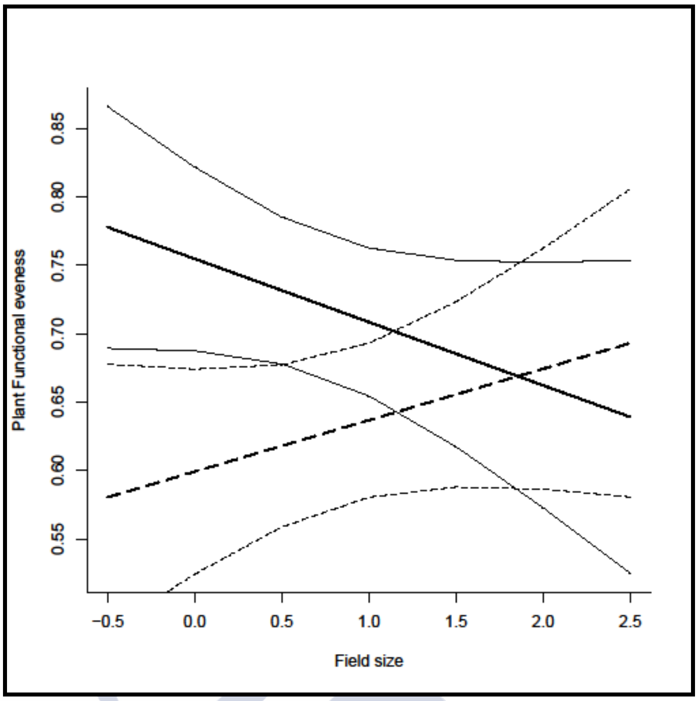

Fig. 2: Effect of field size on plant functional evenness in landscapes with high (solid line) and low (dashed line) proportion of surrounding agriculture. Predicted relationship and 95% confidence intervals shown.

2.3.2. Butterflies

We found a total of 22 species of butterflies, out of which 404 individuals of 19 species were found in organic farms and 241 individuals of 19 species in conventional farms. For each pair of farms, there was an average of 5.1 (± 2.9) species and an abundance of 20.5 (± 19.7) per organic farm, whereas 3.9 (± 3.04) species, with an abundance of 20.1 (± 20.1), were observed on average at the conventional farms (Appendix A). There were three species only observed in organic farms (*Kanetisa circe*, *Mellicta parthenoides* and *Zerynthia rumina*), and three only in conventional farms (*Colias hyale*, *Maculinea arion* and *Pararge aegeria*) (Appendix B). Although our indicator analysis did not identify any butterfly species being significantly more abundant in either organic or conventional farms, the species richness of butterflies was significantly influenced by farm type ($F_{1,12} = 5.17$, $p = 0.0422$), being higher in organic than conventional farms (Fig. 3). Butterfly species richness was not affected by field size ($F_{1,12} = 0.43$, $p = 0.6738$), proportion of agriculture ($F_{1,12} = 0.79$, $p = 0.4462$) or shrubs ($F_{1,12} = -0.83$, $p = 0.4235$). In addition, butterfly species richness was significantly correlated to functional richness ($R^2 = 0.74$, df = 23, $p < 0.0001$).

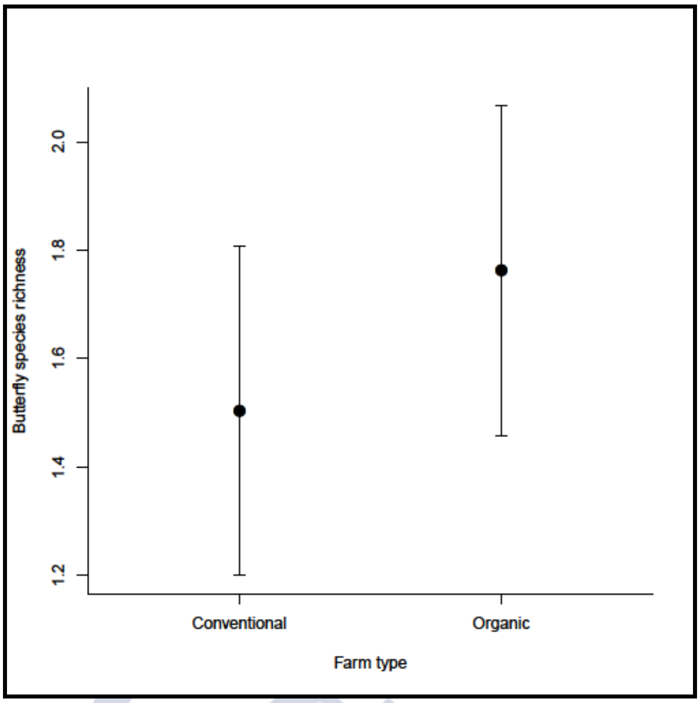

Fig. 3: Effect of farm type on butterfly species richness. Means and 95% confidence intervals shown.

The functional richness of butterflies was significantly related to farm type ($F_{1,10.6} = 5.55$, $p = 0.0388$), being higher in organic than in conventional farms (Fig. 4). In addition, functional richness was significantly related to an interaction between field size and proportion of shrubs in the surroundings ($F_{1,12.2} = 8.11$, $p = 0.0145$); functional richness decreased with increasing focal field size and a high proportion of shrubs, but functional richness did not significantly change with field size when the proportion of shrubs surrounding the fields were low (Appendix C).

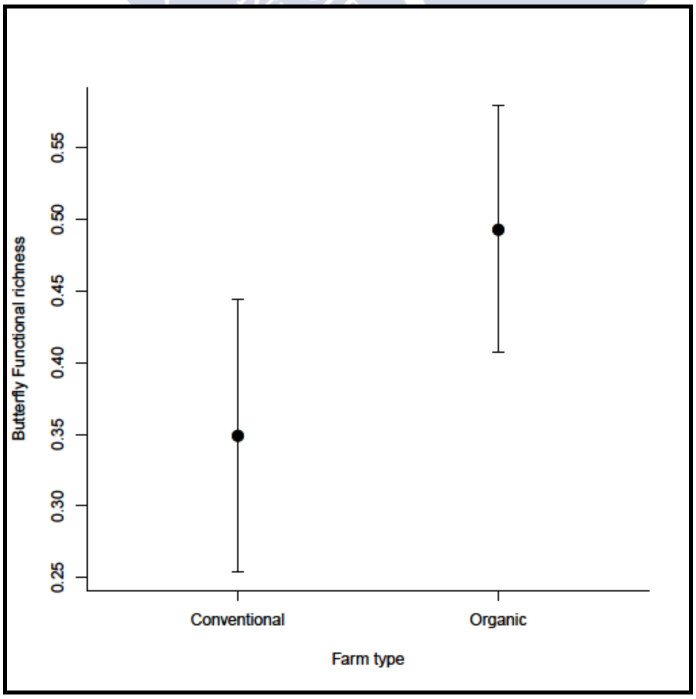

Fig. 4: Effect of farm type on butterfly functional richness. Means and 95% confidence intervals shown.

Butterfly functional evenness was significantly related to an interaction between farm type and proportion of agriculture in the landscape ($F_{1,19}$ = 5.05, p = 0.0366), by which functional evenness increased with increasing proportion of agriculture surrounding conventional ($t_{1,19}$ =2.605, p = 0.0174), but not that surrounding organic farms ($t_{1,19}$ =-0.521, p = 0.6083; Fig. 5). Finally, similarly to plants, neither farm type nor field size or proportion of surrounding agriculture or shrub significantly affected plant functional divergence ($F_{1,10.3}$ = 0.98, p = 0.3456; $F_{1,14.004}$ = 0.01, p = 0.9927; $F_{1,16.7}$ = 0.68, p = 0.4198 and $F_{1,16.06}$ = 0.06, p = 0.8049, respectively) or dispersion ($F_{1,20}$ = 0.32, p = 0.5774; $F_{1,20}$ = 0.01, p = 0.9271; $F_{1,20}$ = 1.42, p = 0.2478 and $F_{1,20}$ = 0.46, p = 0.5044, respectively).

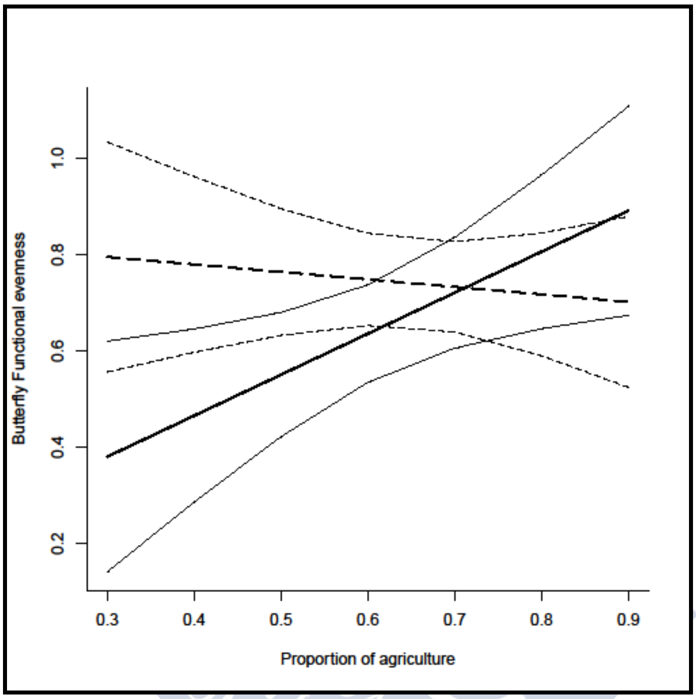

Fig. 5: Effect of the proportion of agriculture in the surrounding landscape on butterfly functional evenness in conventional (solid line) and organic (dashed line) farms. Predicted relationships and 95% confidence intervals shown.

2.4. DISCUSSION

We found no effects of organic farming on plant species richness or the different components of functional diversity. Since earlier studies have found effects mostly in simplified landscapes (Rader *et al.*, 2014; Tuck *et al.*, 2014), the lack of effect in this study may be caused by the generally high landscape heterogeneity (but see Ekroos *et al.*, 2010). It is also possible that effects of organic farming on species richness are smaller in pasture-based farming systems, such as the one studied here, due to longer crop rotations, compared to arable systems. Alternatively, the combination of farming system and high landscape heterogeneity contributed to our result. However, as revealed by species indicator analyses, three plant species were significantly associated with organic farming. Amongst these, *Trifolium pratensis* (the red clover) is known to attract and benefit flower-visiting insects (Rundlöf *et al.*, 2014).

