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Plant diversity and ecosystem services in agricultural landscapes along different spatial scales

Xavier Oriol Solé-Senan

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Universitat de Lleida

TESI DOCTORAL

Plant diversity and ecosystem services in agricultural landscapes along different spatial scales

Xavier Oriol Solé-Senan

Memòria presentada per optar al grau de Doctor per la Universitat de Lleida
Programa de Doctorat en Ciència i Tecnologia Agroalimentària

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2017

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This PhD has been carried out within the consolidated group of research “Weed Science and Plant Ecology” (2014SGC008) from the Universitat de Lleida. The author was funded by a PhD grant from the Universitat de Lleida. The study was funded by Ministerio de Educación y Ciencia (Projects AGL 2007-60828 and AGL 2010-22084-C02-01).

Al padrí i la padrina

Agraïments

Vull donar les gràcies als meus dos directors de tesi per haver-me donat l'oportunitat de fer aquesta tesi doctoral i de tots els aprenentatges que se n'han desprès, en particular els coneixements de botànica. Gràcies Josep Antoni i Jordi. En aquest mateix context, agrair el mateix al Joan Pedrol per tot el que he après amb ell al camp, en particular del territori de Monegros o de les sortides de Botànica Forestal i Botànica de Camp amb l'alumnat de Forestals. Josep Antoni i Joan, que n'hem passat d'hores pels Monegros buscant endemismes... ☺

Agraïments també a la resta de membres del Grup de Recerca de Malherbologia i Ecologia Vegetal, a aquells que hi són i a aquells que hi han estat: Aritz, Bàrbara, Joel i Núria. Gràcies a la Núria Llop (eficiència burocràtica al 100%). Demanava un document o un tràmit administratiu i en un tres i no res tot solucionat.

A les companyes del despatx per les estones viscudes, els tutorials de R i els scripts fets i refets; les discussions sobre temes de malherbologia i altres banalitats: Addy, Valentina, Jordi i Fran. Esment a part mereixen l'Alex i la Irene (*Madrid team*). Hem passat i hem après moltes coses col·lectivament; més de bones que de dolentes. Els viatges a la Camarga o a Tolossa amb la Irene pel tema *Farmland*, excursions a Bilbo per fer algun curset d'estadística on vam conèixer el Francesco De Bello i que ens va permetre entrar colze a colze en el camp de la diversitat funcional i moltes més situacions que no esmentaré perquè ara no toca. Irene, te'n recordes d'aquells fulls d'inventaris on algú havia escrit *Bomus driandrus*? Alex, a tu et podria agrair un sense fi de coses però aniré al gra i em centraré en el camp científic; gràcies per les teves *hard revisions* en les cartes de resposta a revisors, pel teu sentit crític i sobretot per haver-me permès entrar en el món de l'ecologia de les espècies invasores. Un aprenentatge més. I un més de la família ☺

Natàlia, gràcies per la portada que m'has fet. Tu has fet la teva part del tracte i ara jo faré la meva. Quan vinguis ja saps que et vindré a buscar a l'aeroport de BCN. A tot això... quan véns?

Tunica, ves pensant a quin curs o a quina cosa he d'inscriure'm ara per seguir ocupant temps. August, ves reservant hores que ara tindrem temps per anar a treure herbes de l'hort.

Agraïments als *coperos* de dijous. Érem assidus de ser a les 8 a l'Arms –o Casa de les Amfores pels nouvinguts a Lleida-. A vosaltres; César, Agnès, Moderna, Jonatan, Paula, Jorge, Carles, Eva, Carmen, etc... Per cert Carmen, la propera sardinada què... Vinga que a aquest pas hi haurà aturada de pesca! Gràcies pels moments divertits i alegres que hem passat totes i tots.

Potser em deixo més gent. Si és així disculpeu-me però ja sabeu que, com que sóc del ram de la botànica, si el vostre nom fos en llatí, segur que me'n recordaria. Així de cop; Tere (quines magdalenes), Ana (i Matilda), Sònia i Arnau (*allotment team*), etc...

Gràcies a la tesi he conegut gent que ja coneixia perquè havien estat professors i professores meves però en un altre vessant. Tranquils, la cosa queda aquí i no explicaré res ;)

No puc concloure sense fer referència a la meva família. Als que hi són i a aquells que han marxat. Ja veus padrí, mira si n'arriba a haver de plantes tu que sempre em preguntaves. Padrina, seguirem anant a Aitona a la primavera a veure aquella brolla i llistonar florit que sempre em deies que hi havia pel secà. Mare, Maria i Pepe; gràcies per tot. Us estimo.

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Llistat de publicacions

This thesis is based on the work contained in the following paper:

I. How does boundary structure affect the inner-field weeds in arable fields? A classification base on a structural typology Alicia Cirujeda A, Gabriel Pardo, Ana Isabel Marí, Joaquín Aibar, Yessica Pallavicini, Jose Luís González-Andújar, Jordi Recasens, **Xavier Oriol Solé-Senan**. Resubmited after revision to *Weed Research*.

II. Plant species, functional assemblages and partition of diversity in a Mediterranean agricultural landscape mosaic. **Xavier Oriol Solé-Senan**, Alejandro Juárez-Escario, Josep Antoni Conesa y Jordi Recasens. Resubmited after major revision to *Agriculture, Ecosystems and Environment*.

III. Plant diversity in Mediterranean cereal fields: Unraveling the effect of landscape complexity on rare arable plants. **Xavier Oriol Solé-Senan**, Alejandro Juárez-Escario, Josep Antoni Conesa, Joel Torra, Aritz Royo-Esnal y Jordi Recasens. *Agriculture, Ecosystems and Environment*, 185, 221-230. https://doi.org/10.1016/j.agee.2014.01.003

IV. Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services of Mediterranean arable plants. **Xavier Oriol Solé-Senan**, Alejandro Juárez-Escario, Irene Robleño, Josep Antoni Conesa i Jordi Recasens. *Agriculture, Ecosystems and Environment,* 247, 255-264. https://doi.org/10.1016/j.agee.2017.07.005

Summary

This thesis is aimed at disentangling how the structure and the diversity of arable plant communities are affected at different spatial scales within agricultural landscapes. The reduction of diversity in European arable plant communities, which stems from the negative impact of the raising agricultural intensification (represented by the use of pesticides and fertilizers and a landscape structure simplification), is increasing the awareness of its impact in such ecosystems, as arable plants are one of the main ecosystem services providers. The use of species and functional diversity indexes is expected to provide new insights in such issues. At field scale, shifts in the structure of field boundaries affect the hosted plant communities.

At field scale, those structurally simply boundaries lead to an increase of the abundance of harmful weeds such as *Lolium rigidum, Papaver rhoeas, Bromus diandrus* and *Avena sterilis*. On the other hand, intermediate levels of complexity have been found to positively affect the presence of rare arable plants, whereas structurally complex boundaries enhance perennial species that entail a reduction of the presence and abundance of annual plant species. Furthermore, the species richness and diversity are reduced from boundaries to inner-fields, whereas field edges host more rare arable plants than the adjacent boundaries, indicating the dependence of this species group to intermediate disturbance levels.

Within a mosaic of agricultural landscape, the diversity of habitats improves much more the species and functional diversity than the different levels of agricultural intensification at which such habitats are subjected. Regarding landscape heterogeneity, the increasing compositional landscape heterogeneity enhances the species richness and diversity of arable plant communities, being the positive effect stronger at field boundaries than in inner-field positions. On the other hand, the increasing configurational landscape heterogeneity enhances the species richness and diversity of rare arable plants, being the positive effect stronger in field edges than at boundaries and in inner-fields. From a trait-based approach perspective, compositional landscape heterogeneity is linked to traits that provide suitable habitat for farmland diversity, whereas configurational landscape heterogeneity is related to floral traits, thus impacting the provision of resources for pollinators.

In conclusion, this study aims at improving the current conservation measures by providing valuable information about the different aptitudes of management strategies, according to the preferences of the target species and ecosystem functions studied. The proposed response-effect trait framework appears to be an effective tool to assess the most effective conservation strategies in order to accomplish the objectives that society may demand from agroecosystems.

Resum

Aquesta tesi està adreçada a esbrinar com l'estructura i diversitat de les comunitats vegetals arvenses varien a diferents escales espacials en els paisatges dominats per l'agricultura. La reducció de diversitat dins les comunitats vegetals arvenses en el territori europeu, conseqüència de l'efecte negatiu de la intensificació agrícola creixent basada en l'ús de pesticides i fertilitzants i en una simplificació en l'estructura del paisatge, ha fet que augmenti la preocupació sobre el seu possible impacte en l'aportació de serveis ecosistèmics. L'ús d'índexs de diversitat taxonòmica i funcional pot aportar nous coneixements amb utilitat en l'establiment de mesures adreçades a fer front a aquesta reducció de diversitat.

A nivell de camp, les espones estructuralment més simples afavoreixen la presència i abundància d'aquelles males herbes més problemàtiques com *Lolium rigidum, Papaver rhoeas, Bromus diandrus* i *Avena sterilis*. Per l'altra banda, les espones amb un nivell intermedi de complexitat estructural afecten positivament a la presència d'espècies arvenses rares, mentre que aquelles espones dominades per espècies perennes promouen una reducció en la presència i abundància de les espècies anuals (tant de les rares com de les males herbes perjudicials). A més a més, la riquesa i diversitat de flora arvense dins d'un camp es redueix de l'espona al centre del camp, mentre que els marges acullen més espècies arvenses rares que les espones, indicant la dependència d'aquest grup d'espècies a nivells intermedis de pertorbació.

Dins d'un paisatge agrícola en mosaic, les diversitats taxonòmica i funcional es veuen més afavorides per la diversitat d'hàbitats dins del mosaic que no pas pels nivells d'intensificació agrícola a la qual es troben sotmesos aquests hàbitats. Pel que respecta a l'heterogeneïtat del paisatge, l'increment d'heterogeneïtat composicional augmenta la riquesa i diversitat de les comunitats vegetals arvenses, essent l'efecte positiu molt més intens en l'espona que no pas en els centres dels camps. Per altra banda, l'increment de l'heterogeneïtat configuracional augmenta la riquesa i diversitat d'espècies arvenses rares, amb un major efecte en els marges que no pas en les espones i els centres dels camps. A nivell funcional, l'heterogeneïtat composicional està promou plantes amb atributs funcionals relacionats amb la provisió d'un hàbitat adequat per la diversitat d'aus i d'insectes, mentre que l'heterogeneïtat configuracional es relaciona amb atributs

funcionals florals i que, per tant, poden influir directament en la provisió de recursos pels pol·linitzadors.

Per concloure, els resultats d'aquest estudi aporten nova informació relativa a les preferències de les espècies arvenses i al manteniment de les funcions dels agroecosistemes, la qual cosa pot permetre millorar les actuals estratègies de conservació a partir de la inclusió d'aquesta informació. La proposta d'un model funcional en funció dels atributs resposta-efecte es presenta com una eina efectiva per establir aquelles mesures més efectives per tal d'assolir els objectius que la societat demandi dels agroecosistemes.

Resumen

Esta tesis está dirigida a averiguar como la estructura y diversidad de la comunidades vegetales arvenses varían a distintas escalas espaciales dentro de los paisajes dominados por la agricultura. La reducción de la diversidad en las comunidades vegetales arvenses en el territorio europeo, consecuencia del efecto negativo de la creciente intensificación agrícola (representada en el uso de pesticidas y fertilizantes y en una simplificación de la estructura del paisaje), ha dado lugar a una preocupación creciente sobre su posible impacto en la provisión de servicios ecosistémicos. El uso de índices de diversidad taxonómica y funcional puede aportar nuevos conocimientos útiles para establecer nuevas medidas dirigidas a hacer frente a dicha reducción de diversidad.

A nivel de campo, los ribazos estructuralmente más simples favorecen la presencia y abundancia de aquellas malas hierbas más problemáticas como *Lolium rigidum, Papaver rhoeas, Bromus diandrus* y *Avena sterilis*. Por otro lado, los ribazos con un nivel intermedio de complejidad estructural afectan positivamente la presencia de especies arvenses raras, mientras que los ribazos dominados por especies perennes promueven una disminución significativa en la presencia y abundancia de las especies anuales (tanto de las raras como de las malas hierbas perjudiciales). Además, la riqueza y diversidad de flora arvense dentro de un campo se reduce del ribazo al centro del campo, mientras que los márgenes acogen un mayor número de especies arvenses raras que los ribazos, indicando la dependencia de dicho grupo a niveles intermedios de perturbación.

Dentro de un paisaje agrícola en mosaico, la diversidad taxonómica y funcional se ve más favorecida por la diversidad de hábitats dentro del mosaico que por los distintos niveles de intensificación a les que se encuentran sometidos dichos hábitats. En relación a la heterogeneidad del paisaje, el incremento de heterogeneidad composicional incrementa la riqueza y diversidad de las comunidades arvenses, siendo dicho efecto mucho más intenso en el ribazo que en el centro del campo. Por otro lado, el incremento de heterogeneidad configuracional incrementa la riqueza y diversidad de especies arvenses raras, siendo dicho efecto más intenso en los márgenes. A nivel funcional, la heterogeneidad composicional está ligada a atributos funcionales relacionados con la provisión de un hábitat adecuado para la diversidad de aves e insectos, mientras que la

heterogeneidad configuracional se relaciona con atributos funcionales florales y que por tanto, pueden influir directamente en la provisión de recursos tróficos para polinizadores.

En conclusión, los resultados de este estudio aportan nueva información relativa a las preferencias de las especies arvenses y al mantenimiento de las funciones de los agroecosistemas, lo que puede permitir mejorar las estrategias actuales de conservación, a partir de la inclusión de dicha información. La propuesta de un modelo funcional basado en los atributos respuesta-efecto se presenta como una herramienta efectiva para establecer aquellas medidas más efectivas para alcanzar los objetivos que la sociedad demande a los agroecosistemas.

CHAPTER 1

General Introduction

GENERAL INTRODUCTION

Background

Agricultural landscapes in the Mediterranean area are characterized by a mosaic of patches of different habitats (Folch et al., 1997). These patches and the surrounding boundary networks sustain biocenosis that can be exceptionally rich, as has been shown for birds (Cardador et al., 2015), butterflies (González-Estébanez et al., 2011) and plants (José-María et al., 2010; Bassa et al., 2011; Concepción et al., 2012). The structure of Mediterranean agricultural landscapes depends on the local topography. Thus, in broad plains, fields are huge and patches of natural and semi natural vegetation are reduced to networks of boundaries, whereas in areas where topography is abrupt, cultivation is concentrated in small and convoluted fields (Folch et al., 1997). Furthermore, in contrast to agricultural landscapes of central and northern Europe, Mediterranean agricultural landscapes often show a high abundance of species that are relevant for conservation such as rare arable plants (Holzner and Immonen, 1982; José-María et al., 2010, Rotchés-Ribalta et al., 2015).

The ongoing increasing agricultural intensification operating both at field and landscape scale (Roschewitz et al., 2005; José-María et al., 2010), has triggered a decline across taxa (Benton et al., 2003), which has been particularly pronounced on arable plants, (Tscharntke et al., 2005). Agricultural intensification is defined by different trends in management practices such as an intense use of herbicides and pesticides, mineral nitrogen fertilizers, seed cleaning, monoculture as well as increasing field size and landscape homogenization (Tilman et al., 2002; Storkey et al., 2012).