Butterfly species richness was positively affected by organic farming, with consequences also for functional richness and evenness. Earlier studies have mainly compared species richness between organic and conventional farming (reviewed in Tuck *et al*., 2014; Lichtenberg *et al*., 2017), whereas only few studies have considered effects on functional diversity (Rader *et al.*, 2014; Forrest *et al.*, 2015), none of which considered butterfly functional diversity. In addition, while earlier studies have found stronger effects of organic farming in intensively farmed landscapes, in this study we found effects in a generally heterogeneous landscape and the effect on functional evenness was in fact only evident when the proportion of agricultural land was low. It has been argued that the effect of organic farming on the species richness of flower-visiting insects is mediated by higher in-field flower diversity (Holzschuh *et al.*, 2007). Although we only found subtle shifts in plant communities, it is also possible that butterflies are directly affected by the use of pesticides on conventional farms (Brittain *et al*., 2010), or benefit from higher resource continuity in the organic farms with more complex crop rotations (Schellhorn *et al.*, 2015). Nevertheless, our results show that organic farming has the potential to promote arthropods in agricultural habitats, such as butterflies, in heterogeneous, mosaic landscapes (also see Lichtenberg *et al.*, 2017).

2.4.1 Effects of organic farming on plant and butterfly species richness

Organic farming did not significantly affect local plant species richness in our study, in contrast to earlier research which has found plants to benefit strongly from organic farming (Tuck *et al.*, 2014). However, our indicator analysis showed that three plant species, typical on wet pastures (*Trifolium pratensis*) or cereal fields (*Cerastium glomeratum* and *Anthemis arvensis*), were significantly more abundant in organic than conventional farms. In our study, organic farming thus had much more subtle effects on plant communities compared to the majority of earlier studies, most of which have been carried out in cereal systems (Tuck *et al*., 2014). Compared with typical cereal systems at least in Europe, herbicide use may be a key reason for diverging results between our study and earlier research. In total, 29 out of the observed 77 plant species were grassland specialist species, typical from mesophile to wet meadows and pastures communities on deep and moist soils, which are often manured, constituting 57% of the abundance of all observed plants (Appendix A). Amongst the 12 species only found in organic farms, eleven were species typical on manured/wet pastures or cereal fields (Rivas-Martínez *et al*., 2002; Appendix A). In contrast, the 16 species only found in conventional farms were typical for a wide variety of habitats, including manured to wet pastures, deciduous forest soils, semi-shaded perennial communities and scrubland (Rivas-Martínez *et al*., 2002; Appendix A). These differences might suggest that grassland and farmland specialist plants are present in organic farms to a higher degree than in conventional farms (see also Boutin *et al*., 2008), although they were not identified as significantly associated to organic farming by our indicator analysis.

Although we found the same total number of species of butterflies in organic and conventional farms, and no particular species significantly associated to either farm type, local species richness was significantly higher on organic compared to conventional farms. While earlier research have found butterflies to benefit in homogeneous landscapes (Rundlöf *et al*., 2008a), similar results have not been found in heterogeneous landscapes (Ekroos *et al*., 2008). Although some earlier studies have suggested that higher plant diversity in organic farms increase butterfly species richness (Feber *et al*., 1997), we did not find such a link. In our study, the higher butterfly species richness in organic farms could be due to increased availability of plant resources, in particular red clover (*T.pratensis*), or to the required practices in organic farming, such as non-use of synthetic pesticides, or other practices which are non-required but commonly used to accommodate farming to the prohibition of pesticides and inorganic fertilizers, like long rotation of crops (Schellhorn *et al.*, 2015), or a combination of both (see Goded *et al*., 2018).

2.4.2. Effects of organic farming on plant and butterfly functional diversity

We found no effects of organic farming on plant functional diversity in our studied fields, most of which were grasslands in both organic and conventional farms. Our a priori hypothesis was that plants should respond more strongly to farming system compared with mobile butterflies, both concerning species richness, as has been observed previously (Bengtsson *et al*., 2005; Fuller *et al*., 2005), or in functional diversity. In theory, organic farming could increase plant functional diversity by i) allowing a larger coexistence of plants, occupying a wider niche space e.g. because of higher environmental stability, or ii) by providing more niches because of longer crop rotations of lack of use of synthetic pesticides. However, in accordance with the only study which explicitly compared plant functional diversity between organic and conventional farms (Rader *et al*., 2014), we did not find higher plant functional diversity in organic farms. Although plant functional diversity was not influenced by farming system in our study, we acknowledge that there could be systematic effects on individual traits that may not be captured by diversity indices. A formal trait-based analysis would be needed to confirm if there is an effect of plant species composition.

We found a higher butterfly functional richness in organic than conventional farms. Effects of organic farming on butterfly functional diversity have not previously been studied, although the abundance of butterflies with some specific traits, such as high mobility and reproductive rate, has been shown to be higher in organic farms in homogeneous landscapes (Jonason *et al*., 2012). Although organic farming may not counteract the negative effect of landscape homogenisation on butterflies (Jonason *et al.*, 2012), organic farming may still increase the functional richness in farmland butterfly assemblages (this study). Hence, organic farming may, in addition to benefitting butterfly species richness, support butterfly communities which are more resilient to environmental change (Chillo *et al*., 2011).

2.4.3. Effects of landscape factors on plant and butterfly functional diversity

We found that plant functional richness and evenness were influenced by the landscape context, but in different ways. Plant functional richness decreased with increasing proportions of surrounding agricultural land, being highest in landscapes with low proportions of agricultural land and lowest in landscapes with high proportions of agricultural land. Our results therefore show that the highest cover of functional space for plants appears in fields embedded in heterogeneous landscapes, characterised by low proportions of arable land. Increasing land openness, as an indicator of increasing land-use intensification, therefore decreases functional richness of plants, in line with previous findings for plants (Rader *et al.*, 2014), and other taxonomic groups (Flynn *et al*., 2009 for birds and mammals, and Jonason *et al*., 2017 for butterflies). In addition, plant functional evenness was highest in small fields in open agricultural areas and lowest in small fields in landscapes with low proportions of agricultural land. Hence, plants are more evenly distributed in functional space in small fields situated in homogeneous than heterogeneous landscapes, whereas in big fields plants are equally evenly distributed in functional space regardless of surrounding landscape openness, (also see Van Halder *et al*., 2017). Small isolated grasslands may be dominated by clonal plant species (Lindborg *et al*., 2007), which could reduce the functional evenness in plant communities. In our study, more than half of the total plant abundance belonged to grassland specialist species, which may benefit from larger grassland fields because of isolation effects in small grassland fields situated in highly heterogeneous landscapes. Therefore, a relatively large area surrounding a focal grassland can affect the distribution of life-history traits in a local plant community (Lindborg *et al.*, 2007), highlighting once more the importance of considering functional diversity, rather than exclusively species richness, in order to understand the effects of isolation on local communities (Öckinger *et al*., 2010; Marini *et al*., 2012).

Butterfly functional richness was influenced by an interaction between proportion of surrounding shrubs and field size, such that it decreased with increasing field size in landscapes surrounded by high proportion of shrubs. Functional richness of butterflies was high in small fields surrounded by high proportions of shrubs, and in large fields surrounded by low proportions of shrubs, but low in large fields surrounded by high proportions of shrubs. This diverging pattern probably reflects the fact that butterflies as mobile organisms can swiftly concentrate in habitats with complementary resources, such as sheltered microhabitats provided by small fields surrounded by shrubs or hedgerows (also see Öckinger and Smith, 2007), and patches with larval host plants (Fred *et al.*, 2006) or floral resources (Loertscher *et al.*, 1995), which larger grassland fields might contain to a higher degree, given that they provided a higher functional evenness of plants in our study area. Alternatively, both habitats sustain a wider niche space for butterfly communities, and therefore the high butterfly functional richness in these two habitats could be an effect of a wider realised niche space locally. Finally, the diverging pattern in functional richness might also reflect species turnover, considering that half of the observed butterfly species were typical grassland species mainly occurring in open meadows, whereas the other half were species associated with grassy habitats close to scrubland or deciduous woodland (Tolman, 2008).

2.4.4. Interactive effects of farming practice and landscape structure

We did not find an interaction effect of farm type with any landscape predictor for plant functional diversity. However, landscape heterogeneity and field size significantly influenced plant functional diversity. Therefore, in our study, both landscape and field structure had a larger effect on plant functional diversity than farming system, as has been previously observed for butterflies (Jonason *et al.*, 2012).

Butterfly functional evenness was significantly influenced by an interaction between farm type and proportion of agricultural land in the surrounding landscape, with increasing functional evenness with increasing proportions of agricultural land, but only when farming was conventional. This result suggests that there might be a more unequal distribution in trait-space in conventional agriculture at low presence of agriculture, possibly because the butterfly community becomes defined by the surrounding landscape structure, as fields have less complementary food resources compared to fields on organic farms. Therefore, our result might show that organic fields constitute higher quality habitats for butterflies than conventional fields, as the functional diversity of butterflies was more evenly distributed in organic fields regardless of surrounding landscape, contrary to what occurs in conventional fields. As noted above, another possible explanation is that organic fields have more available ecological niche spaces for butterflies independently of landscape context and, therefore, they harbour a higher butterfly functional evenness than conventional fields.

2.5. CONCLUSIONS

Plants were not affected by farming system either in species richness or functional diversity. However, plants seem to be more affected by landscape structure, as functional diversity of plants is affected by landscape heterogeneity and field size. In particular, functional richness declined as the landscape becomes more homogeneous, but this effect is modulated by field size for plant functional evenness. In addition, we found that three species of plants were significantly more abundant in organic farms, one of which is a particularly important feeding resource for several flower-visiting insect groups. Nonetheless, butterflies have been shown to benefit from organic farming in the study area, as evidenced by higher species richness in organic farms than in conventional farms. In addition, functional diversity was higher in organic than conventional farms, although it is also dependent on landscape heterogeneity. The positive effect of organic farming on butterflies could be due to higher presence of plant species which are important for butterflies. However, it could be also a result of a wider availability of niche spaces present in organic farms, as a result of the management practices typical from organic farming, such as the non-use of synthetic pesticides or long crop rotations. Future studies on the effect of organic farming on functional diversity are needed to better understand these effects.

The benefit of organic farming on biodiversity has not only an effect on species richness and abundance, but on the effectiveness of how plants and butterflies can use the available resources that each agricultural system provides them. Therefore, organic farming might have the potential to offer a more functionally rich ecosystem for agricultural species than conventional farming system.

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2.7.APPENDICES

APPENDIX A

Plant species observed in the study, with their corresponding phytosociological class and typical habitat (following Rivas-Martínez *et al*., 2002), being "AWCF": Annual weeds in cereal fields; "AWSF": Annual wood and shrub fringes; "MPBG": Mediterranean perennial basophilous grasslands; "MWMP": Mesophile to wet meadows and pastures; "NNP": Non nitrophilic pastures; "NSSWF": Nitrified and semi-shaded wood fringes; "PGMP": Perennial grazed and manured pastures; "PHFW": Perennial herbs of fresh waters; "PPRS": Perennial pastures on rich soils; "PSRB": Permanent or serial reed beds; "SC": Scrubland; "SCDF": Scrubland in borders of deciduous forests; "SPG": Silicicolous perennial grasslands; "SSFE": Semi-shaded forest edges and "TDMF": Temperate decidious or mixed forests. Together with the functional traits used to calculate the four functional indices: "Pollinator": pollinator type; "LDMC": Leaf Dry Matter Content; "Seed mass": average seed mass; "Velocity": terminal velocity and "Life span": life span, together with the total frequency values found in all organic ("Org.") and conventional ("Conv.") farms added together.

Species	**Phytosociological class**	**Habitat**	**Pollinator**	**LDMC**	**Seed mass**	**Velocity**	**Life_span**	**Org.**	**Conv.**
Achillea millefolium	*Molinio-Arrhenatheretea*	*MWMP*	insects	196.00	0.13	1.34	perennials	4	28
Agrostis capillaris	*Molinio-Arrhenatheretea*	*MWMP*	wind	281.66	0.07	0.75	perennials	24	32
Agrostis stolonifera	*Molinio-Arrhenatheretea*	*MWMP*	wind	284.00	0.02	0.78	perennials	4	0
Aira caryophyllea	*Tuberarietea guttatae*	NNP	wind	NA	NA	NA	annuals	0	12
Andryala integrifolia	*Lygeo stipetea*	MPBG	insects	NA	0.19	NA	perennials	6	16
Anthemis arvensis	*Stellarietea mediae*	AWCF	insects	112.91	0.50	2.71	perennials	156	58
Anthoxantum odoratum	*Molinio-Arrhenatheretea*	*MWMP*	wind	273.17	0.88	2.45	perennials	0	2
Anthyllis vulneraria iberica	*Juncetea maritimi*	PSRB	insects	170.00	3.25	1.52	perennials	18	32
Arenaria montana	*Querco-Fagetea*	TDMF	insects	NA	0.08	2.21	perennials	0	2

Arrhenatherum elatius	*Molinio-Arrhenatheretea*	*MWMP*	wind	NA	3.50	3.29	perennials	50	42
Bartsia trixago	*Stellarietea mediae*	AWCF	insects	198.44	0.24	1.69	annuals	0	2
Bellis perennis	*Molinio-Arrhenatheretea*	*MWMP*	insects	118.00	0.09	1.58	perennials	108	62
Briza maxima	*Tuberarietea guttatae*	NNP	wind	358.00	1.74	2.28	annuals	8	4
Bromus hordeaceus	*Stellarietea mediae*	AWCF	wind	278.00	1.17	1.92	annuals	54	10
Bromus rigidus	*Stellarietea mediae*	AWCF	wind	NA	10.32	NA	annuals	2	6
Campanula lusitanica	*Tuberarietea guttatae*	NNP	insects	143.60	0.19	2.30	perennials	12	4
Campanula rapunculus	*Trifolio-Geranietea*	SSFE	insects	152.09	0.03	2.30	annuals	26	12
Capsella bursa-pastoris	*Stellarietea mediae*	AWCF	insects	140.00	0.08	1.61	annuals	66	32
Cardamine pratensis	*Molinio-Arrhenatheretea*	*MWMP*	insects	205.00	0.57	3.01	perennials	0	2
Carum verticillatum	*Molinio-Arrhenatheretea*	*MWMP*	insects	177.15	0.95	NA	perennials	28	18
Centaurea nigra	*Trifolio-Geranietea*	SSFE	insects	147.00	2.16	4.03	perennials	0	4
Cerastium fontanum vulgare	*Molinio-Arrhenatheretea*	*MWMP*	insects	140.00	0.14	2.72	perennials	26	6
Cerastium glomeratum	*Stellarietea mediae*	AWCF	insects	186.00	0.06	1.56	annuals	90	24
Coleostephus myconis	*Stellarietea mediae*	AWCF	insects	NA	NA	NA	annuals	10	12
Crepis capillaris	*Molinio-Arrhenatheretea*	*MWMP*	insects	133.00	0.26	0.42	annuals	184	106
Cynosurus cristatus	*Molinio-Arrhenatheretea*	*MWMP*	wind	282.00	0.50	2.17	perennials	12	4
Cytisus scoparius	*Cytisetea scopario-striati*	SCDF	insects	198.00	0.36	4.53	perennials	0	4
Cytisus striatus	*Cytisetea scopario-striati*	SCDF	insects	NA	6.27	4.53	perennials	0	4

Dactylis glomerata	*Molinio-Arrhenatheretea*	*MWMP*	wind	320.00	1.20	2.84	perennials	178	206
Echium plantagineum	*Stellarietea mediae*	AWCF	insects	142.00	2.39	2.86	annuals	126	42
Erodium cicutarium	*Stellarietea mediae*	AWCF	insects	224.00	1.53	1.95	annuals	80	28
Erodium moschatum	*Stellarietea mediae*	AWCF	insects	98.50	1.81	2.90	annuals	4	0
Festuca grex *rubra*	*Molinio-Arrhenatheretea*	*MWMP*	wind	289.00	0.42	2.79	perennials	196	238
Geranium columbinum	*Cardamino hirsutae*	AWSF	insects	301.00	3.15	NA	annuals	1	0
Geranium molle	*Galio-Urticetea*	*NSSWF*	insects	196.00	1.24	3.83	annuals	44	16
Geranium pyrenaicum lusitanicum	*Festuco-Brometea*	*SSFE*	insects	209.00	1.41	3.16	perennials	80	70
Holcus lanatus	*Molinio-Arrhenatheretea*	*MWMP*	wind	204.22	0.36	2.74	perennials	146	148
Holcus mollis	*Querco-Fagetea sylvaticae*	TDMF	wind	230.00	0.35	1.43	perennials	0	12
Hypochoeris radicata	*Molinio-Arrhenatheretea*	*MWMP*	insects	130.00	0.66	0.36	perennials	32	44
Juncus effusus	*Molinio-Arrhenatheretea*	*MWMP*	wind	279.74	0.02	1.63	perennials	16	0
Lepidium heterophyllium	*Stellarietea mediae*	AWCF	insects	172.06	1.38	3.73	annuals	6	0
Linum bienne	*Molinio-Arrhenatheretea*	*MWMP*	insects	189.04	1.24	1.96	perennials	4	0
Lolium multiflorum	*Molinio-Arrhenatheretea*	*MWMP*	wind	265.00	3.06	3.47	annuals	96	190
Lolium perenne	*Molinio-Arrhenatheretea*	*MWMP*	wind	219.00	2.02	3.41	perennials	428	338
Lotus corniculatus	*Molinio-Arrhenatheretea*	*MWMP*	insects	188.00	1.65	4.09	perennials	24	32
Lupinus luteus	*Stellarietea mediae*	AWCF	insects	102.20	155.00	5.61	perennials	2	0
Malva sylvestris	*Stellarietea mediae*	AWCF	insects	170.01	2.78	4.13	perennials	0	10

Malva tournefortiana	*Stipo giganteae*	SPG	insects	220.00	2.03	3.32	perennials	8	10
Medicago arabica	*Stellarietea mediae*	AWCF	insects	252.00	2.10	3.68	perennials	98	28
Mentha spicata	*Phragmito-Magnocaricetea*	MWMP	insects	170.00	0.05	1.75	perennials	2	8
Myosotis cespitosa	*Phragmito-Magnocaricetea*	PHFW	insects	139.00	0.26	2.23	annuals	6	0
Myosotis discolor discolor	*Cardamino hirsutae*	AWSF	insects	132.57	0.15	1.88	annuals	0	8
Ornithopus compressus	*Tuberarietea guttatae*	NNP	insects	222.00	1.35	1.60	annuals	78	68
Ornithopus perpusillus	*Tuberarietea guttatae*	NNP	insects	222.00	1.05	1.60	annuals	12	28
Ornithopus sativus	*Tuberarietea guttatae*	NNP	insects	222.00	3.65	1.60	annuals	2	0
Parentucellia viscosa	*Poetea bulbosae*	PGMP	insects	NA	0.02	NA	annuals	2	0
Picris hieracioides	*Artemisetea vulgaris*	PPRS	insects	188.90	1.18	0.59	perennials	0	2
Plantago lanceolata	*Molinio-Arrhenatheretea*	*MWMP*	wind	158.00	2.01	3.27	annuals	330	344
Poa pratensis	*Molinio-Arrhenatheretea*	*MWMP*	wind	342.00	0.31	2.14	perennials	88	4
Pteridium aquilinum	*Cytisetea scopario-striati*	SCDF	wind	338.00	NA	NA	perennials	14	26
Quercus pyrenaica	*Querco-Fagetea sylvaticae*	TDMF	wind	277.00	2996.00	NA	perennials	0	8
Ranunculus bulbosus	*Molinio-Arrhenatheretea*	*MWMP*	insects	205.00	2.23	3.50	perennials	0	52
Raphanus raphanistrum	*Stellarietea mediae*	AWCF	insects	129.00	33.72	4.18	annuals	122	14
Rhinanthus minor	*Molinio-Arrhenatheretea*	*MWMP*	insects	204.00	2.84	1.72	annuals	8	0
Rubus ulmifolius	*Rhamno-Prunetea*	SCDF	insects	263.00	2.17	3.60	perennials	0	4
Rumex acetosa acetosa	*Molinio-Arrhenatheretea*	*MWMP*	wind	115.56	0.74	1.90	perennials	12	8