Understanding how plant diversity reduction operates at different spatial scales has become one of the major concerns in agro-ecology. Arable plants are of great importance to agriculture since they provide many benefits to agro-ecosystems as well as affecting both directly and indirectly to human welfare by the provision of vital goods and ecosystem services (Storkey et al., 2013). The study of ecosystem services has increased awareness of the impact of diversity loss on the ecosystem functioning, stability and sustainability (Wood et al., 2015). In this scenario, an effective management of plant diversity in agricultural landscapes requires an assessment of the drivers of species diversity along multiple spatial scales and how other organisms of the food chain (i.e. insects and birds) underpin on arable plants.

Increasing or preserving arable plants diversity in agricultural landscapes can enhance the ecological health of these agroecosystems with regard to the potential delivery of ecosystem services to other organisms. In this sense, this thesis seeks to debate on how best to promote the persistence of arable plants in Mediterranean agricultural landscapes by looking at the factors and processes that determine the diversity of arable plants both at field and landscape scale. The results of this thesis are expected to be a breakthrough on the ecological knowledge of arable plants.

Arable plants

Arable plants are those annual species that thrive in arable fields without being intentionally sown and whose persistence relies on regular disturbance. Most arable plant species are adapted to soil tillage, low fertilization, mechanical weeding and little seed cleaning (Fried et al., 2008). Despite being an important constraint on yield in cereal and arable crops, arable plants significantly contribute to the overall species diversity since they are key primary producers and thus, of central importance to arable system food web (Hawes et al., 2003; Marshall et al., 2003). As it has been previously mentioned, agricultural intensification has entailed to a reduction in the richness and diversity of these species, as it has been showed in United Kingdom (Sutcliffe and Kay, 2000; Storkey et al., 2012), France (Van Calster et al., 2008; Fried et al., 2008), Germany (Meyer et al., 2013), Spain (Cirujeda et al., 2011), Catalonia (Chamorro et al., 2016) and Denmark (Andreasen et al., 1996), thus being an unequivocal evidence that arable plant diversity decline is a process taking place on an European-scale. As a result, many species have become rare (Storkey et al., 2012). The increasing awareness on these rare species (Romero et al., 2008; José-Maria et al., 2010; Epperlein et al., 2014; Pinke and Gunton, 2014; Rotchés-Ribalta et al., 2015; Rotchés-Ribalta et al., 2016) has focused on unravelling the best strategies aimed at promoting their persistence (Aboucaya et al., 2000; Fried et al., 2009; Storkey et al., 2012; Albrecht et al., 2016).

Arable plant species own a notorious ecological relevance (Tscharntke et al., 2005). They play an important role in supporting biodiversity, on account of their multiple interactions within and among trophic levels in agroecosystems, serving as immediate food sources by providing environmental benefits. Furthermore, arable plants maximize important ecosystem services such as pollination and biological pest control and furthermore, provide forage and shelter for fauna (Marshall et al., 2003). Consequently, arable plant diversity reduction jeopardizes the ecosystem services provided by arable fields. Understanding how arable plant diversity reduction affects the organisms that rely on these plant species has become one of the major issues in agroecology.

Processes determining plant diversity in arable fields

Species diversity in one environment is based upon a balance between species colonization, establishment and local extinction (MacArthur and Wilson, 1967). In the case of plants, the ability of a seed to colonize a new site depends on its dispersal capacity and size (Moles et al., 2004), as well as on the distance and the spatial configuration of neighbouring populations (Devlaeminck et al., 2005; Thomson et al., 2011). Before their germination, seeds have to survive a period in the soil facing predation (Baraibar et al., 2009). After germination, plant survival is affected by interspecific competition (Jing et al., 2015). For example, perennial plants are known to determine the exclusion of annual species (see Marshall, 2009), leading to the local extinction of arable plant species, although some plant species do better with neighbours of other different species (Tilman, 1982).

In Europe, arable crops represent nowadays over 60% of the total cultivated agricultural land (Eurostat, 2016). The majority of these arable lands are managed by conventional cropping practices, which are underpinned on the use of herbicides and fertilizers (Pywell et al., 2002; Hyvönen et al., 2003). As a result of these farming practices, plant species sensitive to herbicides and fertilizers may encounter difficulties in ensuring their establishment and survival, leading to a reduction of species diversity (Wilson and Aebischer, 1995; Roschewitz et al., 2005; Romero et al., 2008; José-María et al., 2010), as well as local extinction (Fried et al., 2009). In addition to management practices, local field factors, such as soil properties and elevation, can act as important determinants of arable plant diversity and species composition (Lososová et al., 2004). However, the homogenization in cultivation techniques has promoted the development of largely similar arable communities within-fields across a broad range of local conditions (Romero et al., 2008; Pinke et al., 2012).

Factors affecting plant diversity at field scale

Among the main factors that trigger changes in plant diversity at field scale, the boundary structure (Kleijn and Verbeek, 2000; Smart et al., 2002; Bassa et al., 2011), the use of agrochemicals (Kleijn and vanderVoort, 1997; Kleijn and Verbeek, 2000; Tilman et al., 2002; Fried et al., 2009; José-María et al., 2010) and soil management (Wilson and Aebischer, 1995; Hernandez Plaza et al., 2015) stand out.

Boundary structure

Boundary structure influences the hosted plant species. Flat boundaries are usually used for cultivation and therefore, agricultural inputs (e.g. machinery, fertilisers and herbicides loads) select species adapted to them (Schippers & Joenje, 2002). Conversely, sloping boundaries are less disturbed than flat boundaries. In sloping boundaries, the reduced disturbance promotes the success of perennial species, which is accompanied by a reduction in the establishment of weedy annual species (Marshall, 2009) and leads to differentiated species assemblages in boundaries compared to those in inner-fields (Marshall & Arnold, 1995; Aavik & Liira, 2010). Regarding boundary width, Schipper and Joenje (2002) suggested that the widest boundaries are more diverse than the narrowest because large width provides an opportunity for plant species to escape from fertilizers and herbicides loads, as well as there is an increasing in species number with a larger area. Therefore, boundary slope and width are expected to strongly modify the species assemblages thriving in those semi natural habitats. However, the effect of these indicators on rare weeds has been scarcely studied.

Agrochemicals

Arable plants density and species number are known to decline with increasing herbicide rates, although some species are able to survive in reduced rates (Hyvönen and Salonen, 2002). However, the impact of herbicides differs along field positions. While in field edges and inner-field herbicides are applied directly on plant species, at boundaries the herbicide drift may arrive from the arable field (Kleijn and Snoeijing, 1997). When comparing the effect of herbicides with that of fertilizers on arable plant communities, the former can affect species diversity and composition more than nitrogen fertilization (Hyvönen and Salonen, 2002). However, Kleijn and Snoeijing (1997) found that the negative impacts of herbicides at boundaries appear to be small compared to those of the fertilizer drift. Indeed, Kleijn and Snoeijing (1997) and Pysek and Leps (1991) argued that fertilizers are the main drivers of the species composition in arable plant communities since the increase of nutrient availability potentially benefit ruderal species with high biomass (Grime, 1979). In such situations, arable plants may suffer from increased competition. Many rare species are characterized by short stature (Storkey et al., 2010), which makes them particularly susceptible to the high levels of shading brought about by cereal canopies and ruderal weeds (Kleijn and van de Voort, 1997).

Soil disturbance

Soil disturbance caused by machinery may have two major effects on arable plants. On the one hand, it increases the extinction rate of non-annual species, leading therefore to species loss of perennial species. On the other hand, the regular recurring soil disturbance provides new habitats for species with similar niche requirements such as annual plants (Willcox, 2012) and in particular for rare arable plants (Albrecht et al., 2016). This pressure on plant species lies behind species' functional traits selection (Hernández Plaza et al., 2015). Hence, recurrent disturbance will avoid the colonization of perennial species, whereas the absence of soil disturbance will promote perennial species against annual plants (Marshall et al., 2009). Regarding rare arable species, Pointereau et al. (2010) observed that mechanical soil disturbance of stubble immediately after harvest disrupted the reproduction cycle of the rare species. On the other hand, Meyer et al. (2013) found that increased intensity of and depth of soil tillage particularly affected bulbous geophytes considered as rare arable plants such as *Gagea* spp. and *Ornithogalum umbellatum* L.

Factors affecting plant diversity at landscape scale

Centuries of low-intensity farming have created cultural landscapes characterized by a mosaic of different land cover types, patches of natural and semi-natural vegetation and the presence of networks of boundaries and stone walls (Plieninger and Bieling, 2012). These landscapes are recognized as high nature farmland areas since a wide range of species are hosted in them (Bennet et al., 2006). Likewise, landscape structure can influence the temporal and the spatial presence of arable plants (Kremen et al., 2007). Therefore, the increase of landscape heterogeneity in agricultural landscapes can benefit plant diversity (Gabriel et al., 2005; Gaba et al., 2010; José-María et al., 2010; Fahrig et al., 2011; Fahrig et al., 2015; Rotchés-Ribalta et al., 2015). Landscape heterogeneity is driven by the presence of patches of semi-natural and agricultural habitats (compositional heterogeneity) and their arrangement and shape (configurational heterogeneity) (Fahrig et al., 2011). It has been showed that increased compositional heterogeneity may promote more niches to support more species, whereas increased configurational heterogeneity promotes connectivity, edge and mass effects for plant species distributions along boundaries networks (Fahrig et al., 2011). Permanent boundaries, stone walls and seminatural habitats may function as plant propagule sources, dispersal corridors, alternative habitats and sources for recolonisation (Roschewitz et al., 2005). Therefore, more richness of plant species should be found in fields with a higher proportion of edges (Gabriel et al., 2005). Regarding configurational heterogeneity, some studies have found strong positive relationships between arable plants richness and the perimeter-area ratio of the fields (Weibull et al., 2003; Gabriel et al., 2005). Besides, field size could be used as an indirect measure of agricultural intensity (Roschewitz et al., 2005). Finally, at landscape scale, it has been suggested that landscape heterogeneity may buffer in-field management intensification, favors species spill-over and supports the species pool for individual traits, thus supporting the landscape-moderated traits selection hypothesis (Tscharntke et al., 2012).

At landscape scale, land consolidation processes have been identified as the main threats to rare arable plants since they lead to a reduction of field edges that provide favourable habitats for rare plants (Fried et al., 2009). Likewise, habitat fragmentation has also negatively affected the survival of rare species populations (Le Corre et al., 2014).

From diversity to ecosystems functioning

It is known that biodiversity drives ecosystems functioning and processes, which determine the provision of ecosystem services (Storkey et al., 2013). Therefore, the loss of diversity in arable ecosystems has increased the awareness regarding the reduction in the supply of ecosystem services. For this reason, disentangling the potential effects of land-use changes on the provisioning of ecosystem services has become an urgent task for ecologists. At this point, it is important to highlight that diversity includes taxonomical and functional aspects.

In this sense, plant community composition stems from the responses of plant functional traits to environmental filters, which are abiotic factors that prevent species establishment or persistence in a particular location (Violle et al., 2007). A trait is any morphological, physiological or phenological characteristic measurable at individual level that impacts plant fitness. Therefore, functional diversity captures information that is absent in measures of species diversity, and which highlight the interaction between organisms and their environment since ecosystem functions appear to be strongly controlled by plant traits (Ricotta and Moretti, 2010). Furthermore, the trait-based methodology enables us to identify more general patterns of species response between regions with different environmental conditions, allowing the prediction of vegetation changes in response to future environmental variations (Pakeman and Stockan, 2013). Thus, the application of functional approaches in agricultural science to understand the ecosystem processes that lay behind species assemblages is needed (Wood et al., 2015).

In this context of interaction among plants and other organisms, the importance of splitting functional traits between response and effect traits has been described (Lavorel and Garnier, 2002). Response traits are those that govern how plants respond to different environmental filters, whereas effect traits are those that determine how plants affect their environment (Lavorel and Garnier, 2002). Although several studies have disentangled how agricultural intensification affects response traits (see José-Maria et al., 2011; Fried et al., 2012; Fontana et al., 2014; Guerrero et al., 2014; Hernandez Plaza et al., 2015; Kormann et al., 2015), it is scarcely known how these changes on trait composition affect the provision of ecosystem services (Lavorel et al., 2013). In this sense, the response-effect trait framework has been identified as a useful tool for predicting the impact of environmental changes on ecosystem services delivery in multi-trophic systems (Lavorel et al., 2013). In consequence, a functional perspective is essential to unravel the functional rules that govern mechanisms of plant persistence in agricultural landscapes at different spatial scales in order to develop recommendations regarding management and conservation not only of the arable plants species, but also the ecosystems services they can provide to other organisms. These measures can be aimed at facing diversity loss.

From arable plants to pollination and suitable habitat for farmland biodiversity

From the high variety of ecosystem services that arable plants deliver to agricultural landscapes, two major functions can be highlighted: (1) pollination services and (2) the provision of suitable habitat for farmland biodiversity. Regarding the former, the positive relationship between plant diversity and pollinators imply that spatial and temporal changes in abundance, diversity or distribution of flowering plants may strongly affect the pollinator populations that depend on them, and vice versa (Kohler et al., 2007; Bretagnolle and Gaba, 2015). Regarding the latter, functional traits of arable plants are known to affect richness and diversity of many arthropod species (see Woodcock et al., 2005; Moretti et al., 2013; Storkey et al., 2013), as well as other organisms as birds (Jiguet and Bretagnolle, 2001; Storkey et al., 2013). The development of frameworks aimed at understanding how arable plants affect their environment from a trait-based approach appears to be a mandatory activity due to the current shift of nature conservation from species management based on target species, to ecosystem management based on ecological dynamics of ecosystems (Bengtsson et al., 2003)

MAIN OBJECTIVES OF THE THESIS

This thesis investigates how plant diversity on arable fields responds to different abiotic factors such as management practices and landscape heterogeneity from local scale – patch– up to landscape scale. The effect of these abiotic factors on arable plants has been studied at different arable field positions and habitats within a Mediterranean mosaic landscape as well as at different trophic levels. This framework is specified in these particular objectives:

1. Evaluate the impact of boundaries structure in species assemblages as well as the role of these boundaries as a refuge for harmful weeds and rare arable plants.
2. Determine how different levels of agricultural intensification entail shifts in taxonomical and functional diversity in plant communities at different spatial scales within a Mediterranean agricultural landscape mosaic.
3. Identify how landscape heterogeneity affects the diversity of plant species and in particular of rare arable plants in Mediterranean rainfed cereal fields from field scale up to landscape scale.
4. Identify how landscape heterogeneity affects the compositional and the functional structure of arable plant communities in Mediterranean rainfed cereal fields from field scale up to landscape scale.

5. Define a suite of functional traits linked to the success and persistence of arable plants regarding gradients of agricultural intensification within-field and within-landscape.
6. Propose a response-effect trait framework to characterize the impact of agricultural intensification at different trophic levels and therefore, on the potentiality of arable plants communities to deliver pollination services and the provision of suitable habitat for farmland biodiversity.

These objectives are included in the following chapters of this thesis in the form of scientific papers (i.e., structured in the sections: abstract, introduction, material and methods, results, discussion, conclusions and references), which allow readers to understand each one independently of the others (see Table 1). These chapters correspond to: (1) How does boundary structure affect the inner-field weeds in arable fields? A classification base on a structural typology; (2) Plant species, functional assemblages and partition of diversity in a Mediterranean agricultural landscape mosaic; (3) Plant diversity in Mediterranean cereal fields: unraveling the effect of landscape complexity on rare arable plants and (4) Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services of Mediterranean arable plants. Finally, and to address the main target of the thesis, results from the different chapters are jointly discussed, leading to the main conclusions.