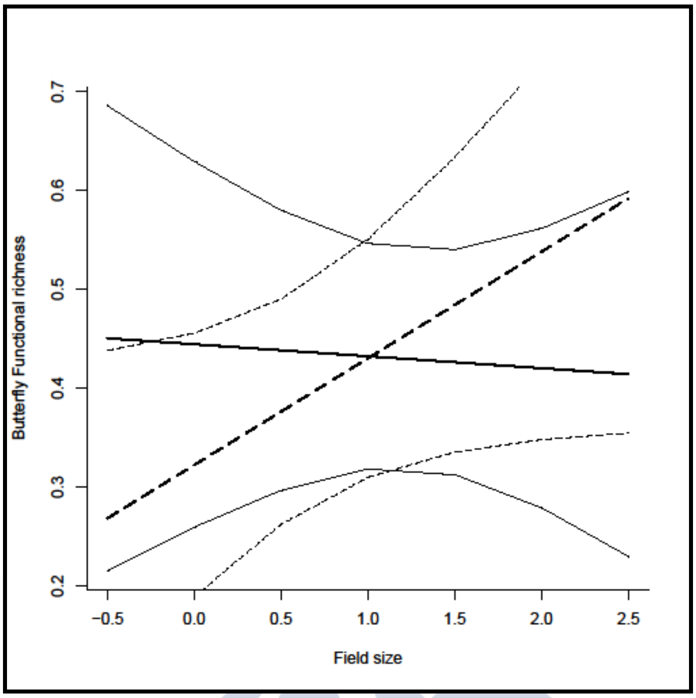
Rumex acetosella	*Sedo-Scleranthetea*	*LRS*	wind	141.00	0.44	2.36	perennials	82	96
Rumex obtusifolius	*Molinio-Arrhenatheretea*	*MWMP*	wind	150.00	1.25	2.39	perennials	0	1
Simethis mattiazzi	*Calluno-Ulicetea*	SC	insects	NA	NA	NA	perennials	2	0
Trifolium dubium	*Molinio-Arrhenatheretea*	*MWMP*	insects	212.00	0.23	2.56	annuals	0	26
Trifolium pratense	*Molinio-Arrhenatheretea*	*MWMP*	insects	208.00	2.37	3.38	perennials	182	44
Trifolium repens	*Molinio-Arrhenatheretea*	*MWMP*	insects	209.43	0.48	3.33	perennials	312	210
Ulex europaeus	*Calluno-Ulicetea*	SC	insects	267.00	6.20	4.50	perennials	2	0
Veronica serpyllifolia	*Trifolio-Geranietea sanguinei*	SSFE	insects	175.00	0.24	2.11	annuals	12	6
Vicia angustifolia	*Trifolio-Geranietea sanguinei*	SSFE	insects	234.00	14.26	5.04	annuals	42	58
Vicia cracca	*Trifolio-Geranietea sanguinei*	SSFE	insects	250.00	14.29	5.03	perennials	10	4
Vulpia myurus	*Tuberarietea guttatae*	NNP	wind	307.00	0.52	2.61	annuals	18	0

APPENDIX B

Butterfly species observed in the study, with the functional traits used to calculate the four functional indices: "Winglength": average winglength; "Phagy": larval phagy type; "Eggprod": potential egg production, and the total abundances found in all organic and conventional farms added together.

Butterfly species	Winglength	Phagy	Eggprod	Organic	Conventional
Aglais io	28	G	900	2	1
Anthocharis cardamines	20	O	230	23	9
Artogeia rapae	25	G	430	73	7
Coenonympha pamphilus	15	G	143	47	20
Colias croceus	25	O	500	27	18
Colias hyale	22	O	210	0	1
Erynnis tages	13	O	86	5	1
Eurodryas aurinia	18	O	430	16	6
Gonepteryx rhamni	28	O	600	4	3
Hyponephele lycaon	20	O	100	8	4
Kanetisa circa	35	O	NA	1	0
Leptotes pirithous	13	G	112	5	1
Maculinea arion	20	O	280	0	21
Maniola jurtina	25	G	300	79	62
Melanargia lachesis	25	O	90	41	26
Mellicta parthenoides	17	G	320	1	0
Pararge aegeria	21	O	185	0	4
Pieris brassicae	30	G	1100	2	13
Polyommatus icarus	15	O	300	34	1
Pyronia tithonus	19	O	240	28	41
Vanessa atalanta	29	S	900	7	2
Zerynthia rumina	25	S	NA	1	0

APPENDIX C



Interactive effect of field size with high (solid line) and low (dashed line) proportion of shrubs around 500m from field centre on butterfly functional richness. Mean values and Confidence Intervals shown.

CHAPTER III:

Effects of *Eucalyptus* plantations on biodiversity in North-West Spain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DE COMPOSTELA

3.1. INTRODUCTION

During the past 60 years, increasing human demands for wood and paper have favoured the use of fast-growing tree species for plantation forestry (Barlow *et al.*, 2007). An estimated 25% of the planted forest area globally (264 million ha) consists of fast-growing exotic species, while natural forests are rapidly declining and increasingly fragmented (FAO, 2010). Exotic plantations are often preferred because of their high productivity and economic profitability.

Due to their fast growth, wide adaptability and profitability for paper production (Turnball, 1999), *Eucalyptus* species are one of the most widely used *taxa* as exotic plantations outside their natural range, currently covering c. 20 million ha in temperate, tropical and subtropical regions (Rejmánek and Richardson, 2011). *E. globulus* Labill. is currently one of the most important planted tree species in the world, with an estimated 2.5 million ha being planted worldwide by 2004, mainly in the Iberian Peninsula (Potts *et al*., 2004). In Spain, *Eucalyptus* plantations cover 633,000 ha (Montero and Serrada, 2013), having their highest densities in the North-West region (IFN, 2017). In this region, plantations of both *Eucalyptus globulus* and *E. nitens* have been established in scrublands and farmlands, thus replacing traditional elements of the agrarian mosaic (Loidi, 2017). Furthermore, *Eucalyptus* plantations have also replaced native forests directly (Teixido *et al*., 2010). These plantations have been supported by the government (Calviño-Cancela *et al*., 2012), aiming at economically benefitting rural livelihoods. In NW Spain, this development has been reinforced by rural abandonment. Because of low opportunity costs and management requirements, *Eucalyptus* plantations are commonly regarded as one of the few options for land owners not living in rural areas to make use of their lands, which in turn provokes a profound change in land use.

Research has shown that *Eucalyptus* plantations have a lower species diversity of plants (Barlow *et al*., 2007; Proença *et al*., 2010; Calviño-Cancela *et al*., 2012) and birds (Bongiorno, 1982; Pina, 1989; Tellería and Galarza, 1990; Barlow *et al*., 2007; Proença *et al*., 2010; Calviño-Cancela, 2013; De la Hera et al., 2013), compared to native forests. This difference is not only caused by plantations tending to be younger than native forests, since also *Eucalyptus* plantations older than 25 years do not provide habitat as suitable as native forests for many plant species (Calviño-Cancela *et al*., 2012). However, surprisingly few studies have analysed if the replacement of native forests by exotic plantations affect rare or specialist species to a greater extent than common generalist species (Proença *et al*., 2010; Calviño-Cancela *et al*., 2012), e.g. by analysing if there are systematic patterns in community dissimilarity between native forests and *Eucalyptus* plantations (Olden *et al*., 2004). Changes in community dissimilarity can in turn be explained by analysing species nestedness and turnover (Baselga *et al*., 2007). Species nestedness occurs when species assemblages in sites with fewer species are subsets of species assemblages at richer sites (Ulrich & Gotelli, 2007). In contrast, spatial turnover implies a systematic replacement of some species by others, as a consequence of environmental sorting or spatial and historical constraints (Qian *et al*., 2005).

In this study, we analysed whether patches of native forest have a higher species richness and diversity of birds and plants than patches of *Eucalyptus* plantation. Higher biodiversity in native forests can be expected as a result of a long history of low-intensity land-use resulting in species-rich plant and bird communities, as well as because of more benign habitat characteristics of native forests (Cordero, 2011). In addition, we analysed if *Eucalyptus* plantations lead to biotic homogenization driven by a systematic loss of rare or specialist species (McKinney and Lockwood, 1999), or species turnover, where different species predominantly occur in either native forests or in plantations. We focused on herbs and birds as they are commonly used as biodiversity indicators but characterized by different mobility and degree of habitat specificity, and therefore can be expected do respond differently to local habitat characteristics (Ekroos *et al*., 2013).

3.2. MATERIALS AND METHODS

3.2.1. Study area

The study was performed in the centre of Galicia (Ulloa Shire), in the North West of the Iberian Peninsula. The study area consisted of a hilly mosaic farmland-forest mixed landscape, of a 421 km^2 and at an altitude of between 400 and 750 m above sea level. 46% of the area is forested, both by natural forests and plantations (IGE, 2012). Native deciduous forest is largely comprised of oak (*Quercus robur*), chestnut (*Castanea sativa*) and birch (*Betula alba*), classified as *Rusco aculeati – Quercetum roboris* and *Holco mollis – Betuletum celtiberiace* forest associations (Amigo *et al*., 2017). However, during the past 25 years, *Eucalyptus* plantations have increased rapidly in Galicia (Manuel and Gil, 2002), and now cover an area larger than that of native forest (500.000 ha *Eucalyptus* vs 400.000 ha native forests in 2016) (IFN, 2017). Most land in Galicia is privately owned, and 83% of the *Eucalyptus* plantations in the region are on private land. During the past 30 years, 70% of the agricultural land in Galicia was abandoned (IGE, 2012), paving the way for *Eucalyptus* plantations, which are normally harvested 15-18 years after plantation, in order to re-grow or re-plant them.

The plantations of *Eucalyptus* species in the study region have mainly replaced natural and semi-natural habitats that would have been covered by native forests by natural succession if left unmanaged (Calviño-Cancela, *et al*., 2012). *Eucalyptus* plantations have also directly replaced native forest (even though this is restricted by law; DOG, 1989). Thus, although native forest still remain, particularly in mountainous areas, increasing *Eucalyptus* plantations have contributed to an increasing fragmentation of native oak forests (Teixido *et al*., 2010). Because *Eucalyptus* plantations are replacing land that otherwise would develop into native forests if left undisturbed, a comparison of biodiversity between these plantations and native forests can inform about how planting of *Eucalyptus* will affect future biodiversity (Stephens and Wagner, 2007).

We performed a comparative study based on 14 pairs of matched patches of native forest and *Eucalyptus* plantation. Patches within each pair were matched on proximity (max 10 km apart) and size (with a minimum of 10 ha). Of the 14 *Eucalyptus* plantations studied, only two were pure stands. The remaining plantations had other marginal tree species (mainly oak), comprising 0.33-25% of the trees, that grew scattered between the *Eucalyptus* trees (Appendix A). Only four out of 14 *Eucalyptus* plantations were actively managed, mainly by removal of undergrowth each year. The four managed plantations had less than 50% cover of shrubs (mainly *Erica, Ulex* and *Cytisus* species), while shrub cover in the remaining plantations ranged between 50 and 80% (see Appendix A for information about patch vegetation characteristics). There was no significant difference in patch sizes between patch types (native forests: mean size 33.7 ha, range 11–62 ha; *Eucalyptus* patches: mean size 31.3 ha, range 10–70 ha; Appendix A).

3.2.2. Surveys

Data were collected between early May and late July in 2017, when two visits to each pair of patches were performed. All surveys were done by the same person. Each pair of patches was surveyed on the same day (cf. Kleijn *et al.*, 2006) and the order in which the surveys were carried out within the pair was systematically switched between visits, to avoid effects of time of day (cf. Dänhardt *et al.*, 2010).

3.2.2.1. Plant surveys

In three 20 x 20-m square plots within each patch, separated by 250 m along a 500 m transect across the centre of the patch, herbs were identified to species (cf. Santos *et al.*, 2010). We used the total number of plant species observed during both survey rounds to calculate species richness and composition. As a proxy for plant abundance used the frequency of 20 x 20m plots each plant species was recorded at in a site (range 0 to 3) during the second survey round when most herbs were flowering.