METHODOLOGY AND OUTLINE OF THE THESIS

Field experiments of this thesis have been conducted in Catalonia and Aragon (NE of Iberian peninsula) during spring and summer seasons between 2008 and 2013 coinciding with the flowering onset period of plant species thriving in rainfed crops of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.) and alfalfa (*Medicago sativa* L.) and the surrounding seminatural habitats, such as boundaries, roadverges and fallow lands. Some of the prospected areas are included in Special Protection Areas (SPA); sites established under the 2009/147/EC Birds Directive and included in the Natura 2000 network (the European network of protected natural areas). The climate of the study area is semiarid Mediterranean, with mean annual temperature ranging from 13.5°C to 15°C and annual precipitation from 250 mm to 450 mm, mainly concentrated in spring and autumm (Ninyerola et al., 2005). Height above sea level ranges from 200 m up to 800 m. Most of the study sites were composed of rainfed barley fields (*Hordeum vulgare* L.) interspersed with patches of woodlands of *Quercus ilex* L., *Quercus faginea* L., *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco and *Pinus hapelensis* Mill. scrublands (mainly of *Salsola vermiculata* L., and *Rosmarinus officinalis* L.) and dry-mediterranean grasslands of *Lygeum spartum* L. and *Brachypodium retusum* Pers. Occasionally, fields with almond trees (*Prunus dulcis* (Mill.) D.A. Webb), olive trees (*Olea europaea* L. var. *europaea* L.) and vineyards (*Vitis vinifera* L.) shelter close to the study sites. Agricultural management in the study sites is based on conventional farming practices such as at least one application of herbicides per year and mineral nitrogen fertilizers. The mean size of the fields chosen as study sites was 1.67 ± 0.18 ha. Throughout the study sites of Catalonia, there was no east–west or north–south gradient of landscape complexity, as XY-coordinates of the localities do not correlate with landscape context (X-coordinates vs. percentage of natural vegetation: $\rho = 0.03$, $P = 0.83$; Y-coordinates vs. percentage of natural vegetation: $\rho = 0.15$, $P = 0.32$). At each chapter of this thesis study sites are detailed.

To answer objective 1, floristic trials were conducted throughout 200 arable fields (110 fields in Aragon and 90 fields in Catalonia). The six-point scale of Braun-Blanquet (1979) was used to quantify species abundance. Field boundaries were characterized defining three structural descriptors: the boundary width (more or less than 3m wide), the boundary slope and the presence of stonewalls in such boundaries. By determining a threshold of tolerance based on the abundance of four harmful weeds (*Papaver rhoeas* L., *Lolium rigidum* Gaudin, *Bromus diandrus* Roth and *Avena sterilis* L.), we linked such threshold with the presence and abundance of perennial plants species. Species assemblages of each boundary were compared to its respective within-field composition. By linking the structural descriptors and the abundance of perennial species we identified up to five different types of boundaries. Furthermore, in the boundaries of Catalonia, the presence of rare arable plants was studied. Results from a similar sample conducted in another region (Andalusia, south of Iberian Peninsula) were joinly analyzed to confirm our findings. Results of this study are reported and discussed in Chapter 2. This chapter has been resubmitted to *Weed Research*.

Table 1. Overview of the conducted studies presented from chapter 2 to chapter 6. Summarised are the investigated predictor and response variables, and methods employed.

	Predictor variables	**Response variables**	**Nº of fields surveyed**	**Experimental methods**	**Statistical methods**	**Scale of study**
C.2	Boundary width, percentage of perennial species thriving at boundaries, boundary slope and presence of stone-walls	Species assemblages, abundance of harmful weeds, species richness of rare arable plants	200	Observational unit. Species abundance in sampling quadrats of 5m^2	Descriptive analysis, Linear regression, redundancy analysis (RDA) and non-metric multidimensional scaling (NMDS)	Field scale: Boundary
C. 3	Levels of agricultural intensification	Species richness, Rao's entropy index of response traits –traits related to agricultural intensification-. Rao's entropy index of effect traits- traits related to the provision of resourses to pollinators-. Community-weigthed means of response and effect traits.	140	Observational units. Species presence in sampling quadrats of 1m^2	Descriptive analysis by the additive partitioning of the species diversity, and non-metric multidimensional scaling (NMDS), redundancy analysis (RDA) with the patch value of Rao's entropy index and Community-weighted means of response and effect traits. Permutational analysis of variance (PERMANOVA)	From patch up to local landscape scale
C.4	Landscape heterogeneity, field position (Boundary, edge and inner-field)	Species richness and Shannon entropy index of the total species and rare arable plants. Species assemblages	90	Observational unit. Species abundance in sampling quadrats of 5m^2	Linear mixed-effect models (LME), Permutational analysis of variance (PERMANOVA), and non-metric multidimensional scaling (NMDS).	From field, local landscape up to region.
C.5	Landscape heterogeneity, field position (Boundary, edge and inner-field)	Functional assemblages and functional trait values in terms of Rao's quadratic entropy index and Community-weighted means both for response and effect traits	90	Observational unit. Species abundance in sampling quadrats of 5m^2	Linear mixed-effect models (LME), redundancy analysis (RDA) with the patch value of Rao's entropy index and Community-weighted means of response and effect traits	From field up to local landscape scale. Development of a response-effect trait framework for the delivery of pollination services and the provision of suitable habitat for farmland biodiversity.
C.6	General discussion and general conclusions					

To meet objective 2, the presence of the plant species was recorded in 1m^2 plots in 20 patches of different habitats in a local landscape scale (Ager Valley) in spring and summer of 2010 and 2011. The study was aimed at understanding how three levels (Low, Medium and High) of agricultural intensification (based on a proxy of the disturbance caused by herbicides and fertilizers applications, below-ground disturbances and vegetation removal) affected richness and functional diversity of plant species. Diversity trends were studied at different spatial scales –from the within-patch diversity up to the local within-landscape diversity- by using the additive partitioning method of the species richness and the Rao's quadratic entropy index (Q), which takes into account intraespecific trait variability (Leps et al., 2006). Furthermore, species traits were split between response traits –those that govern how respond to agricultural intensification- and effect traits –those that determine how plants affect their environment-. Specifically, I focused on floral trait potentially linked to pollinators. The results of these objectives are reported and discussed in Chapter3. After major revision this chapter has been resubmitted to *Agriculture, Ecosystems and Environment*.

Objective 3 was assessed by comparing the assemblages, the richness and the Shannon diversity of arable plants and in particular of rare arable plants throughout transects of five plots in 90 rainfed fields of wheat and barley at three different field positions (boundary, edge and inner-field) along a gradient of landscape complexity (Fig.1). Landscape heterogeneity was characterized in the surrounding area of 1 km of radius. Landscapes were situated along a gradient of complexity ranging from simple landscapes with high percentage of arable land (95%) up to complex landscapes with a low percentage of arable land (5%) (Fig.2). Landscape structure was characterized by a set of landscape metrics widely used in landscape ecology (McGarigal and Marks, 1994), namely: the percentage of natural natural vegetation, the perimeter-area ratio of patches of natural vegetation and arable fields and the shape index of patches of natural vegetation and arable fields. Species richness and Shannon diversity were partitioned at different spatial scales. Changes in within-landscape (α landscape diversity) of both plant species and rare arable plants due to gradients of landscape heterogeneity were tested at three different field positions. Results of this study are reported and discussed in Chapter 4. This chapter has been published in *Agriculture, Ecosystems and Environment*.

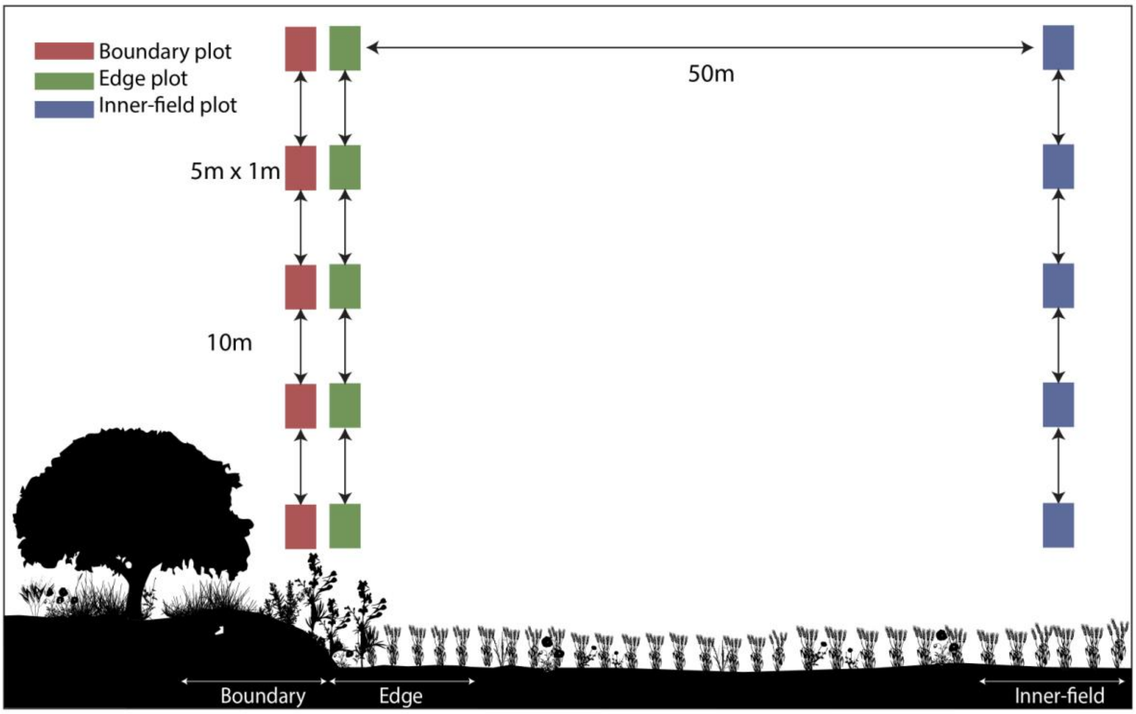

Figure 1. Scheme of the sampling design conducted in chapter 3 and 4. The three transects run parallel to the field boundary.

Figure 2. Buffer area of 1 km of radius representing the study sites in which landscape heterogeneity was characterized

In order to achieve objectives 4, 5 and 6 the functional composition of the arable plant community was assessed at three different field positions (boundary, edge and inner-field) (Fig.1), throughout 90 rainfed fields of wheat and barley at three along a gradient of landscape heterogeneity (Fig.2). Landscape heterogeneity was decomposed by composition heterogeneity (percentage of natural vegetation) and configurational heterogeneity (perimeter-area ratio of arable patches). Functional traits were split between response and effect traits. I linked response to effect traits and the latter to potential ecosystem services along several trophic levels. To assess the functional approach, Rao's quadratic entropy index (Q), which takes into account intraspecific trait variability) (Lepš et al., 2006) and the community-weighted mean (CWM, which reflects the average trait value of the most dominant species in a community) (Garnier et al., 2004) were used. It was tested how functional diversity at landscape scale varied due to gradients of landscape heterogeneity. A proposal of response-effect traits framework is presented and discussed. The study represented the first attempt to analyze the effect of agricultural intensification on ecosystem services (pollination services and the provision of suitable habitat for farmland biodiversity), both at field and landscape scale in the Mediterranean area, by integrating plant functional traits in a response-trait framework. The results of these objectives are reported and discussed in Chapter 5. After minor revision, this chapter has been published in *Agriculture, Ecosystems and Environment*.

In Chapter 6 results from the previous chapters are jointly discussed. This chapter includes the main conclusions

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CHAPTER 2

How does boundary structure affect the inner-field weeds in arable fields? A classification base on a structural typology

Resubmitted to *Weed Research* after revision

How does boundary structure affect the inner-field weeds in arable fields? A classification base on a structural typology

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Abstract

Any assessment on whether plant assemblages at boundaries favour weed infestations in inner-fields needs to be based on structural indicators, otherwise contradictory results could be obtained. In this study we present a classification of arable fields boundaries based on four structural descriptors (slope, width, percentage of cover of perennial species and presence of stone walls). Five types of boundaries are identified, ranging from those structurally simple ones (flat, narrow, dominated by annual species) to those structurally complex ones (slope, more than 3 meters wide, dominated by perennial species). Data from three Spanish regions were used to validate that classification and to assess the role of these boundaries in hosting weeds. Assessment of weed frequency and abundance gave complementary information. The descriptors explained the differences observed in terms of species assemblages. Boundary structure can hinder or facilitate disturbances (herbicide and fertiliser drift, cultivation). Our typology is aimed at transmitting a common message to researchers, farmers and legislators concerned about boundaries acting as weeds reservoir.

Keywords: slope, perennial species, width, multivariate analysis, non-metric multidimensional scaling (NMDS).

1. Introduction

During the last decades, increased attention has been paid to the functionality of boundaries in arable fields such as reducing soil erosion, providing suitable habitats for biodiversity, or connecting semi-natural habitats in agricultural landscapes (Marshall and Moonen, 2000; Aavik et al., 2010). Although numerous papers have focused on their role in northern and central Europe, hardly any work has been conducted in southern Europe (but Cirujeda et al., 2007; Bassa et al., 2011; Bassa et al., 2012).

Boundaries consist in a strip of semi-natural vegetation surrounding arable fields, which harbour a very diverse plant spectrum (Marshall and Moonen, 2000). However, farmers mostly consider them as a source of weeds even though few real data support their perception (for United Kingdom, Marshall and Arnold, 1995; Germany, Mante and Gerowitt, 2009; Netherlands, Kleijn and Verbeek, 2000 and USA, Reberg-Horton et al., 2011). Conversely, boundaries have been found to host rare arable plants (Bassa et al., 2011; Solé-Senan et al., 2014).

In Spain the relationship between boundary structures and weed communities has shown contradictory results. While Pallavicini et al. (2013) found shared weed species between boundaries and their respective inner-fields, Cirujeda et al. (2013) described few harmful species coinciding in both positions. Further discussion has suggested that structural differences such as boundary slope, width or the structure of the hosted vegetation, filter the success of weeds in these boundaries. For instance, flat boundaries tend to be cultivated and therefore, these disturbances (e.g. machinery, fertilisers and herbicide drifts) promote species adapted to it (Schippers and Joenje, 2002; de Cauwer et al., 2008; Pallavicini et al., 2013). Conversely, lack of disturbance promotes the success of perennial species preventing the colonization by annual species (Marshall, 2009) and thus leading to different species assemblages in boundaries and inner-fields (Mashall and Arnold, 1995; Hovd and Skogen, 2005; Aavik and Liira, 2010; Cirujeda et al., 2013). Although it has been reported that boundary vegetation could be mainly determined by management (Hovd and Skogen, 2005; de Cauwer et al., 2008; Reberg-Horton et al., 2011; Bassa et al., 2011), few studies found that boundary structure, such as slope and width, may drive its community composition (Hovt and Skogen, 2005; Schippers and Joenje, 2002; Bassa et al., 2011). Regarding boundary width, Schippers and Joenje (2002) suggested that wider boundaries host more diverse plant communities than narrower boundaries since (1) wide boundaries buffer against agro-chemical drift, which is one of the major cause of diversity decline and homogenization, and (2) species number increases with increasing area. Similarly, Gove et al. (2007) found that the abundance of plant species sensitive to herbicides increased in boundaries at a distance of between 2m and 4m from the edge compared to those located between 0m and 2m because of the reduction in the herbicide drift effect.

Furthermore, some species have become extremely rare and under threat due to increasing agricultural intensification (Fried *et al.*, 2009). Concerns about the conservation status of these rare arable plants are raising in northern and central Europe and, consequently, polices aimed at their conservation have been developed (Aboucaya *et al.*, 2000; Byfield and Wilson, 2005). Concurrently, recent studies have increased the awareness of how agricultural intensification is jeopardizing these species in the Mediterranean area (Solé-Senan et al., 2014). The presence of rare arable plants is expected to be greater in boundaries with an intermediate level of complexity than in those subjected to regular cultivation (Fried et al., 2009). Likewise, the increasing abundance in perennial species is expected to entail decreases of rare plants abundance due to their inability to thrive in competitive habitats (Marshall, 2009).

Although non-crop plants are usually confined to boundaries due to lesser negative impact of management than in inner-fields (Kleijn and van der Voort, 1997), we expect boundary structure to affect species the hosted plant communities. Most weeds are assumed to be enhanced in most structurally simple boundaries (narrow, with no slope, absence of perennial species), whereas they are expected to decrease in more structurally complex boundaries (wide, with slope, presence of perennial species). Therefore, we expect a reduction in infestation with increasing boundary complexity. Our aims were: (1) to propose a structural typology based on easily measurable indicators to support further research, (2) to appraise weed and rare arable plant occurrence in boundaries and inner-fields, and (3) to validate the typology with available data from Spain. The typology should be useful to transmit a common message to researchers, farmers, stakeholders and legislators indicating which factors favour boundaries to host weeds potentially affecting crop production. The typology is intended to contribute towards managing boundaries with specific Agri-Environmental Schemes (AES) aimed at reducing weeds but enhancing rare arable plants.

2. Material and methods

2.1. Study regions

The study was conducted in three different regions of Spain (Andalusia, Aragon and Catalonia), which encompass a cereal production farming area under rainfed conditions. The regions provide a gradient of the structural complexity of boundaries. Environmental characteristics and farming practices applied in the fields of each region are summarized in Table S1.

2.2. Plant survey

Sampling was conducted in boundaries (B) and inner-fields (IF) of rainfed cereal fields between April and July before harvest from 2008 to 2012. The number of fields surveyed per region is summarized in Table S1.

In Andalusia, boundaries were sampled along one transect of five quadrats of 1 x 1m at 5m intervals, whereas in the inner-fields (IF) the first quadrat was positioned 25m away from the boundary and the following four ran diagonally to the edge towards the inside of the field. In each quadrat, all species were identified and individuals were counted. In Aragon boundaries were sampled by three squares of boundary width x 2m in length. Sampling in the adjacent inner-field in other same-sized three squares was generally made at 20m. In Catalonia, surveys were performed at the boundaries and 30m from the boundaries in inner-fields. At each position, surveys were conducted by one transect of five plots (1 x 5m) that ran parallel to the edge at 10 m intervals. Percentage of cover of each species within the plot was estimated both in Aragon and Catalonia (details in Table S1).

2.3 Boundaries classification

Data from Aragon and Catalonia were used to check the effect of the boundary structure on both species assemblages and the presence of weeds at boundaries. Data from Andalusia were not used in this classification because of the differences in the sampling method. We used four descriptors to classify boundaries: (1) percentage of perennials covering the boundary, (2) boundary width, (3) boundary slope and (4) presence of a stone wall. The importance of these four descriptors was checked in two steps. Firstly, linear regressions were performed to quantify the effect of the percentage of plant cover of perennial species on the percentage of plant cover of four harmul weed. Data from Aragón and Catalonia were analyzed together for this purpose. The percentage of cover of each harmulf weed in both areas following Cirujeda et al. (2001) i.e. *Avena sterilis* L., *Bromus diandrus* Roth., *Lolium rigidum* Gaud. and *Papaver rhoeas* L, as well as the sum of the cover of the four species were related to the percentage of plant cover of perennial species (using Minitab v. 13.1). All five regressions were significant, fitting to decreasing straight lines, demonstrating the reduction of the cover of the harmful weeds caused by the increasing cover of perennial species (Fig. 1). For all the species, the maximum percentage of plant cover was reached in absence of perennial vegetation, being weed cover in these situations below 5% for *A. sterilis* and *P. rhoeas* and 5.3% for *L. rigidum* (Fig. 1). Only *B. diandrus* reached a possible troublesome soil cover of 15.8% in absence of perennials, as well as the sum of the four species, reaching 28.6%. Gerowitt and Heitefuss (1990) established the general economic threshold inside a cereal field in 5-10% for broad-leaved species. Similar, the Integrated Pest Management guide published by the Spanish Ministry of Agriculture considers 2, 4, 6 and 8% as economic threshold inside a cereal field for *A. sterilis, B. diandrus, L. rigidum* and *P. rhoeas*, respectively (MAAMA, 2015). Taking into account these limits with the present data a total weed cover of less than 10% were related to a perennials cover of 58% or more. Focusing on *B. diandrus* being the main weed with the highest covers in the boundaries, 62% of perennial soil cover allowed the presence of 5% *B. diandrus* (Fig. 1). The 4% requirement for this species is meant inside fields so that considering this threshold for the boundary is rather demanding. Consequently, 60% of perennials cover was chosen to be the limit to be used as fourth descriptor in field which is a measurable figure in field assessments. Boundaries exceeding this value will most probably not harbour harmful weeds at such densities, whereas boundaries with less than 60% of plant cover can be considered a potential weed reservoir.

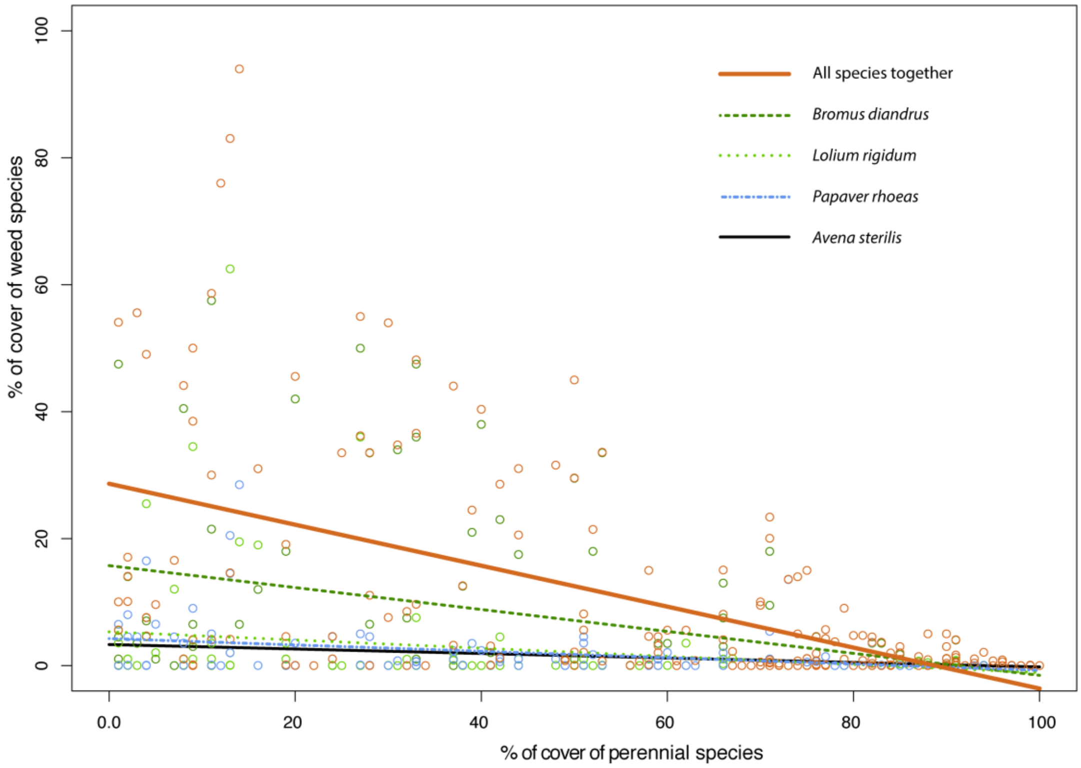

Figure 1. Points and regression lines relating the percentage of cover of the main main weeds *Avena sterilis, Bromus diandrus, Lolium rigidum* and *Papaver rhoeas* and the sum of all four weeds to the percentatge of cover of perennial vegetation. Data from Aragon and Catalonia pooled together.

On the other hand, boundaries were classified into into narrow (<3 m) or wide (>3 m), according to the results of Gove et al. (2007), who defined that a 4-m no-spray buffer zone would be very likely to render spray drift and fertilizer overspread impacts negligible, although even a 2-m buffer would have considerable beneficial effects on vegetation. Consequently, three meters were considered as a mean value to split narrow from wide margins. Boundaries were divided into flat or having slope since Hovd and Skogen (2005) considered slope to affect significantly species assemblages and the percentage of annual species hosted at boundaries. Finally, the presence of stone walls was also considered since these walls entail the establishment of vegetation both on the top and next to the bottom part of the wall because the top cannot be disturbed by cultivation and on the bottom fallen stones provoke a widening of the margin and makes disturbances and cultivation more difficult. Plant species were classified into functional types, namely; (a) annual weeds, (b) annual non-weeds, (c) rare weeds (see Solé-Senan et al., 2014), (d) perennial non-weeds and (e) perennial weeds. Species assemblages and functiona types were constrained to boundary characteristics (% of perennial species, slope and width) using a redundancy analysis (hereafter RDA) with CANOCO 5.0. The Significance of the explanatory boundary characteristics was tested with a Monte-Carlo permutation test (999 permutations).

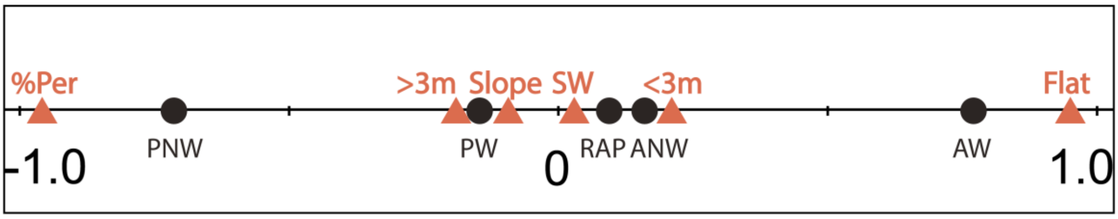

Figure 2. Projection on the first axis of the RDA-analysis showing the effect of boundary width, slope and presence of stone walls on the plant functional groups of the Aragon and Catalonia surveys, grouping the species in annual weeds (AW), annual non-weeds (ANW), perennial weeds (PW), perennial non-weeds (PNW) and rare arable plants (RAP).

The RDA showed that both species assemblages and functional types were significantly explained by boundary characteristics. However, the amount of variation explained was higher for functional types (24.2%) (Fig. 2) than for species assemblages (12.5%) (Figure S1 and Table S2). Both for functional and species assemblages, the percentage of cover of perennial species explained a higher amount of variation than slope, whereas boundary width explained the least. The stone wall had no significant effect neither for functional types nor for species assemblages (Table S2). However, it was considered in the study as these structures are locally protected. The RDA of functional types revealed that the first axis explained 22.9% of the variation, whereas axis 2 accounted for 1.5%. Given that RDA axis 1 accounted for the greatest part of the variability in functional types (Fig. 2), as well as site scores are weighted averages of functional types scores, annual weeds were linked to flat and narrow boundaries, whereas annual non-weeds and rare arable plants were linked to narrow boundaries and boundaries with stone walls. Perennial species were strongly related to boundaries with slope and wide boundaries.

The four descriptors were thus considered valuable including stone walls due to their distinctive feature and their combination led to the margin classification into 5 categories with increasing complexity: flat and narrow boundaries with less than 60%

perennials (B_A) steep with less than 60% perennials (B_B); steep with more than 60% perennials (B_C) next to a stone wall (B_D), steep with presence of trees in the boundary and more than 60% perennials narrow or wide (B_E) (Fig. 3). Previous analyses indicated the absence of different in boundaries within B_B and B_C regarding boundary width. Flat and wide boundaries were not considered because they were not found in the study areas. Inner fields, were accordingly called as IF_A, IF_B, IF_C, IF_D or IF_E.

2.4 Validation of the boundaries classification

After establishing this boundary classification (Fig. 3), vegetation of boundaries and that of their nearby inner-fields from the three regions were analysed taking into account the boundary type. With this purpose the most frequent and most abundant species were identified for each boundary type. Boundaries were also studied from the weed point of view focusing on the four main weed species for the regions including for Andalusia *Phalaris minor* Retz. (González-Andújar and Saavedra, 2003) (Table 1).

Non-metric multidimensional scaling (NMDS) analysis in two dimensions was used to evaluate the differences on species abundance between boundaries and inner-fields regarding the proposed typology, as it is the most robust unconstrained ordination method in community ecology (Leps and Smilauer, 2007). The values of plant cover (Aragon and Catalonia) and plant density (Andalusia) of each plot per position were averaged to obtain a unique value per field and position. The NMDSs were conducted for each region because of the differences on the plant survey among regions. For evaluating species assemblages, we used the Bray–Curtis distance index. Next, we tested the significance of differences in NMDS first axis among the types proposed within each region using ANOVA and Tukey's post-hoc test. Statistical analysis was carried out using R 2.8.1. (R Development Core Team, 2008) by package Vegan (Oksanen et al., 2013). As rare arable species (*sensu* Solé-Senan et al., 2014) in the fields of Aragon and Andalucia were poorly represented, rare arable plants were exclusively projected in the NMDS of Catalonia. Smooth surfaces of the richness of rare arable plants were generated on the NMDS plot by fitting thin plane splines using general additive models from the ordisurf function in R and interpolating the fitted values in the unconstrained ordination diagrams (Oksanen et al., 2013). Rare arable plants that only occurred in one locality were excluded because their presence could be accidental.

% Perennial species: <60%; >60%	**Slope** Yes No	**Field margin width** <3m; >3m; Stone wall	**Final structure**
<60%	No	<3m	
<60%	Yes	<3m or >3m	
>60%	Yes	<3m or >3m	
-	-	Stone wall	
>60% Presence of trees	Yes	<3m or >3m	

Figure 3. Description and diagram of each proposed boundary typology.

Table 1. Data of the four main weeds for each region. Frequency (%) / Mean abundance (%) considered only when found. In bold highest values for each species per region and boundary type. [1]: abundance in plants m^{-2} and species selected following Gonzalez-Andújar and Saavedra (2003), [2]: abundance in % of plant cover and species selected following Cirujeda et al (2011). B: Boundary, IF: Inner-field.