3.2.2.2. Bird censuses

Birds were censused along the 500-m long transects described above. Birds were recorded up to a distance of 25 m at each side of the transect (Tellería and Galarza, 1990). Bird censuses were carried out during a 2-hour period, starting after sunrise. Birds observed flying over the study patches and birds of prey belonging to the family *Strigidae* were not included in analyses due to inadequacy of this method to survey these species (Calviño-Cancela, 2013).

3.2.3. Quantification of vegetation parameters

Eight different vegetation characteristics were recorded: number of trees, number of species of trees, tree diameter at breast height (DBH), tree height, percentage of canopy cover, number of species of shrubs, shrub height, and percentage of shrub cover (De la Hera *et al.*, 2013; Appendix A). All these parameters except number of trees and DBH, were recorded within each of the three 20 x 20 m sample plots described above, which were instead measured in three sub-squares of 8x3 m within each 20 x 20 m plot. All values were averaged between sample plots in order to obtain a single descriptor for each vegetation characteristic for each patch. Number of trees and DBH were first averaged per sample plot and then per patch.

Since the eight vegetation parameters estimated in each study patch were inter-correlated, we used principal components analysis (PCA) to create a set of uncorrelated vegetation descriptors (De la Hera *et al.*, 2013). From the eight original vegetation variables introduced in the PCA, we selected the three first principal components, which together explained 73.1% of the total variation. Our main goal was to characterize the two patch types, rather than directly analyze effects of vegetation structure on birds and herbs. PC1 was positively correlated with the number of trees in each study patch (r_P = 0.49), and negatively to tree species richness (r_P = -0.45), canopy cover (r_P = -0.48) and shrub species richness (r_P = -0.46). Thus PC1 was interpreted as a measure of structural and taxonomic forest diversity. PC2 was negatively correlated with shrub height (r_P = -0.601), and positively with tree height (r_P = 0.595) and tree diameter (r_P = 0.441), characterising a gradient in tree size whereas PC3 was positively correlated with the percentage of cover of shrubs ($r_P = 0.744$).

3.2.4. Statistical analyses

To describe differences in vegetation characteristics and patch type, we compared both the vegetation characteristics and PC-variables between patch types, using paired t-tests. In addition, linear regressions were used to relate response variables to PC-variables describing vegetation characteristics. In all cases, the requirements for normal distribution of residuals were met (Quinn and Keough, 2002).

Linear mixed models (function lme() available in library nlme; Pinheiro *et al.*, 2011) were used to measure the effect of patch type (native vs exotic), and patch size on species richness and Shannon diversity for herbs and birds. Separate models were created for herbs and birds, with species richness and Shannon diversity as response variables, and patch type, patch size and the interaction between patch type and patch size as fixed effects. Patch size was log transformed. Pair identity was used as a random factor, to take into account that the observations within each pair were not independent. Bird species richness was log-transformed to achieve normal distribution of residuals. All models on species richness and diversity were assessed for normality and homoscedasticity. For the bird models, we found heterogeneity of variances between patch types, with a higher residual variance in *Eucalyptus* than native patches. We therefore adjusted the variance-covariance structure for patch type in these models using the varIdent()-function available for mixed models in library nlme (Zuur *et al.*, 2009).

We analysed species nestedness and spatial turnover of both herb and bird species using nestedness and turnover partitioning of community dissimilarity as implemented in library betapart (Baselga *et al.*, 2012). For this approach, we calculated Sörensen's dissimilarity based on presence-absence matrices for herbs and birds, and dissimilarity matrices were used to calculate nestedness and turnover components. Nestedness and turnover in bird and herb communities was thereafter analysed using permutational analysis of variance (function adonis() implemented in library vegan; Oksanen *et al.*, 2013), including patch type as a fixed factor (Jacoboski *et al.*, 2016). P-values were derived based on 999 permutations (Oksanen *et al.*, 2013). All statistical analyses were done using R 3.2.3 (R Core Team, 2008).

3.3. RESULTS

3.3.1. Vegetation parameters

Patch types differed significantly in PC1 ($t = 13.9$, $df = 13$, $P < 0.0001$), indicating that *Eucalyptus* plantations have a much higher density of trees, but a much lower tree diversity, shrub diversity and canopy cover (Fig. 1A). PC2 and PC3 did not significantly differ between patch types ($t \leq 0.78$, $P \geq 0.447$), indicating that tree size and shrub development did not significantly differ between native forests and *Eucalyptus* plantations (Fig. 1B-C).

3.3.2. Herbs

We found a total of 31 herb species in native forest patches and 25 herb species in *Eucalyptus* plantation patches. There were eleven species only observed in native patches and seven species only observed in *Eucalyptus* plantations (Appendix B).

Herb species richness was significantly related to patch type ($F_{1,12}$ = 9.07, P = 0.0108), being higher in native forests than *Eucalyptus* plantations (Fig. 2A). Shannon diversity index was also significantly related to patch type ($F_{1,12}$ = 8.61, P = 0.0125), with consistently higher plant diversity in native forests compared with *Eucalyptus* plantations (Fig. 2B). Neither herb species richness, nor herb Shannon index, were significantly related to patch size ($F_{1,12}$ = 0.26, P = 0.6223; $F_{1,12}$ = 0.36, P = 0.5568). Species richness of herbs was associated with structural and taxonomic forest diversity (i.e. decreasing herb species richness with increasing PC1; r = -0.44, df = 26, P = 0.0186, Fig. 1D), but not with forest maturity or shrub development ($P > 0.83$ in both cases, Fig. 1E-F).

Herb species did not show signs of nestedness between native forests and exotic *Eucalyptus* ($F_{1,1}$ = 0.223, pseudo-R^2 = 0.008, P = 0.653). In contrast, herb communities were significantly different from each other between native forests and *Eucalyptus* plantations, based on significant turnover between patch types ($F_{1,1}$ = 7.623, pseudo-R^2 = 0.227, P = 0.001).

3.3.3. Birds

We found 2,384 birds belonging to 37 species in native forest patches and 548 birds of 34 species in *Eucalyptus* plantation patches. The average number of bird species in native forest patches was 26.6 (*SD* = 1.8) and that of *Eucalyptus* patches 12.9 (± 3.7). Four species were only observed in native patches (*Prunella modularis, Sylvia communis*, *Turdus viscivorus* and *Upupa epops*) and one species only in *Eucalyptus* plantations (*Accipiter nisus*) (Appendix C).

Bird species richness ($F_{1,12}$ = 85.81, $P < 0.0001$) and Shannon diversity ($F_{1,12}$ = 59.41, $P < 0.0001$) were significantly higher in native forests than *Eucalyptus* plantations (Fig. 2C-D). As with herbs, neither bird species richness, nor Shannon index, were significantly correlated to patch size ($F_{1,12}$ = 1.7, P = 0.2169; $F_{1,12}$ = 1.52, P = 0.2414, respectively).

Bird species richness was significantly associated with structural and taxonomic forest diversity (PC1, r = -0.901, df = 26, $P < 0.0001$, Fig. 1G), but not with tree size or shrub development ($P > 0.45$ in both cases, Fig. 1H-I).

Bird communities were strongly nested in response to patch type ($F_{1,1}$ = 109.89, pseudo-R^2 = 0.82, P = 0.001), with exotic plantations leading to a systematic overall homogenisation of bird assemblages. The analysis on bird community turnover returned a negative F-value and was therefore discarded.

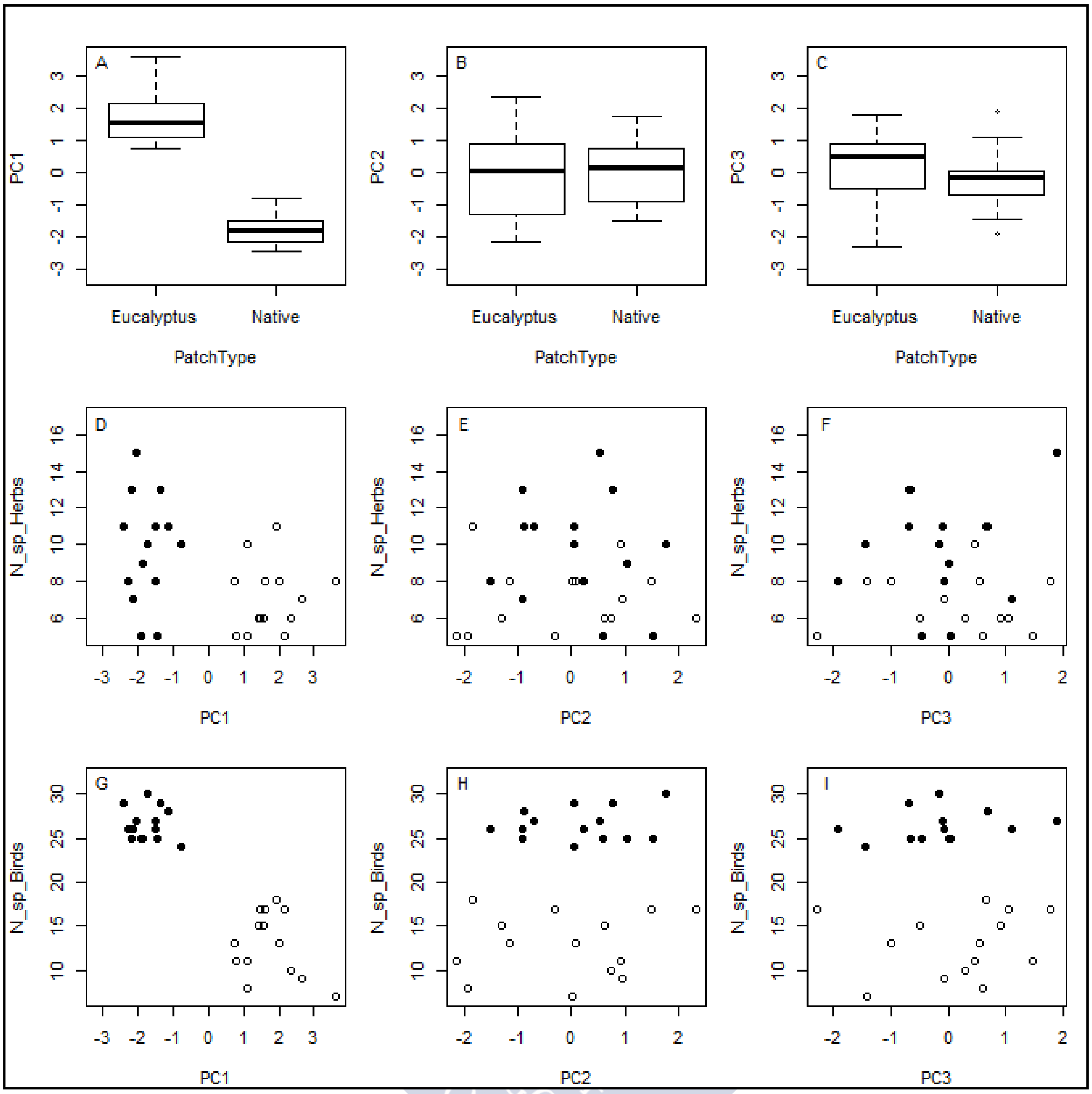

Fig.1. Forest characteristics (PC1-PC3) between forest types (panels A-C) and relationships between herb species (panels D-F), and bird species richness (panels G-I) and forest characteristics (PC1-PC3). PC1 corresponds to patch structural and taxonomic diversity; PC2 relates to tree size and PC3 to shrub development. Filled dots correspond to native forest patches and empty dots correspond to *Eucalyptus* patches.