		Andalusia[1]		Aragon[2]		Catalonia[2]	
		B	IF	B	IF	B	IF
Type A	*Avena sterilis*	**48/5**	44/3	-	-	**44**/13	31/**30**
	Bromus diandrus	-	-	-	-	**75**/10	25/**39**
	Lolium rigidum	**87/13**	30/8	-	-	**87**/10	81/**22**
	Papaver rhoeas	**27/2**	26/1	-	-	**81/11**	75/3
	Phalaris minor	**39/4**	35/1	-	-	-	-
	Mean	**50/6**	34/3	-	-	**72**/11	53/**24**
Type B	*A. sterilis*	-	-	**8/1.0**	3/1	**30**/6	20/6
	B. diandrus	-	-	**41/27**	3/0.4	**80/7**	20/0.1
	L. rigidum	-	-	30/0.6	**68/2**	**80**/0.3	70/**6**
	P. rhoeas	-	-	**30/2**	8/1	**65**/1	55/**4**
	Mean	-	-	**27/8**	21/1	**64**/4	41/4
Type C	*A. sterilis*	-	-	**3/10**	0/0	**27**/8	18/**14**
	B. diandrus	-	-	**30**/6	15/**12**	**91/12**	23/2
	L. rigidum	-	-	30/2	**64/3**	**91/6**	77/4
	P. rhoeas	-	-	15/2	**24/3**	**100**/2	91/**6**
	Mean	-	-	20/5	**26**/5	77/7	52/7
Type D	*A. sterilis*	-	-	-	-	**39**/6	22/**19**
	B. diandrus	-	-	-	-	**44/13**	22/1
	L. rigidum	-	-	-	-	**94**/0.2	83/7
	P. rhoeas	-	-	-	-	44/**2**	**61**/0.2
	Mean	-	-	-	-	**55**/5	47/7
Type E	*A. sterilis*	-	-	**7/1**	0/0	60/2	60/10
	B. diandrus	-	-	**30**/6	7/**9**	**50**/0	0/0
	L. rigidum	-	-	20/1	**45/3**	**60**/1	40/**32**
	P. rhoeas	-	-	**16**/1	9/**3**	**60/1**	40/0.1
	Mean	-	-	**18**/2	15/**4**	**58**/1	35/**11**

3. Results

3.1 Overall results in species assemblages

The total plant species recorded were 208, 170 and 405 in Andalusia, Aragon and Catalonia, respectively. Regarding the field position, 112, 17 and 79 species were exclusive from boundaries, exclusive of inner-fields and shared between the two positions in Andalusia, respectively; 90, 9 and 71 species in Aragon and 252, 9 and 144 species in Catalonia.

3.2 Species dominance depending on the boundary type

In Andalusia, *Polygonum aviculare* L. was one of the four most frequent species at boundaries and in inner-fields. In Catalonia, *L. rigidum*, *P. rhoeas* and *Convolvuls arvensis* L. appeared as the most frequent species at boundaries and inner-fields of types A and B. Likewise, in type C, *P. rhoeas* and *L. rigidum* were within the four most frequent species at boundaries and in inner-fields, whereas, *L. rigidum* apperared at boundaries and inner-field of type D and *C. arvensis* in those of type E (Table 2). Thus, when focusing on the most frequent species in the Catalonian boundaries, similar main species at boundaries and inner-fields were found especially in type A and B but fewer coincident species were found in B_C, B_D and B_E demonstrating a decreasing similarity for boundaries increasing in complexity. The troublesome species *B. diandrus* was more frequent at boundaries of types B_A, B_B and B_C than in the respective inner-fields but decreased in importance in B_D and B_E. In Aragon, no coincident species were found within the four most frequent species between boundaries and inner-fields (Table 2). Moreover, frequency and abundance of these species were in most cases very low or even absent in boundary type B_B, B_C and B_E.

L. rigidum was the most dominant species in IF_A, IF_B and IF_D, whereas *P. rhoeas* and *P. aviculare* were among the most frequent and most abundant species and in IF_C. Exclusively in Aragon, *S. vermiculata* was the most frequent and abundant species irrespective of the boundary type.(Table 2, Table S3).

Table 2. The four most frequent species at boundaries and in inner-fields in three regions. Frequency (%) / mean abundance (%) considered only when found. [1]: abundance in plants m^{-2}; [2]: abundance in % soil cover. a) The most frequent species at boundaries, b) most frequent species in inner-fields. Boundaries (B), inner-fields (IF).

		Andalusia[1]			Aragon[2]			Catalonia[2]		
			B	IF		B	IF		B	IF
Type A		*Lolium rigidum*	**87/13**	30/8				*L. rigidum*	**88**/10	81/**22**
		Glebionis coronaria	**65/9**	4/2				*Papaver rhoeas*	**81/11**	75/3
	a)	*Sonchus oleraceous*	**65**/1	30/**43**				*C. arvensis*	**81**/1	63/1
		Polygonum aviculare	**62/13**	61/8				*Bromus diandrus*	**75**/10	25/**39**
		Anagallis arvensis	57/4	**65/6**				*L. rigidum*	**88**/10	81/**22**
		Convolvulus arvensis	35/5	**65**/5				*P. rhoeas*	**81/11**	75/3
	b)	*Pulicaria paludosa*	48/7	**57/12**				*C. arvensis*	**81**/1	63/1
		P. aviculare	**62/13**	61/8				*Polygonum aviculare*	44/1	**56/3**
Type B					*Salsola vermiculata*	**51/33**	5/0.2	*B. diandrus*	**80/7**	20/0.1
					Sonchus oleraceus	**49/1**	14/0.3	*L. rigidum*	**80**/0.3	70/**6**
	a)				*Bromus rubens*	**46/6**	5/0.4	*P. rhoeas*	**65**/1	55/**4**
					Anacyclus clavatus	**43/5**	27/0.6	*C. arvensis*	**60/2**	50/1
					L. rigidum	21/1	**46/3**	*P. aviculare*	10/1	**75**/1
					C. arvensis	7/1	**46/2**	*L. rigidum*	**80**/0.3	70/**6**
	b)				*Salsola kali*	16/**3**	**39**/2	*P. rhoeas*	**65**/1	55/**4**
					Euphorbia serrata	2/1	**34/5**	*C. arvensis*	**60/2**	50/1

Table 2.(cont)

		Andalusia[1]			Aragon[2]			Catalonia[2]		
			B	IF		B	IF		B	IF
Type C	a)				*Salsola vermiculata*	**70/37**	0/0	*P. rhoeas*	**100**/2	91/**6**
					Phalaris minor	**55/3**	0/0	*L. rigidum*	**91/6**	77/4
					B. rubens	**46/4**	0/0	*B. diandrus*	**91/12**	23/2
					Mantisalca salmantica	**46/2**	0/0	*C. arvensis*	73/**2**	**77**/1
	b)				*L. rigidum*	30/2	**64/3**	*P. rhoeas*	**100**/2	91/**6**
					C. arvensis	15/1	**46/2**	*L. rigidum*	**91/6**	77/4
					Diplotaxis erucoides	9/1	**33/5**	*C. arvensis*	73/**2**	**77**/1
					Salsola kali	3/**20**	**27**/2	*P. aviculare*	41/1	**46**/1
Type D	a)							*L. rigidum*	**94**/0.2	83/**7**
								S. oleraceus	**72/0.1**	28/0
								C. arvensis	61/1	61/1
								Hordeum murinum	**56/8**	6/0
	b)							*L. rigidum*	**94**/0.2	83/**7**
								P. rhoeas	44/**2**	**61**/0.2
								C. arvensis	61/1	61/1
								F. officinalis	**56/2**	39/0.3
Type E	a)				*S. vermiculata*	**98/42**	5/0.2	*C. arvensis*	80/0.3	80/**1**
					T. nodosa	**55/2**	0/0	*Brachypodium phoenicoides*	**60/32**	0/0
					P. minor	**48/4**	2/0.2	*D. glomerata*	**60/5**	0/0
					Dactylis glomerata	**46/9**	0/0	*Genista scorpius*	**60/2**	0/0
	b)				*L. rigidum*	21/1	**46/3**	*C. arvensis*	80/0.3	80/**1**
					E. serrata	7/1	**46/2**	*P. aviculare*	40/0.3	**60/2**
					C. arvensis	16/3	**39**/2	*A. sterilis*	60/2	60/**10**
					Chondrilla juncea	2/1	**34/5**	*L. rigidum*	**60**/1	40/**32**

It is noteworthy that when focusing on the four most abundant species at boundaries and inner-fields (Table S3) no single species for any of the boundary types appeared both as one of the four most abundant at boundaries and in inner-fields at any of the three study areas (Table S3). Considering the data from that point of view, boundaries appear to be very different to inner-fields.

3.3 Main weeds

In the Andalusian boundaries *L. rigidum* exceeded 50% frequency, even more than in the nearby inner-fields (Table 1). None of the four main weeds reached this value in the Aragon boundaries. Opposite, in boundaries in Catalonian included in B_A, B_B, B_C and B_E, *B. diandrus, L. rigidum* and *P. rhoeas* exceeded 50% of frequency. Abundance was 2-4 fold higher in IF_A and IF_E but in some cases higher for species in B_B and B_C (Table 1). But despite frequency was high in many cases, abundance was under 10% in all boundaries for all species excepting for *B. diandrus*. Moreover its abundance tended to decrease in Aragon and Catalonia concurrent to the increasing boundary complexity (Table 1). *B. diandrus* only accounted ≥10% abundance in B_A, B_C and B_D and *L. rigidum* in B_A in Andalusia.

3.4 Community composition and field margin's typology

The NMDS analysis showed differences on species assemblages depending on the boundary type, as well as on the field position i.e. boundaries *versus* inner-fields (Fig. 4a, 4b, 4c). Each of the three NMDS conducted revealed a stress lower than 0.2 indicating a strong structure of community composition.

In Andalusia (Fig. 4a) and Catalonia (Fig. 4c), neither B_A nor IF_A were significantly different according to the ANOVA analysis of the NMDS scores in axis 1. For the rest of the types, differences between species assemblages at boundaries, as well as differences between boundary types and its respective inner-fields were observed within each region. In Aragon, B_B were significantly different to IF_B and at the same time, to the B_C and the B_E. Altought the two latter were not significantly different between them, they differed from their respective inner-fields. In Catalonia, boundaries from B_A, B_B and B_C were not significantly different between them but differed from B_D and B_E. The two latter were different, as well.

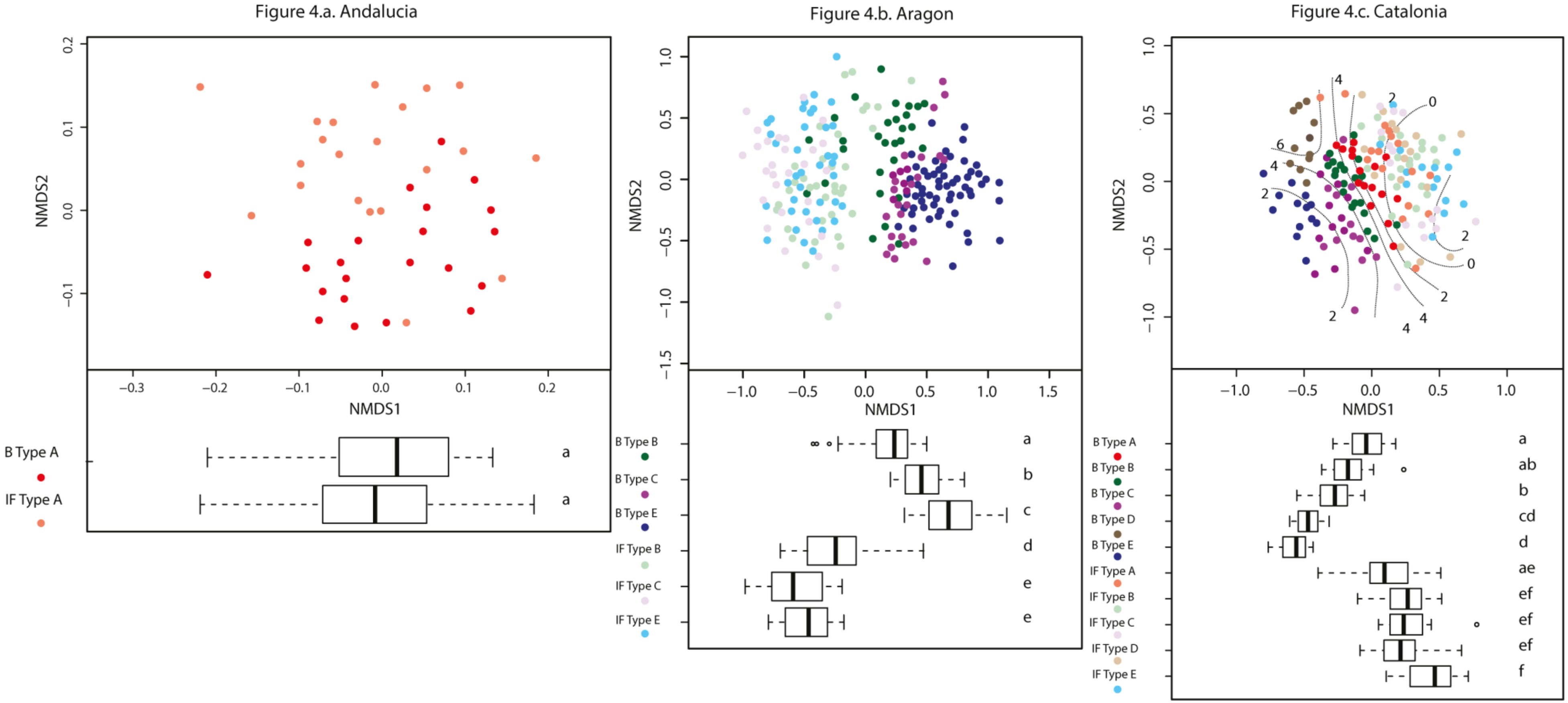

Figure 4. NMDS ordination diagram of species compositional data regarding the region, the field position and the boundary type. Significance of differences in NMDS axis 1 within each region between field positions and each type was tested using ANOVA and Tukey's post-hoc test. Different letters in the boxplot show significant differences between field positions regarding types ($P<0.05$). Smooth surface (contours) representing values of rare arable plant richness (4c). B= boundaries, IF= inner-fields

4. Discussion

4.1 Boundary typology

Our study is the first proposing a structural typology of boundaries in arable fields in the European Mediterranean area. The wide range of boundaries observed has been confirmed to influence the species assemblages hosted at those boundaries (Figs. 1, 2) and states a deeper description of boundaries structure than a simply classification based on the physiognomy of the vegetation such as from woodlands to ruderal vegetation (Marshall and Moonen, 2002).

4.2 Influence of typology on most frequent and most abundant species

The increasing complexity of boundaries in Catalonia lead to increasing differences of the most frequent and abundant species. This trend confirms that the structural typology may be useful to predict the occurrence of weed species in boundaries. Boundary narrowness suggests that both herbicide and fertilizer drift are higher under these circumstances. Likewise, we found that boundaries structurally complex contained among the most highlighted species a pool of perennial species from the surrounding patches of natural vegetation.

While some weeds were hosted in the five boundary types, the subset of the harmful weeds increased their abundance in most structurally simplified boundaries, excepting *B. diandrus* exceeding 10% of cover in several boundary types. This finding partially confirms the common fear of boundaries to host this species confirming Pallavicini et al. (2013) who surveyed simple structured boundaries but contradicting Kleijn and Verbeek (2000) and Marshall and Arnold (1995) who stated that problematic weeds were barely present in boundaries, probably because they studied more complex boundaries. On the other hand, the simplest boundaries hosted very similar species assemblages to those in their respective inner-fields. It is widely known that increasing agricultural intensification impacts on species growing up in boundaries entailing a reduction on species diversity (Kleijn and Verbeek, 2000; Gove et al., 2007; José-Maria et al., 2009). On the other hand, the vegetation in uncultivated boundaries is generally more influenced by fertilization than by the use of herbicides (Marshall and Moonen, 2002), which is corroborated by the values of presence and abundance of nitrophilous species as *Glebionis coronaria* (L.) Cass. ex Spach., *P. aviculare, B. diandrus* or *A.*

clavatus both at B_A and B_B. As B_A type includes the narrowest boundaries, the impact of fertilizer drift may contribute to the persistence of these species tolerant to eutrophization (Robinson and Sutherland, 2002). Therefore, differences found in species assemblages reflected differences on the disturbance impacts between types.

These results bear out the positive effects of perennial species (in B_C, B_D and B_E) by reducing the seedling recruitment of weeds. For instance, the presence of grasses as *L. spartium, B. phoenicoides* or *D. glomerata* are effective in excluding harmful weeds as suggested Critchley et al. (2006), but these species may impact negatively on rare arable plants populations (Marshall, 2009). Following the NMDS, rare plants were harboured in B_B and $B_{D,}$ i.e. on margins with less than 60% of perennials and in margins with stones walls where disturbances are low because of the distance between the wall and the cultivator. Furthermore, our results do not differ from those other studies that revealed significant association between the presence and the amount of perennial species and species assemblages at boundaries (Le Coeur et al., 2002; Aavik et al., 2008). Moreover, in other studies, boundaries tended to be wide and are therefore less affected by disturbances than narrow boundaries. The lack of disturbance as soil cultivation or plant cutting or mowing, promote the exclusion of annual species (Smith et al., 2010).

Only *S. vermiculata* in Aragon boundaries was within the most frequent and most abundant species and the Catalonian boundaries showed a more diverse composition where no species was found within the four most frequent and most abundant species at boundaries of any of the five analysed boundaries types (Table 2, Table S3). Opposite, *L. rigidum* in the inner-fields of Catalonia were within the most frequent and most abundant species demonstrating a uniform weed flora inside the fields. Weed composition in the Aragon inner-fields was more diverse probably due to lower intensification compared to Catalonia. Curiously, IF_A from Catalonia hosted weeds in a higher abundance than in the rest of situations maybe reflecting a more intensive agriculture in these fields.

The species frequencies and abundances generated complementary information. It is recommended to assess both of them in future work. It is important to highlight that the most abundant species in the boundaries of Aragon and Catalonia were mostly non-weed species (excepting *B. sterilis* in boundaries of type A and C and *A. fatua* in boundaries of type A in Catalonia). Thus, focusing on the most frequent species a more negative picture is shown from the weed problem point of view, whereas highlighting the most abundant species shows that mainly different species grow on both environments in boundaries classified as types B, C, D and E.

4.3 Implications for management: enhancing diversity and weed risk assessment

Disturbance ends up in more weed species and less natural vegetation (Schippers and Joenje, 2002; de Cauwer et al., 2008). The present results demonstrate that boundary slope, width, and the percentage of perennial species affect the presence of weeds that colonize from the close patches. Cultivation or mowing and removing cuttings as suggested by de Cauwer et al. (2008) in newly-established margins, cannot be conducted in boundaries acting as slope interruption or on stoned walls but is possible in flat areas. Grazing is also limited by slopes. On the other hand, agronomic practices conducted inside the field can reach the boundary especially when there is no slope interruption and narrow boundaries. But if boundary structure hinders the access of machinery and soil cultivation, the disturbance level at the boundary will be lower, receiving less soil tillage, fertiliser and herbicide drift compared to those applied to the field centre (Schmitz et al., 2014). Boundary width and slope determine the possible management and thus the presence or absence of weeds at boundaries. Unfortunately, few studies take into account boundary structure together or instead of landscape structure descriptors as Marshall and Arnold, (1995) and Aavik and Liira, (2010), possibly because most of the research is conducted in quite homogenous boundary types. It is therefore recommend that researchers include structural and management descriptors as proposed in this work but also see Kleijn and Verbeek (2000) and Reberg-Horton et al. (2011). These descriptors are easy to measure, which would facilitate comparison between studies as well as to define AES focused on promoting boundaries without increasing the risk of hosting weeds which could harm the nearby fields, thus combining environmental and productive interests.

Acknowledgements

We thank S. Murillo and R. Gurrucharri (Dep. de Agricultura, Ganadería y Medio Ambiente, Aragón Government) for her help in choosing and visiting the margins and, FEDER funds and the Spanish Ministry of Economy and Competitiveness funding this work (Projects AGL2007-60828, AGL2010-22084-C02 and AGL2012-33736). YP was supported by a FPI (Spanish Ministry of Economy and Competitiveness) scholarship. XS was supported by an UdL (Universitat de Lleida) scholarship. We thank Joel Torra and Aritz Royo for the field assistance.

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Table Supplementary 1 (Table S1) Environmental characteristics and boundary and crop management data

	Andalusia	Aragón	Catalonia
Sampling information			
Sampling years	2010 and 2011	2011 and 2012	2008
Sampling period	April and May	April and May	May to July
Sampled boundaries and fields	23	120	90
Environmental characteristics			
Altitude (m a.s.l.)	28-675	212-587	250-950
Mean rainfall (mm)[1]	534	318	370-560
Boundary descriptors			
Boundary width (m)	1.5 ± 1.29 [0.3-5.8]	2.8 ± 1.03 [1.0-6.0]	Field margins were classified into narrower or wider than 3m
Boundary height (m)	0.5 ± 0.23 [0.1-0.9]	1.1 ± 0.52 [0.3-2.5]	Data not available
Slope (%)	Flat	7.7 ± 4.98 [0-23.4]	Flat, step
Position of the margin	Outer borders and between-field	Between-field	Outer borders and between-field
Boundary and field crop management			
Boundary age	Unknown, irregular, but intensively managed	Probably more than 20	Probably more than 20
Herbicide use in the field	Usually graminicides	Usually auxinic herbicide in spring	Usually graminicides in winter and dicotyledoneous control in spring
Fertilizer use in the field	Annual or split in two applications	Annual or split in two applications	Annual or split in two applications
Burning / mowing / grazing / herbicide on the boundary?	Sporadic cultivation	No management and sporadic sheep grazing	No management and sporadic sheep grazing
Landscape indicators			
Forest or natural vegetation is abundant near (% soil cover)	50-30	50-80	5-80

[1] Source: Agencia Estatal de Meteorología (1971-2000).

Table Supplementary 2 (Table S2). Monte-Carlo permutation test on the explanatory variables from the RDA analyses.

	Species composition			Functional types		
	Explains %	F-value	p-value	Explains %	F-value	p-value
% perennials	11.9	26.8	0.001	21.2	53.1	0.001
Flat	2.9	5.9	0.001	10.5	23.1	0.001
Slope	2.9	5.9	0.001	10.5	23.1	0.001
> 3m	2.4	5	0.001	4.6	9.6	0.001
< 3m	2.1	4.2	0.002	4.3	9	0.001
Stone wall	0.6	1.1	0.291	0.5	1	0.396

Table Supplementary 3 (Table S3). Data of the four most abundant species at boundaries (B) and in inner-field (IF) in three regions. Frequency (%) / mean abundance (%) considered only when found. [1]: abundance in plants m^{-2}; [2]: abundance in % soil cover. a) Most abundant species at boundaries, b) most abundant species in inner-fields.

		Andalucia[1]			Aragon[2]			Catalonia[2]		
			B	IF		B	IF		B	IF
Type A		*Atriplex prostrata*	**507/4**	0/0				*Elymus repens*	**6/24**	0/0
		Echinochloa colonum	**168/4**	0/0				*Bromus sterilis*	**25/21**	0/0
	a)	*Lythrum acutangulum*	**77**/7	116/**13**				*Bromus tectorum*	**6/16**	0/0
		Torilis glomerata	**73/3**	0/0				*Avena fatua*	**44/14**	19/0
		Juncus hybridus	**124**/4	30/4				*Hordeum murinum*	**31**/12	13/**44**
		Elminthotheca echioides	**120**/17	5/17				*Bromus diandrus*	**75**/10	25/**39**
	b)	*Lythrum acutangulum*	**116/13**	77/9				*Avena sterilis*	**44**/13	31/**30**
		Juncus bufonius	**89/22**	21/13				*Lolium rigidum*	**88**/10	81/**22**
Type B					*Vulpia ciliata*	**5/34**	0/0	*E. repens*	**10/23**	0/0
					Salsola vermiculata	**51/33**	5/0.2	*Brachypodium phoenicoides*	**50/16**	0/0
	a)				*B. diandrus*	**41/27**	3/0.4	*Poa bulbosa*	**5/16**	0/0
					Santolina chamaecyparissus	**14/20**	0/0	*Kochia scoparia*	10/**15**	**15**/0.1
					Descurainia sophia	**14**/2	3/**9**	*Cynodon dactylon*	**30**/8	10/**29**
					Vicia peregrina	11/1	11/**6**	*K. scoparia*	10/**15**	**15**/7
	b)				*Chondrilla juncea*	3/0.2	**32/4**	*A. sterilis*	**30**/6	20/6
					Malcolmia africana	14/1	**16/3**	*L. rigidum*	**80**/0.3	70/**6**

Type C	a)	*S. vermiculata*	**70/37**	0/0	*B. sterilis*	**18/15**	0/0
		Elymus repens	**42/34**	0/0	*Elymus pungens*	**14/14**	0/0
		Lygeum spartium	**39/31**	0/0	*Rubus ulmifolius*	**9/13**	5/1
		Brachypodium retusum	**24/29**	0/0	*Satureja montana*	**5/12**	0/0
	b)	*V. peregrina*	**18**/1	15/**12**	*A. sterilis*	**27**/8	18/**14**
		B. diandrus	**30**/6	15/**12**	*A. fatua*	**14**/2	14/**6**
		D. sophia	6/1	**12/9**	*P. rhoeas*	**100**/2	91/**6**
		Chondrilla juncea	3/1	**21/5**	*P. aviculare*	9/2	**14/5**
Type D	a)				*Rubus caesius*	**6/39**	0/0
					S. vermiculata	**33/38**	6/0
					Scorpiurus muricatus	**6/15**	0/0
					Arrenatherum elatium	**6/15**	0/0
	b)				*A. sterilis*	**39**/6	22/**19**
					B. sterilis	**22**/6	6/**13**
					L. rigidum	**94**/0.2	83/**7**
					Xanthium strumarium	**6**/0	6/**7**
Type E	a)	*S. vermiculata*	**98/42**	5/0.2	*Brachypodium phoenicoides*	**60/32**	0/0
		Atriplex halimus	**11/37**	2/3	*Rosmarinus officinalis*	**10/27**	0/0
		L. spartium	**39/25**	0/0	*Elymus pungens*	**50/24**	0/0
		Rosmarinus officinialis	**4/22**	0/0	*Brachypodium retusum*	**30/18**	0/0
	b)	*Diplotaxis virgata*	**9**/0.7	2/**11**	*L. rigidum*	**70**/1	40/**32**
		Hirschfeldia incana	0/0	**2/10**	*A. sterilis*	**70**/2	60/**10**
		Vicia peregrina	**21**/1	9/**10**	*Polygonum bellardi*	10/0	10/**5**
		B. diandrus	**30**/7	7/**9**	*P. aviculare*	40/0.3	**60/2**

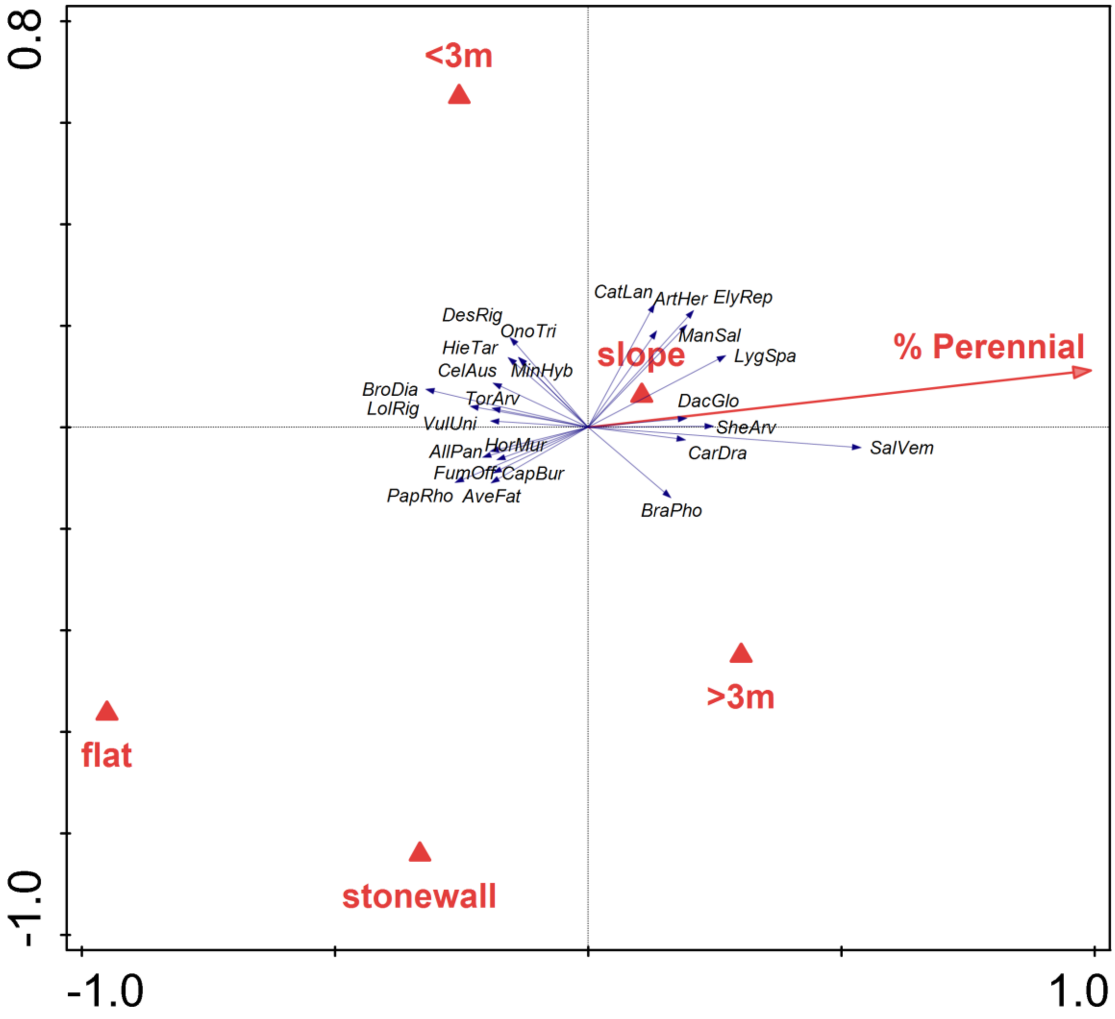

Figure Supplementary 1 (Fig S1). Biplot of the RDA analyses considering the species assemblages as response variable and the structural descriptors as explanatory variables. *AllPan: Allium paniculatum, ArtHer: Artemisia herba-alba, AveFat: Avena fatua, BraPho: Brachypodium phoenicoides, BroDia: Bromus diandrus, CapBur: Capsella bursa-pastoris, CarDra: Cardaria draba, CatLan: Carthamus lanatus, CelAus: Celtis australis, DacGlo: Dactylis glomerata,DesRig: Desmazeria rigida, ElyRep: Elymus repens, FumOff: Fumaria officinalis, HieTar: Hieracium tardans, HorMur: Hordeum murinum, LolRig: Lolium rigidum, LygSpa: Lygeum spartum, ManSal: Mantisalca salmantica, MinHyb: Minuartia hybrida, OnoTri: Ononis tridentata, PapRho: Papaver rhoeas, SheArv: Sherardia arvensis, TorArv: Torilis arvensis, VulUni: Vulpia unilateralis*

CHAPTER 3

Plant species, functional assemblages and partition of diversity in a Mediterranean agricultural mosaic landscape

Resubmitted to *Agriculture, Ecosystems and Environment* after major revision

Plant species, functional assemblages and partition of diversity in a Mediterranean agricultural mosaic landscape

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Abstract

Agricultural landscapes represent mosaics of different habitats that can harbour high plant diversity where plant traits and trait syndromes can be used for predicting either plant responses to agricultural intensification or plant functional effects on other organisms. Understanding the spatial components of diversity within an agricultural mosaic can help to select the appropriate spatial scale for conserving species and ecological functions such as the provisioning of resources for pollinators. We hypothesize that trait syndromes aimed at provisioning resources for pollinators are positively related to non-crop habitats and negatively related to increasing agricultural intensification. To identify the detail at which habitats should be classified and sampled to provide useful information on functional diversity, we sampled plant species in 140 patches distributed among seven habitats (abandoned fields, boundaries, roadverges, and edges and inner alfalfa and cereal fields that were classified into three levels of agricultural intensification: Low, Medium and High. We examined differences in species and functional assemblages, splitting response and effect traits, across various habitats and levels of agricultural intensification. Species richness and functional diversity of response and effect traits were partitioned along spatial scales. Both species and functional assemblages changed across habitats and with different levels of agricultural intensification. Non-cropped habitats and low levels of agricultural intensification promoted trait syndromes with trait-divergence mainly linked to the provisioning of resources for pollinators. The frequent turnover in species at higher spatial scales did not imply a functional turnover. Our study shows that traits are determined by agricultural intensification, and no further details on field position and habitat variability are needed to promote vegetation types with trait syndromes able to support pollinating insects.