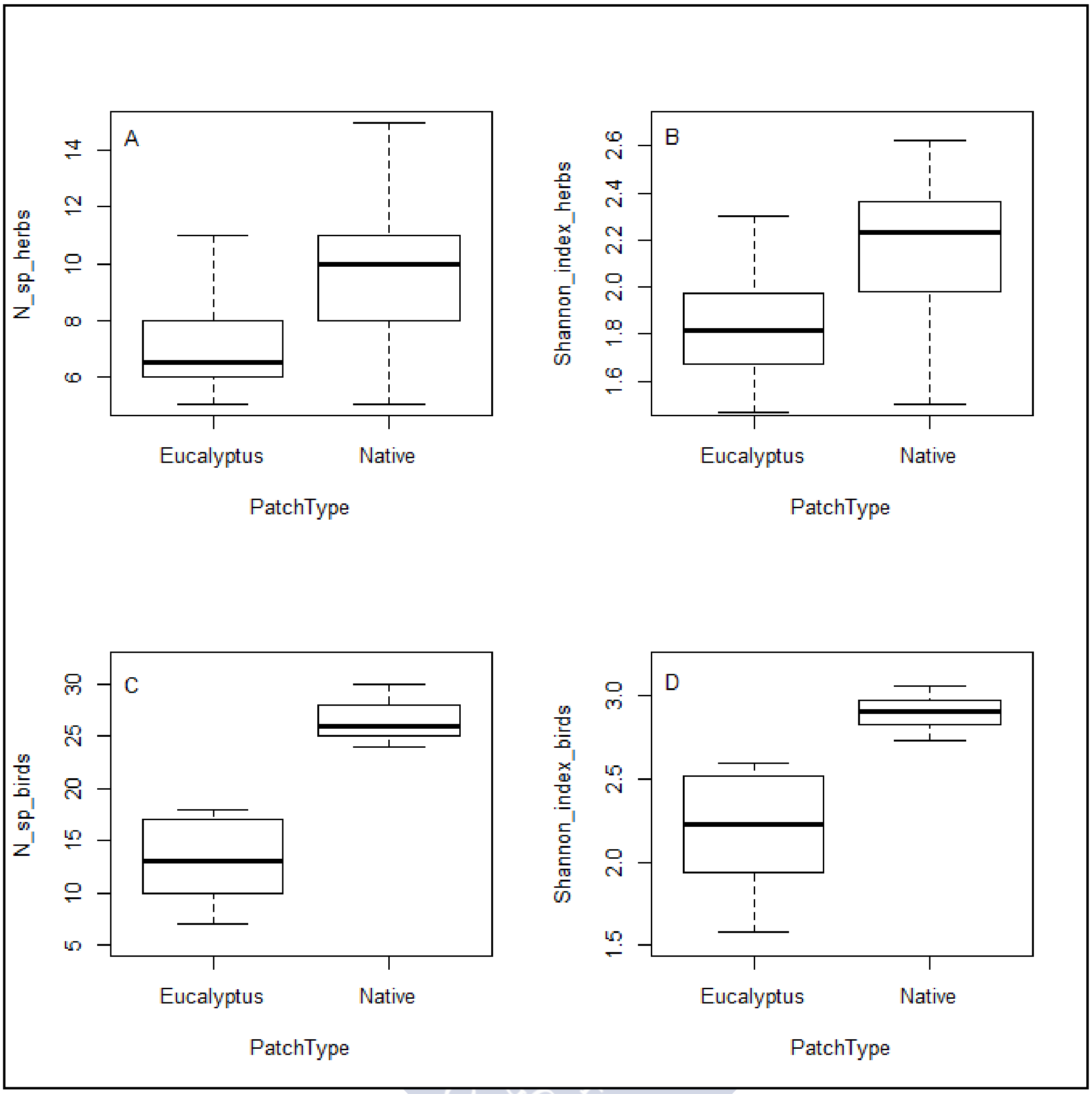

Fig. 2. Boxplots on species richness and Shannon diversity of herbs (panels A-B) and birds (panels C-D) in *Eucalyptus* and native forest patches, respectively.

3.4. DISCUSSION

We found that herb and bird species richness and Shannon diversity were consistently higher in all patches of native forest compared to *Eucalyptus* plantations, demonstrating that native forests provide much richer habitats for birds and herbs compared to *Eucalyptus* plantations. These results agree with previous studies in the North of the Iberian Peninsula, both for plants (Proença *et al*., 2010; Calviño-Cancela *et al*., 2012) and birds (Bongiorno, 1982; Pina, 1989; Tellería and Galarza, 1990; Proença *et al*., 2010; Calviño-Cancela, 2013; De la Hera *et al*., 2013). We also found that *Eucalyptus* plantations significantly contributed to community nestedness in birds, demonstrating that *Eucalyptus* plantations lead to biotic homogenization of bird communities compared to native forests (c.f. Jacoboski *et al*., 2016). Furthermore, we found that there was a significant spatial turnover of herb species between native forests and *Eucalyptus* plantations. Thus, in addition to reducing local herb species richness, exotic plantations are also characterized by different plant species compared to native forests. Our results show that *Eucalyptus* plantations reduce bird and plant diversity in a taxon-specific manner, i.e. by biotic homogenization in bird assemblages and spatial turnover of herb communities.

In our study, the main differences between native and exotic patches were the density of trees and the species richness of trees and shrubs. While the density of trees was much higher in *Eucalyptus* plantations, the species richness of trees and shrubs was much lower. This difference in forest structure between native forests and *Eucalyptus* plantations explained the differences in species richness and diversity for both birds and plants. Decreasing numbers of trees, and increasing tree and shrub species richness in native forests were strongly associated with high species richness and Shannon diversity for both herbaceous plants and birds. Plantations are usually established including one (*Eucalyptus nitens*) or two (*E. nitens* and *Pinus radiata*) tree species which are densely planted, with some naturally occurring species, usually *Quercus robur*, being able to grow between the planted trees. In native forests *Q. robur*, *Castanea sativa* or *Betula alba* typically dominate, and thus the species richness in native patches in our study was 3.7 tree species and 11.1 shrub species on average, compared to only 1.9 and 6.9 in *Eucalyptus* plantations (Appendix A). Furthermore, mechanical and chemical (mineral fertilizers and biocides) land preparations before *Eucalyptus* plantations are carried out may result in loss of important aspects of biodiversity. Other characteristics of plantations, not estimated in this study, such as the homogeneity in tree age, lack of dead wood and old trees of any tree plantation could also contribute to reduce plant and bird biodiversity, as evidenced by that *Eucalyptus* plantations harbour less species than natural *Eucalyptus* forests, even in their native range in Australia (Cunningham *et al*., 2005).

Whilst both herb and bird diversity was consistently lower in plantations, we found that herb species and bird communities were affected in different ways. First, we found a significant turnover in herb species between native forests and *Eucalyptus* plantations. In native forest patches the most frequent herbs were typical of mixed and deciduous temperate forests, whereas plants in *Eucalyptus* patches mainly belonged to scrublands or mesophile to wet meadows and pastures (Rivas-Martínez *et al*., 2002; Appendix B). In addition, we found eleven species of herbs only in native forest patches, all of which are typical for managed pastures, wood fringes or deciduous forests with wet soils. In contrast, the seven herb species that were found exclusively in *Eucalyptus* patches are all typical for pastures and scrubland communities (Rivas-Martínez *et al*., 2002; Appendix B). Therefore, there is a turnover between native forest patches, including species with varying habitat requirements, and *Eucalyptus* plantations, mostly including species typical for meadows and scrublands (also see Proença *et al*., 2010). This result may be explained by a combination of biological legacy (Franklin *et al*., 2000) and habitat variability amongst native forests. Native forests established on abandoned farmland can harbour herb species that are typically found in pastures, due to biological legacy effects. As native forests mature, they acquire wet and shady soil conditions which mainly benefit forest specialist species. Therefore, patches of native forests in our study together contain a big range of herb species, typical for either abandoned pastures or wet forest soils, depending on forest maturity. By contrast, plantations have mostly been established in farm- and scrubland, reflecting the biological legacy of communities present in the area before the plantations were established. With time, *Eucalyptus* plantations are known to change soil conditions (Bargali *et al*., 1993, Souto *et al*., 2001; Martín *et al*., 2011) and induce local scarcity of water (Cordero, 2011), with detrimental effects on forest habitat specialists. Hence, *Eucalyptus* plantations cannot substitute native forest habitats, as they will not support herb species typical for native forests (Calviño-Cancela *et al*., 2012). In addition, intensive management practices in *Eucalyptus* plantations during harvest may further decrease the number of soil quality plant species in the long run (Rab, 1994).

In contrast to herbs, we found that *Eucalyptus* plantations lead to a systematic loss of bird species, consistent with biotic homogenisation. The observed nestedness in bird species was mainly driven by declines in forest species and some habitat generalists, as nine forest species and five habitat generalist species found in native forests were either absent or very infrequently observed in *Eucalyptus* patches (Appendix C). In our study we observed one species that was only present in *Eucalyptus* plantations (*Accipiter nisus*, Appendix C). This species is known to be a forest species that has well adapted to modern tree plantations, although it is not exclusively found on them (Hesterkamp, 2015). Regarding forest species found in both patch types, the 80% of the total abundance was found in native forests (Appendix C). The strong differences in bird assemblages can be partly explained by the presence of old trees and large trunks in native forests, providing tree holes and other nesting sites, which are not present in *Eucalyptus* plantations (Carrascal and Tellería, 1990). In our study, all species nesting in primary or secondary tree holes, such as *Cyanistes caeruleus, Dendrocopus major, Parus major, Periparus ater, Sitta europaea* and *Sturnus unicolor,* were all at least 79% more abundant in native forests patches, except *Picus viridis* which was only 64% more abundant (Appendix C). The physical and chemical characteristics of *Eucalyptus* trees are known to reduce lichens and other epiphytes, as well as herbivorous insects (Cadahia, 1980, Calviño-Cancela *et al*., 2013), and therefore potentially bird food resources, which partly may explain the differences in bird diversity.