Keywords: response traits, effect traits, turnover, trait syndrome, ecosystem service, pollination.

1.Introduction

Agricultural landscapes are characterized by a mosaic of habitats where the range of hosted plant species are affected by the spatio-temporal disturbances featuring agricultural intensification (AI) such as pesticide and fertilizer inputs, tillage operations and vegetation removal (Tscharntke et al., 2005). Since species richness does not always adequately reflect the overall diversity, it is likely that the impacts of AI on plant communities are better reflected by functional traits (José-Maria et al., 2011; Storkey et al., 2013; Armengot et al., 2016). As functional diversity refers to the ecological roles that species have in their community and how their traits influence composition and ecosystem functioning, the response-effect trait framework can be used for predicting the impact of environmental changes on ecosystem services (ESs) delivery in multi-trophic systems (Lavorel et al., 2013). The framework integrates plant traits, divided into response traits that govern how plants respond to different environmental filters and effect traits that determine how plants affect their environment (Lavorel and Garnier, 2002). There is agreement that effect traits cause a response from other organisms driving the ESs (e.g. floral traits to pollinator traits). Therefore, dealing with functional traits instead of species richness helps to predict the role of plant species in providing ESs (Lavorel and Grigulis, 2012). This trait approach has been successfully used to quantify trade-offs between plants and grasshoppers in grasslands (Moretti et al., 2013) and to quantify relationships between plants and invertebrates that can provide ESs to farmland birds in arable lands (Storkey et al., 2013). One of the most studied ES is pollination (Potts et al., 2010) because it entails the maintenance of plant communities and agricultural productivity (Aguilar et al., 2006). Through the possession of a particular trait syndrome, floral traits can be used to predict the identity of flower visitors (Ricou et al., 2014). Understanding how floral trait syndromes change in an agricultural landscape will be ground-breaking in terms of underpinning the provisioning of resources for pollinators.

The additive partitioning approach disentangles diversity patterns across multiple spatial scales (Wagner et al., 2000). Total diversity in a location (γ-diversity) can be partitioned into two components; α-diversity (the mean diversity in a sampling unit) and β-diversity (the turnover of diversity between sampling units). This approach has been applied to the analysis of plant richness in different habitats within-landscape (Wagner et al., 2000) and along gradients of landscape complexity across field positions in arable fields

(Gabriel et al., 2006; Solé-Senan et al., 2014). It has also been used for studying plant, carabid and bird richness across gradients of agricultural intensification (Folhre et al., 2011). Furthermore, this approach can similarly be applied to species richness (S) and measures of functional diversity such as Rao's Quadratic entropy (Q) (de Bello et al., 2009). However, we are not aware of any published studies partitioning both S and Q (response against effect traits) in mosaic landscapes.

This study is aimed at understanding how AI drives changes in plant species and functional assemblages of these species in agricultural landscapes, while also considering the detail at which habitats within mosaic landscapes should be classified and sampled in order to provide useful information on functional diversity. More specifically, we aim to determine how the provisioning of resources for pollinators depends on AI. We hypothesized that the diversity of habitats subjected to different levels of AI should benefit the syndrome diversity of response and effect traits. A landscape with a higher diversity of effect trait syndromes should provide resources for different pollinator species than a landscape dominated by habitats providing low trait syndrome diversity. Furthermore, we suspect that habitats subjected to low AI provide resources to specialized pollinators, whereas habitats subjected to high AI will select for plant species with trait syndromes for generalist pollinators. We suspect that the species diversity turnover along spatial scales will not be concurrent to a shift in terms of functional diversity, highlighting a strong filtering effect of plant traits due AI. Hence, AI can be used as the main driver of the spatio-temporal patterns of species and functional diversity in landscapes that host high habitat variability. The questions forming the basis for the analysis conducted address: (1) how habitats and levels of AI affect plant species and functional assemblages (2) how AI variability affects the availability of pollinator resources, (3) how the contribution of the diversity-components differs between species and functional diversity and (4) what vegetation types should be promoted to support pollinating insects. Our study is aimed at disentangling the relationships between patch disturbances and the provisioning of floral resources eventually available for insects, thus providing guidance for diversity maintenance in agricultural mosaic landscapes.

2.Material and methods

2.1. Study area and plant survey

The study was conducted in the Ager Valley (UTM 31N E(X): 313990, N(Y): 4652740, 187km^2, Catalonia, NE Iberian Peninsula). The climate is continental-mediterranean with an average annual rainfall and temperature of 670mm and 12ºC respectively. The Valley is covered by a mosaic of rain-fed alfalfa, arable and abandoned fields bordered by a complex network of permanent boundaries and roadverges surrounded by oak forest (*Quercus ilex*-*Quercus faginea*). The presence of vascular plants was recorded in 2800 plots of 1m^2 within an area of 50 km^2, from April to July in 2010 and 2011 in abandoned, alfalfa and cereal fields, boundaries and roadverges. We subdivided the alfalfa and cereal fields into a 1m-wide edge strip and the inner-field was located 25m from the edge. Plots of edges and inner-fields were located in different fields so as to avoid the error caused by spatial dependence. A total of 20 patches of abandoned fields, boundaries, roadverges and edges and inner alfalfa or cereal fields were selected. Non adjacent patches were surveyed. Within every patch, 20 plots of 1m^2 were randomly conducted to record plant presence. Distance between plots was at least 10m to prevent spatial dependence (Solé-Senan et al., 2014). The surveyed boundaries were surrounded by cereal fields and they were at least 3m wide

We checked the spatial autocorrelation in species assemblages along the surveyed patches with the Mantel test (Bray-Curtis distance for species assemblages, Euclidean distance for geographic distance for patches and based on Spearman correlation with 999 permutations) (Legendre and Legendre, 1998). No spatial autocorrelation effect was found (all patches, R=-0.019, p-value=0.782; abandoned fields, R=0.101, p-value=0.162; alfalfa edges, R=-0.012, p-value=0.512; inner alfalfa fields, R=-0.108, p-value=0.899; boundaries, R=-0.098, p-value=0.891; cereal edges, R=-0.118, p-value=0.918; inner cereal fields, R=0.038, p-value=0.328; roadverges, R=-0.016, p-value=0.534). To test differences in species assemblages between years, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) on the mean frequency of each species per patch. No differences in species assemblages between years were found (F=3.02, R^2=0.02, p-value>0.05). Species accumulation curves with first-order jack-knife estimates of total species richness of each habitat were calculated to check the adequacy of the sampling effort, ranging from 92.5% (abandoned fields) to

97.5% (inner cereal fields) (Supplementary Appendix 1). Both analyses were conducted using the vegan package (Oksanen et al., 2013) in R (R Development Core Team, 2008).

2.2. Levels of agricultural intensification

A farmer-subjective score of the intensity of the farming management practices was considered. It included disturbance indicators that are known to influence plant diversity such as mean fertilizer and herbicide inputs (Kleijn and van der Voort, 1997), belowground disturbances and vegetation removal (Kühner and Kleyer, 2008). The score provided a proxy of agricultural intensification (AI) intensity, namely: (1) Low ($\mathrm{Low}_{\mathrm{AI}}$): intensification shared in abandoned fields, boundaries and roadverges; (2) Medium ($\mathrm{Medium}_{\mathrm{AI}}$): intensification shared between field edges and inner alfalfa fields; (3) High ($\mathrm{High}_{\mathrm{AI}}$): intensification shared between field edges and inner cereal fields.

2.3. Functional traits

For each encountered species, five response and four effect traits were compiled from literature. Response traits such as growth form (GF) (Juarez-Escario et al., 2016), plant height (H) (Fried et al., 2012; Storkey et al., 2013), month of flowering (MF) (Fried et al., 2012; Juarez-Escario et al., 2013) specific leaf area (SLA) and seed mass (SMass) (Storkey et al., 2013) have been related not only to the disturbance response caused by AI, but also to species persistence in herbaceous vegetation. Regarding effect traits, corolla shape (CShap), duration of flowering (DFlow), flower colour (FCol) and flower symmetry (FSym) are known to affect the provisioning of resources for pollinators as they are known to predict the identity of flower visitors (Ricou et al., 2014). Categories of each trait, as well as the references from where data were obtained are compiled in Table 2. SMass values were previously log transformed to achieve normality.

2.4. Species and functional assemblages

Species assemblages were analyzed using the mean frequency of each species per patch. A matrix of similarities was obtained with the Bray-Curtis dissimilarity index, using species frequency at each patch per habitat (20 patches x 7 habitats = 140 sites). This matrix was used to conduct a non-metric multidimensional scaling (NMDS) analysis. To explore patterns of species assemblages regarding habitats and levels of AI (Table 1), a hierarchical cluster based on Ward's criterion was conducted using the Bray-Curtis similarity matrix. Three cluster groups were selected in order to relate the clustered plots with the three levels of AI previously established. The clustered groups were overlaid on the NMDS. These analyses were performed using the 'vegan' package (R Development Core Team, 2008).

Table 1. Characterization of farming practices of each level of agricultural intensification (AI) regarding the variation of four disturbance measures and the proposed habitats included in each level.

Disturbance measure	**Low$_{AI}$**	**Medium$_{AI}$**	**High$_{AI}$**
Fertilization (N-P-K) kg/ha	No	0-80-250	150-60-120
Herbicide application	No	No	Yes
Below-ground disturbance	No below-ground disturbance in the previous 5 years	Ploughing 1-5 years previously	Ploughing in the same year of sampling
Vegetation removal	No	Yes	Yes
Selected habitats	Abandoned fields Boundaries Roadverges	Alfalfa fields: edges and inner-fields	Cereal fields: edges and inner-fields

To examine relationships between functional assemblages regarding habitats and levels of AI (Model$_1$ and Model$_2$ from Fig. 1 respectively), we conducted a distance-based redundancy analysis (dbRDA), which is the most useful community-based analysis to reveal the extent to which functional community composition changes along environmental gradients (Kleyer et al., 2012). Two complementary approaches were used to characterize functional assemblages of single-traits: 1) Rao's Quadratic Entropy (Q) and 2) community weighted-means (CWM). Q and CWM single-trait values of both response (Q_R and CWM_R) and effect traits (Q_E and CWM_E) (Table 2) were calculated with a species frequency matrix. A principal coordinates analysis (PCoA) based on the Gower distance was used to obtain the Q values for categorical and fuzzy traits (Smilauer and Leps, 2014). For quantitative traits, Q was quantified using the Euclidean distance. These matrices were used to calculate functional diversity based on Q. For dummy and fuzzy traits, CWM trait values represented the proportion of the different levels of the factor. Matrices including Q_R, CWM_R, Q_E and CWM_E single-trait values per habitat (Model$_1$) and per level of AI (Model$_2$) were used as response variables, which were constrained to the habitats and to the levels of AI, respectively (Q_R-dbRDA, CWM_R-dbRDA, Q_E-dbRDA and CWM_E-dbRDA). A Monte Carlo Permutation test (9999 permutations) was conducted to test the significance of the habitats, as well as that of the levels of AI for each analysis regarding the variation of Q and CWM values. Single-trait values were centered and standardized. These analyses were performed using CANOCO 5.0 (ter Braak and Smilauer, 2012).

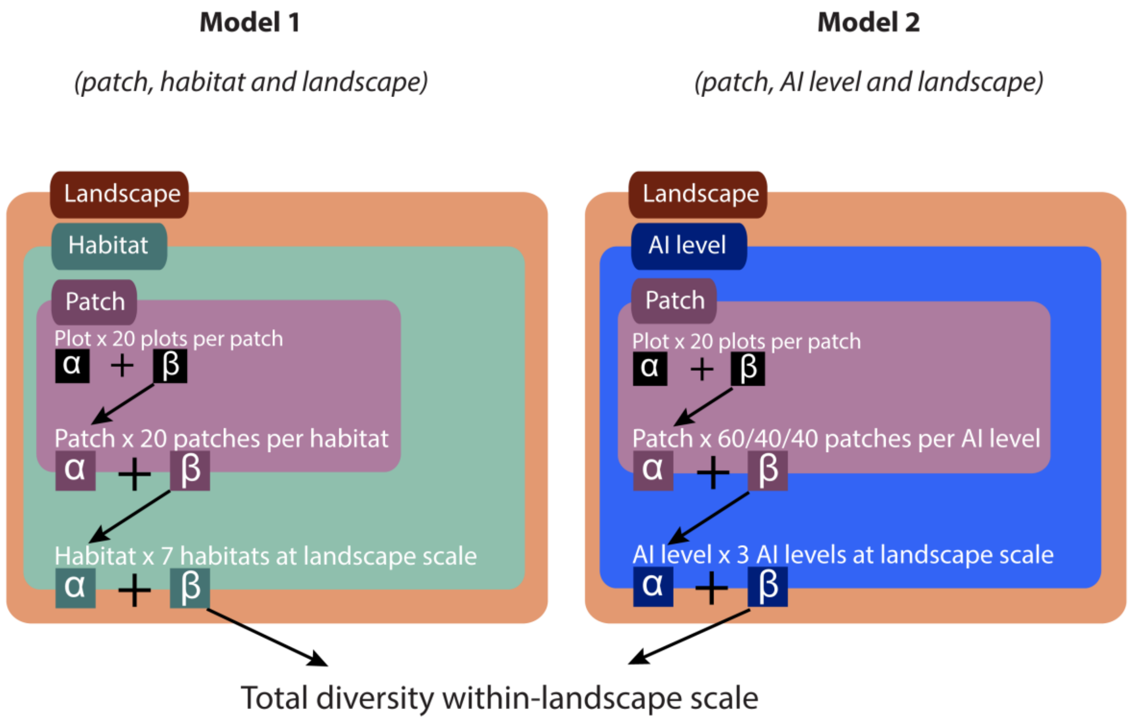

Figure 1. The proposed hierarchical model of species diversity in which α-diversity and β-diversity components at one specific scale are linked additively to form the diversity at the next higher level. Model$_1$ considers the diversity of habitats within-landscape, whereas Model$_2$ considers the different levels of agricultural intensification to which patches within-landscape are subjected.