We found a higher variance in bird species richness and Shannon index within the *Eucalyptus* patches studied compared to native patches. This heterogeneity was driven by the differences in management practices in the *Eucalyptus* plantations, and in particular by structural forest diversity (see Fig. 1A, D and G). Our results show that more diverse *Eucalyptus* plantations are associated with higher bird diversity, but structural diversity in plantations is not allowed by legislation, stating that tree plantations must be managed and the undergrowth cut in order to prevent fires (BOE, 2012). In our study, only two plantations had the understory cleared every year, which is the common scenario in the area due to rural abandonment (Marey-Pérez *et al*., 2006). We therefore suggest that allowing more diverse plantation stands could mitigate bird biodiversity loss, by increasing nesting sites and food availability (Calviño-Cancela, 2013), although it would never replace native forest habitats and their biodiversity richness.

It has been suggested that increasing plantation age might mitigate biodiversity loss (Calviño-Cancela *et al*., 2012). In our study, we compared biodiversity in natural mature forests with *Eucalyptus* plantations that were predominantly young, as in our study region the vast majority of *Eucalyptus* plantations are harvested much before reaching maturity, i.e. 15-18 years after establishment. Therefore, we could not analyse if increasing age of *Eucalyptus* plantations could benefit bird or plant diversity in the study area. However, whereas allowing for longer rotations in *Eucalyptus* plantations may palliate biodiversity loss in these plantations, the dramatic differences in bird nestedness and herb turnover are unlikely to compensate for native forest loss. Therefore, the conservation of native forest patches and mosaic landscape should be the priority in order to conserve biodiversity in the area.

3.5. CONCLUSION

Our results showed that *Eucalyptus* plantations constitute a much poorer habitat for both plants and birds than native forests, with significantly lower species richness, abundance and diversity in both taxa. In addition, because *Eucalyptus* plantations drive biotic homogenization of birds and species turnover in herbs, an increasing extent of exotic plantations would most likely lead to further loss of biodiversity, with highest effect on forest specialist species. In addition, other studies have shown that *Eucalyptus* plantations also lead to biodiversity loss of other taxa, such as aquatic macroinvertebrates (Cordero-Rivera *et al*., 2017), and thus the consequences of increasing these plantations in the area would possibly affect many habitats and taxa. Therefore, the conservation of native forest patches in the study area needs to be prioritised if biodiversity loss is to be avoided.

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3.7.APENDICES

APPENDIX A

Vegetation characteristics for each 14 native and 14 eucalyptus patches in the study, showing their type (Native vs *Eucalyptus*); Size (in Ha); Patch ID; Pair, distance in metres from transect to nearest edge ("Dist. Trans. Edge"); average number of trees ("N. trees"); tree diameter at breast height in centimeters ("DBH"); tree height in metres ("Tree height"); number of species of trees ("N. sp. trees"); percentage of canopy cover ("P. can. cov."); number of species of shrubs ("N. sp. shrub"); percentage of shrub cover ("P. cov. shrub") and shrub height in metres ("Shrub height") in the three 20 x 20 plots for each patch.

Patch Type	Size	Patch ID	Pair	Dist. Trans. Edge	N. trees	DBH	Tree height	N. sp. trees	P. can. cov.	N. sp. shrub	P. cov. shrub	Shrub height
Native	38	14A	1	30	27.22	73.33	19.67	6	78.33	9	60.00	1.23
Eucalyptus	30	11E	1	30	533.33	40.00	10.67	1	46.67	6	40.00	0.43
Native	62	0A	2	100	19.78	25.56	19.00	5	73.33	11	56.67	0.55
Eucalyptus	70	14E	2	150	383.33	55.00	18.67	3	43.33	6	45.00	0.80
Native	58	6A	3	80	15.11	91.11	16.33	5	76.67	9	53.33	0.63
Eucalyptus	70	13E	3	150	200.00	65.00	11.67	4	41.67	5	50.00	1.02
Native	49	11A	4	100	17.78	53.33	20.67	7	68.33	13	70.00	0.50
Eucalyptus	39	9E	4	80	363.33	75.00	27.33	3	43.33	11	63.33	0.40
Native	43	3A	5	140	13.56	113.33	16.67	4	78.33	11	56.67	0.40
Eucalyptus	35	5E	5	50	280.00	100.00	20.00	3	46.67	6	53.33	0.95
Native	42	13A	6	20	12.56	71.11	17.00	8	56.67	14	56.67	1.17
Eucalyptus	33	0E	6	30	240.00	29.67	29.67	1	36.67	7	56.67	0.80
Native	32	7A	7	110	13.00	80.90	13.67	4	80.00	11	81.67	0.95
Eucalyptus	33	2E	7	30	206.67	40.00	16.67	3	45.00	8	80.00	1.27
Native	30	9A	8	150	35.33	35.56	19.00	5	86.67	11	53.33	0.60
Eucalyptus	25	1E	8	40	218.67	26.67	22.50	5	40.00	6	26.67	1.03
Native	28	5A	9	100	15.22	86.67	28.00	4	78.33	10	56.67	0.86
Eucalyptus	25	4E	9	50	307.67	93.33	28.00	2	41.67	8	63.33	0.87
Native	23	1A	10	50	15.89	57.78	14.00	4	78.33	14	66.67	1.18
Eucalyptus	25	7E	10	30	286.67	33.33	11.67	2	33.33	8	70.00	0.92
Native	21	4A	11	30	26.56	100.00	22.33	3	78.33	11	81.67	0.93
Eucalyptus	17	3E	11	30	100.00	46.67	14.67	4	40.00	6	75.00	0.75
Native	19	8A	12	100	20.78	73.61	17.33	6	86.67	12	60.00	0.85
Eucalyptus	14	8E	12	40	250.67	60.00	22.33	3	30.00	6	48.33	0.60
Native	16	2A	13	60	28.11	61.11	14.67	3	80.00	9	76.67	0.87
Eucalyptus	10	12E	13	20	183.33	73.33	20.67	5	43.33	6	66.67	0.47
Native	11	12A	14	50	12.67	85.56	18.33	4	81.67	12	65.00	0.53
Eucalyptus	13	6E	14	30	123.33	40.00	14.67	4	33.33	7	70.00	1.08

APPENDIX B

Herb species observed in the study, with their corresponding phytosociological class and habitat (following Rivas-Martínez *et al.*, 2002), being "FLP": Freshwater lakes and ponds; IGAG": Intensely grazed acidophilous grasslands; "LRS": Lithosols and rock surfaces; "MWMP": Mesophile to wet meadows and pastures; "NNP": Non nitrophilic pastures; "NSSWF": Nitrified and semi-shaded wood fringes; "NWC": Nitrophilic walls and caves; "PG": Perennial grasslands; "SC": Scrubland; "SSFE": Semi-shaded forest edges and "TDMF": Temperate decidious or mixed forests. Together with the total frequencies found in all native and *Eucalyptus* patches added.

Species	Phytosociological class	Habitat	Native	Eucalyptus
Agrostis curtisii	*Calluno-Ulicetea*	*SC*	0	1
Agrostis stolonifera	*Molinio-Arrhenatheretea*	*MWMP*	4	7
Agrostis tenuis	*Molinio-Arrhenatheretea*	*MWMP*	3	6
Anthoxanthum amarum	*Galio-Urticetea*	*NSSWF*	2	0
Arenaria montana	*Querco-Fagetea*	*TDMF*	16	22
Arrhenatherum elatius ssp. bulbosum	*Molinio-Arrhenatheretea*	*MWMP*	27	22
Arrhenatherum longifolium	*Calluno-Ulicetea*	*SC*	9	2
Briza maxima	*Tuberarietea guttatae*	*NNP*	0	3
Centaurea nigra	*Trifolio-Geranietea*	*SSFE*	0	2
Clynopodium vulgare	*Trifolio-Geranietea*	*SSFE*	1	0
Daboecia cantabrica	*Calluno-Ulicetea*	*SC*	0	1
Dactylis glomerata	*Molinio-Arrhenatheretea*	*MWMP*	14	5
Digitalis purpurea purpurea	*Carici piluliferae*	*NSSWF*	23	5
Galium aparine	*Galio-Urticetea*	*NSSWF*	8	0
Geranium robertianum	*Galio-Urticetea*	*NSSWF*	5	3
Gladiolus illyricus	*Festuco-Brometea*	*SSFE*	0	1
Halimium lasianthum ssp. alyssoides	*Calluno-Ulicetea*	*SC*	0	16
Holcus mollis	*Querco-Fagetea sylvaticae*	*TDMF*	35	25
Hypochoeris radicata	*Molinio-Arrhenatheretea*	*MWMP*	3	0
Iris pseudacorus	*Magnocarici-Phragmitetea*	*FLP*	7	2
Lamium maculatum	*Galio-Urticetea*	*NSSWF*	1	1
Lithodora prostrata	*Calluno-Ulicetea*	*SC*	7	13
Lolium perenne	*Molinio-Arrhenatheretea*	*MWMP*	9	12
Malva tournefortiana	*Stipo giganteae-Agrostietea castellanae*	*PG*	0	1
Mentha spicata	*Molinio-Arrhenatheretea*	*MWMP*	3	0
Mercurialis annua	*Galio-Urticetea*	*NSSWF*	10	0
Poa nemoralis	*Molinio-Arrhenatheretea*	*MWMP*	2	1
Potentilla erecta	*Nardetea strictae*	*IGAG*	3	1
Ranunculus repens	*Molinio-Arrhenatheretea*	*MWMP*	2	0
Scilla verna	*Nardetea strictae*	*IGAG*	2	0
Sedum acre	*Sedo-Scleranthetea*	*LRS*	1	0
Stellaria holostea	*Querco-Fagetea*	*TDMF*	18	3
Teucrium scorodonia	*Querco-Fagetea sylvaticae*	*TDMF*	5	0
Umbillicus rupestris	*Parietarietea judaicae*	*NWC*	5	1
Urtica dioica	*Galio-Urticetea*	*NSSWF*	2	1
Veronica chamaedrys	*Trifolio-Geranietea sanguinei*	*SSFE*	7	0
Xolantha gutatta	*Tuberarietea guttatae*	*NNP*	0	1

APPENDIX C

Bird species observed in the study, with their typical habitat (following EBCC, 2014), being “AG”: Agricultural; “IN”: Indetermined; “FO”: Forestal and “SH”: Scrubland; the proportional abundances in native (“Prop. Native”) and *Eucalyptus* (“Prop. Eucalyptus”) patches related to the total abundance per species; the total abundances observed per patch; together with the total number of species and abundance in each patch type.

Species	Habitat	Prop. Native	Prop. Eucalyptus	Native	Eucalyptus
Accipiter nisus	IN	0.00	1.00	0	3
Aegithalos caudatus	IN	0.92	0.08	54	5
Anthus trivalis	IN	0.71	0.29	24	10
Buteo buteo	IN	0.82	0.18	18	4
Carduelis carduelis	AG	0.71	0.29	5	2
Carduelis chloris	AG	0.58	0.42	15	11
Certhia brachydactyla	FO	0.97	0.03	28	1
Columba palumbus	FO	0.82	0.18	123	27
Corvus corone	AG	0.70	0.30	65	28
Cuculus canorus	IN	0.91	0.09	21	2
Cyanistes caeruleus	FO	0.97	0.03	74	2
Dendrocopus major	FO	0.85	0.15	40	7
Emberiza cirlus	AG	0.60	0.40	3	2
Erithacus rubecula	FO	0.73	0.27	232	87
Fringilla coelebs	FO	0.93	0.07	147	11
Garrulus glandarius	FO	0.73	0.27	61	23
Hippolais polyglotta	SH	0.71	0.29	5	2
Lophophanes cristatus	FO	0.71	0.29	42	17
Motacilla alba	AG	0.33	0.67	1	2
Oriolus oriolus	FO	0.96	0.04	26	1
Parus major	FO	0.91	0.09	138	13
Periparus ater	FO	0.79	0.21	201	52
Phylloscopus ibericus	IN	0.85	0.15	80	14
Picus viridis	IN	0.64	0.36	16	9
Prunella modularis	SH	1.00	0.00	2	0
Pyrrhula pyrrhula	FO	0.88	0.13	14	2
Regulus ignicapillus	FO	0.89	0.11	154	19
Serinus serinus	AG	0.72	0.28	13	5
Sitta europaea	FO	0.99	0.01	72	1
Streptopelia turtur	AG	0.83	0.17	49	10
Sturnus unicolor	AG	0.94	0.06	16	1
Sylvia atricapilla	IN	0.83	0.17	151	32
Sylvia communis	IN	1.00	0.00	1	0
Troglodythes troglodythes	SH	0.73	0.27	346	127
Turdus merula	IN	0.89	0.11	98	12
Turdus philomelos	FO	0.91	0.09	40	4
Turdus viscivorus	FO	1.00	0.00	7	0
Upupa epops	AG	1.00	0.00	2	0
Total Num sp.				37	34
Total Abund.				2384	548


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GENERAL CONCLUSIONS

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CONCLUSIONS

This thesis addressed the effects on biodiversity of contemporary agricultural and forest practices in an agro-forest mosaic landscape of North-West Spain. As the main land use changes that have occurred in Europe during the last 50 years are agricultural intensification and the plantation of fast-growing exotic tree species, I aimed to study if these changes have an effect on biodiversity and community composition of birds, butterflies and plants.

I demonstrated that birds were affected by agricultural intensification in mosaic landscapes, as there was higher bird species richness on organic farms, and that this effect was more important during winter than during other seasons. The higher bird species richness in organic farms in winter is probably a result of higher food availability in organic farms resulting from fields not being ploughed as frequently as on conventional farms, as a result of long crop rotations and the use of permanent pastures. In addition, I showed that a combination of organically managed farmland and surroundings with patches of native forest, resulted in particularly high bird abundance, especially for seedeater bird species, most likely because the agro-forest mosaic offers birds both feeding and roosting habitats. Finally, my results showed that birds concentrate more on organic farms in very heterogeneous areas, where there are small proportions of agricultural land overall, and that therefore these organic farms could serve as attraction points, providing resource-rich patches in poor areas for agricultural birds. When placing this study into a broader context, our study showed more subtle positive effects of organic farming on birds compared to other studies in Northern and Central Europe, which is most probably due to the heterogeneous landscape of the region, which mitigates the effects of agricultural intensification. However, studies like this one are very important in order to understand if and how organic farming can mitigate the loss of farmland biodiversity that agicultural intensification has produced in mosaic landscapes.

In addition to this, I demonstrated that agricultural intensification also affects butterflies negatively, since I found higher species richness in organic than in conventional farms. Moreover, also the functional diversity of butterflies was affected, i.e. the butterfly communities were more functionally rich in organic compared to conventional farms. This suggests that organic farming practices could positively affect the effectiveness by which butterflies can use the resources that are available in farmland habitats and, thus make butterfly communities more resilient to environmental or land use changes. In addition, although we found no effect of organic farming on plant species richness or plant functional diversity, we showed that some species of plants, mainly grassland specialists, were more abundant in organic than in conventional farms, therefore enhancing the positive effect of organically-managed farms to restore the heterogeneity that agricultural intensification has eroded.As explained before, this lack of difference in plant species richness between organic and conventional farms could be due to the heterogeneity of the landscape in the study region, very different to the homogeneous landscapes of Central and Northern Europe, where most studies have been done, and the fact that this study was done mostly on grasslands and not cereal crops. Therefore, I predict that the differences in plant species richness would be much higher between organic and conventional maize fields, as an example.

Finally, I studied the effects that the increasing plantations of *Eucalyptus* trees have on the plants and birds that live or depend on the agro-forest mosaic landscapes. I demonstrated that both the species richness and diversity indices of plants and birds were much higher in native forests than in *Eucalyptus* plantations, showing that both the direct and indirect replacement of native forests by these exotic plantations affect biodiversity, as they constitute a much poorer habitat than native forests. In addition, I showed that the *Eucalyptus* plantations result in biotic homogenisation of birds (i.e. loss of rare or forest specialist species), and species turnover of plants, with more scrubland plant species and less forest specialist plant species in *Eucalyptus* plantations. Therefore, I predict that the large-scale plantations of this exotic tree will have profound negative effects on biodiversity. Given the big amount of land at a global scale destined to *Eucalyptus* plantations, more studies like this one should be done in order to understand their negative effects on biodiversity and promote more sustainable forest uses by prioritising native species plantations and management.

To sum up, I was able to demonstrate how habitat degradation, by means of agricultural intensification; overexploitation, by means of native forest loss; and introduction of exotic species like *Eucalyptus spp*., are affecting biodiversity negatively in a mosaic agro-forest landscape of North-West Spain. If these agricultural and forest practices are further expanded, their consequences on organisms could seriously compromise the long-term conservation of biodiversity. Thus, my results suggest that one way to mitigate biodiversity loss is the promotion and implementation of alternative agricultural practices, such as organic farming, or forest practices preserving native Atlantic forests, and that these should be prioritised and promoted by local and national governments. In addition, I was able to demonstrate that some plant species, such as grassland specialists, are particularly affected by agricultural intensification, as they are more present in organic farms, thus, if organic farms are promoted, these species could be benefited. On the same line, forest specialist plant and bird species were negatively affected by the plantations of *Eucalyptus* trees, and therefore the expansion of these plantations could significantly reduce the densities of these species.

PRACTICAL RECOMMENDATIONS

From the many conversations and time spent with farmers and landowners, the general impression I got is that the economical incentives given by the government for the sustainable use of their lands is either non-sufficient or even absent. In the case of organic farmers, there is an economic incentive to manage organically for farms that are registered in the Regional Board of Organic Farming, which, in some cases, is the only reason why they changed their farms from being conventionally to being organically managed. Even so, their opinion is that the incentives are not sufficient for the effort and time spent in managing their lands under organic requirements. Here, it is important to point out that the laws and restrictions for organic farming in North-West Spain are very lax. Many farming practices with known positive effects on biodiversity such as long crop rotations, reduced ploughing of lands or use of composted manure to fertilise, are completely dependent on the farmer´s decision to use them and not directly incentivized by policy. Therefore, under organic farming there is a wide variability in sustainability, with a large opportunity to increase the environmental value of organic farming if these practices were required and not optional for organic farmers. As mentioned before, the requirements for organic farming in Spain are lax when compared to the ones in other countries, and so the implementation of required practices such as long crop rotations or use of composted manure could increase farmland biodiversity in Spain. In addition, the implementation of these practices on conventional farming could produce a more sustainable farming overall, possibly without the yield losses that may occur as a result of organic farming. The disappearance of the separation between organic and conventional agriculture, with all agricultural practices being sustainably managed, would probably be the most efficient and useful way of conserving farmland biodiversity.

In the case of forest landowners, there is a complete lack of government incentives for using the native forest and not cutting it in order to plant *Eucalyptus*, and therefore many landowners see these exotic plantations as the only viable solution to make a living on their lands. There are very reduced market facilities and available information for land owners to conserve and manage native forests or plant native tree species. Nevertheless, the many conversations with land owners of native forests and *Eucalyptus* plantations have shown me that sustainably managing and using the many resources that native forests directly provide (including chestnuts, wood, mushrooms, acorns, medicines, provision of honey, etc.), is up to a 60% more economically viable than planting *Eucalyptus* trees, which only provide wood. However, this information is not available to most land owners. In addition, the regulating (temperature regulation, prevention of fires, land erosion or floods) and cultural (traditional, recreational, landscape or welfare) ecosystem services provided by native forests, are crucial for our living and completely ignored when these forests are cut or replaced by *Eucalyptus* plantations. There is an obvious loss of traditional cultural knowledge on the use and value of the resources that native forests give, provoked by the increasing rural abandonment, the lack of appreciation of traditional local knowledge by new generations, and the lack of interest of conserving traditional knowledge and use of natural resources by governments. Therefore, the existence of economic incentives, spread of knowledge and promotion of both sustainable agriculture and use and conservation of native forests, could help in conserving these valuable habitats and the biodiversity that depends on them, together with conserving rural inhabitants and attracting more people to make a living in rural areas.

CONSTRAINTS

The development of this thesis was affected by some constraints that impeded and slowed the progress of producing the thesis. The main problem was that the work with the thesis was not funded by either public scholarships or by private grants, even though most available national grants and scholarships were applied for. This apparent lack of interest to fund the project had as a main consequence that I, the doctorate, had to work part-time while at the same time developing the thesis, resulting in a prolonged time for its production. Secondly, the lack of funding prohibited the use of paid field assistants to carry out field work, as well as the use of students because of the lack of funding for travel to the relatively remote study sites. As a result, the extensive field work required for this thesis was done entirely by myself, combined with the part-time job. Finally, I did an internship in Sweden, which helped me hugely to develop my thesis, which had to be paid with my own private money, as there were no scholarships or grants either from the university or from the administrations to cover it. Thus, the funding of the internship was based on money raised from other employment both before and after the internship.

The development of the thesis required skills, for example in statistics, for which a lack of courses at the home university slowed my progress. I benefitted from having an international supervisor, but the fact that many of the official documents were exclusively in Spanish resulted in unnecessary additional work.

In conclusion, the development of this thesis would have been much easier, quicker, less stressing and effortless with financial and administrative help, both from public, private and university institutions.

APPENDIX

Effects of organic farming on bird diversity in North-West Spain