Table 2. Response (R) and effect (E) traits used in the analyses. Abbreviators used throughout the manuscript are included. References appear in a superscript after the name of the functional trait

Plant Functional trait		Acronyms	Classes and abbreviations
R	Growth form[a]	GF	Qualitative: Annual forb (ForbA), perennial forb (ForbP), annual grass (GrassA), perennial grass (GrassP), Legume (Leg), Woody plants (W)
	Height[a]	H	Quantitative (cm)
	Month of flowering[a]	MF	Quantitative (1 to 12)
	Specific leaf area[e,f]	SLA	Quantitative ($mm^2 \cdot mg^{-1}$)
	Seed mass[d]	SMass	Quantitative (g)
E	Corolla shape[a]	CShap	Fuzzy: Anemophilous (Ane), flat (Flat), tubular (Tub)
	Duration of flowering[a]	DFlow	Quantitative (1 to 12)
	Flower colour[a]	FCol	Fuzzy: Blue (Blue), green (Green), pink, red & brown (P/R/B), white (White), yellow (Yellow)
	Flower symmetry[a]	FSym	Fuzzy: Actinomorphous (Acti), apetalous (Ape), zygomorphous (Zygo)

List of references a) De Bolòs & Vigo (2011), b) Klimešová J. & Klimeš (2008), c) Klimešová & de Bello (2009), d) Royal Botanic Gardens Kew (2015), e) Kleyer et al. (2008), f) Storkey et al. (2013)

2.5. Diversity partitioning at landscape scale

Additive partitioning was applied to identify the detail at which habitats and AI should be classified and sampled to provide the most useful information on diversity along spatial scales. The design involved three hierarchical spatial scales in two different models: a balanced design from patch, habitat to landscape-scale (Model_1) and an unbalanced design from patch, levels of AI to landscape-scale (Model_2) (Fig. 1). Total diversity (γ_{obs}) was partitioned into -diversity (average diversity within a particular spatial scale) and β-diversity (i.e., species variation among patches of the selected scale). The β-diversity component can be calculated as the total diversity minus the average local diversity $(\beta = \gamma_{obs} - \bar{\alpha})$. Consequently, total diversity observed at landscape-scale (γ_{obs}) was partitioned into:

$$\text{eq1) } \gamma_{obs} = \bar{\alpha}_1 + \beta_1 + \beta_2$$

Where $\bar{\alpha}_1$ and β_1 and β_2 were the averaged diversity among patches and the species variation among patches respectively within habitats (Model_1) or within levels of AI (Model_2). were the averaged diversity among habitats within landscape (Model_1) and among levels of AI within landscape (Model_2). These components can be calculated using the following equations:

$$\text{eq2) } \beta_1 = \bar{\alpha}_2 - \bar{\alpha}_1$$

$$\text{eq3) } \beta_2 = \gamma_{obs} - \bar{\alpha}_2$$

Where $\bar{\alpha}_1$ and β_1 were the averaged diversity within patches from each habitat (Model_1) or within patches from each level of AI (Model_2). The above-mentioned steps were used to calculate components of S and Q since they can be calculated with the same mathematical formula (de Bello et al., 2009). Q values were separately calculated for response and for effect traits, thus obtaining a unique value of Q_R and Q_E at each spatial scale representing the whole functional diversity. Components of S were the number of species found in the pooled plots at each spatial scale, whereas to calculate each component of Q, each hierarchic-scale was treated as a single unit (being the proportion of species occurring at each hierarchic-scale equal to the average over all the within-scale sampling points). For the latter, two different matrices were needed: one containing mean species frequency per scale and the other containing species traits. Q_R

and Q_E at each hierarchical within-scale were calculated using CANOCO 5.0 to obtain the between-component. Since quantitative and qualitative traits were combined, a principal coordinates analysis based on the Gower distance was used to obtain a PCoA scores matrix of the pool of traits. The PCoA scores represent the same information as the original traits values, but with the added dimension of being on a fully quantitative scale (Smilauer and Leps, 2014). The score matrices were used to calculate a single value of Q representing the multi-trait functional diversity. These procedures were conducted to calculate Q using eq1, eq2 and eq3 for $Model_1$ and $Model_2$ respectively.

Shapiro tests indicated that mean values of α_{patch} and β_{patch} of each diversity measure and model (Fig. 1) achieved the normality of the data. Thus, ANOVA tests followed by a post-hoc Tukey test for the values α_{patch} and β_{patch} of each model (Fig. 1) were conducted. These analyses were performed using R (R Development Core Team, 2008).

3.Results

3.1. Species and functional assemblages

The NMDS analysis (k=2, non-metric fit: r^2=0.962) showed a clear distribution of the sites based on the floristic similarities of the patches (Fig. 2). The labels of each habitat correspond to the averages obtained after being fitted onto the ordination diagram (p-value<0.001). The circles projected on the site ordination represent the 95% confidence interval of the three clustered groups.

The distance-based analyses (dbRDA) indicated that habitats explained 32.1% and 37.9% of the variance of Rao's Quadratic Entropy of response (Q_R) and effect traits (Q_E) respectively. In terms of community weighted-means (CMW), habitats explained 46.8% and 44.7% of response (CWM_R) and effect traits (CWM_E) respectively (Table 3). On the other hand, levels of AI explained 32.2% and 38.4% of the variance of Q_R and Q_E respectively and 51.3% and 51% of the variance of CWM_R and CWM_E respectively (Table 3).

The arrangement of single-trait values along axis 1 showed a consistent functional resemblance between habitats and levels of AI (Fig. 3). Q_R values were higher at boundaries, roadverges and abandoned fields (Fig. 3a) and at Low_{AI} (Fig. 3b) than in edges and inner alfalfa and cereal fields edges and at $Medium_{AI}$ and $High_{AI}$, respectively. Q_E values were higher in abandoned fields, roadverges, alfalfa field edges and boundaries than in inner alfalfa and cereal fields and cereal field edges (Fig. 3c). Concurrently, Q_E values were higher at Low_{AI} and $Medium_{AI}$ than in $High_{AI}$ (Fig. 3d).

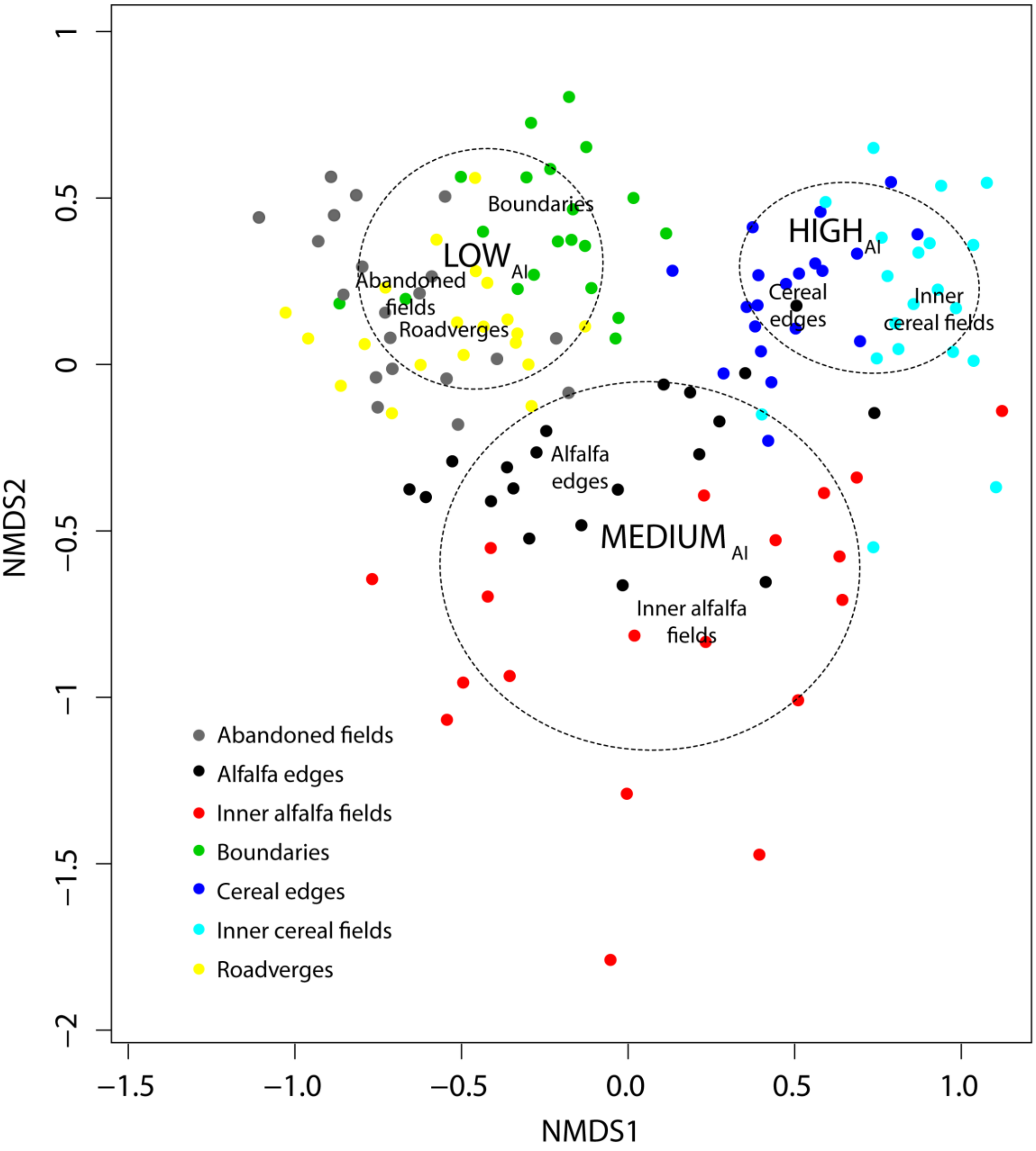

Figure 2. Species assemblages ordination (NMDS) of 140 patches. Dashed circles correspond to the groups regarding cluster ordination at a 95% confidence interval, using the Ward distance and the Bray-Curtis dissimilarity matrix.

Table 3. Percentage of variance explained for each habitat on functional assemblages according to Monte-Carlo permutation on the distance-based redundancy analysis (dbRDA) of Rao's Quadratic Entropy of response (Q_R), effect traits (Q_E), community weighted-mean of response (CWM_R) and effect traits (CWM_E), depending on a) the diversity of habitats and b) the diversity of levels of agricultural intensification (AI) considered in the Ager Valley. Significance of each environmental variable according to Monte-Carlo permutation test (***P <0.001; **P <0.01; *P <0.05; •P <0.1)

		Q_R-dbRDA		CWM_R-dbRDA		Q_E-dbRDA		CWM_E-dbRDA	
a) Habitats	Abandoned fields	2.6	**	6.6	***	5.3	***	8.5	***
	Alfalfa edges	1	•	2.3	**	2.1	*	0.6	•
	Alfalfa inner-fields	2.9	**	8.3	***	7.6	***	4.4	***
	Boundaries	7.6	***	9.8	***	1.6	•	2.7	*
	Cereal edges	3.1	**	5.4	***	8.7	***	7	***
	Cereal inner-fields	9.7	***	9.5	***	8.4	***	14.3	***
	Roadverges	5.2	***	4.9	***	4.2	***	7.2	***
Total variance explained		32.1		46.8		37.9		44.7	
b) AI	Low_{AI}	16.9	***	23.9	***	13.4	***	24	***
	Medium_{AI}	3.9	***	10.8	***	8.1	***	4	**
	High_{AI}	11.9	***	16.6	***	16.9	***	23	***
Total variance explained		32.7		51.3		38.4		51	

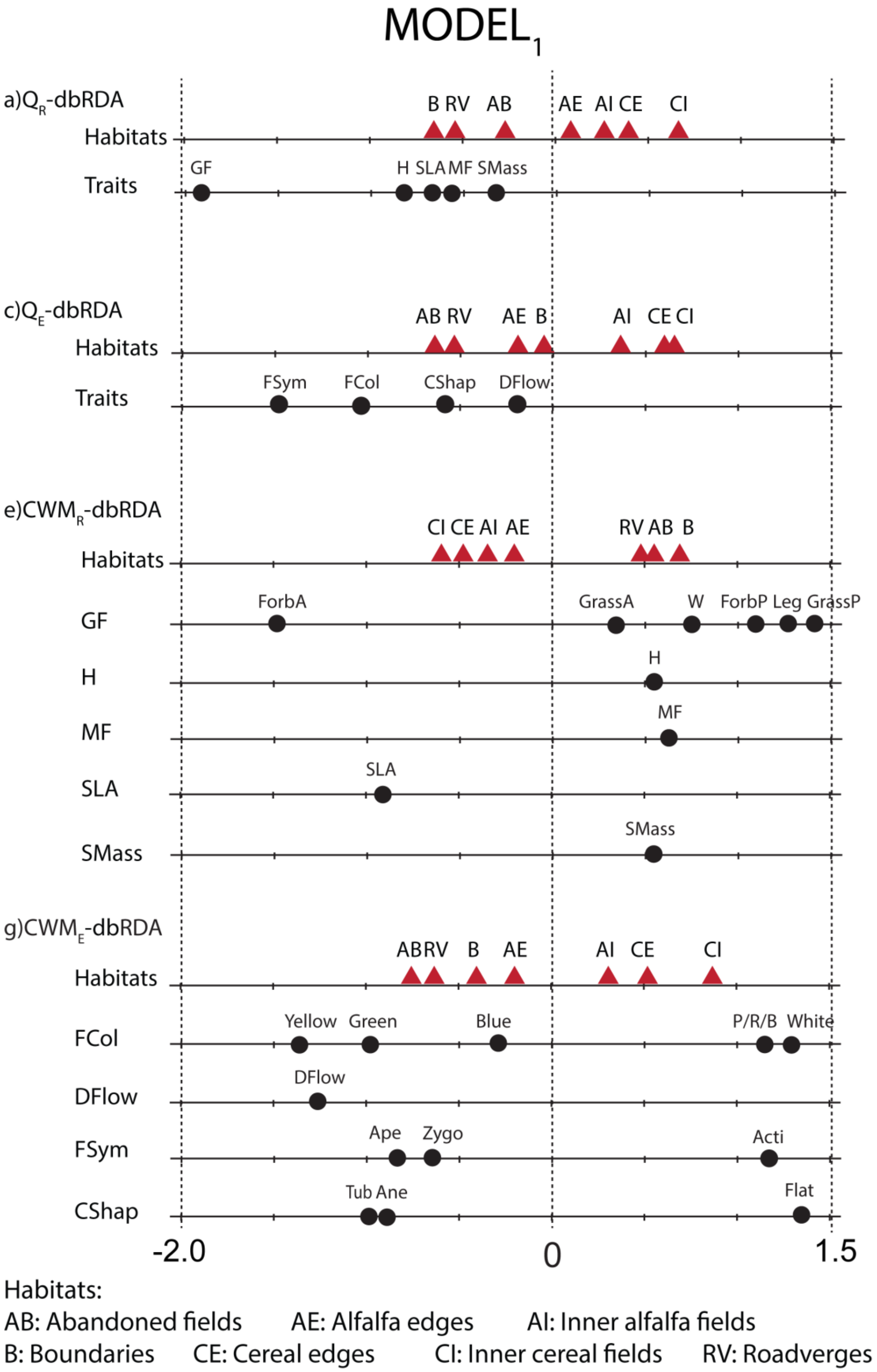

Figure 3. Mean scores along distance-based redundancy analysis (db-RDA) axis 1 of each single trait value of Rao's Quadratic Entropy (Q) and community weighted-means (CWM), of response (Q_R-db-RDA, CWM_R-db-RDA) and effect traits (Q_E-db-RDA, CWM_E-db-RDA), permuted with the surveyed habitats. Trait abbreviators are given in Table 1.

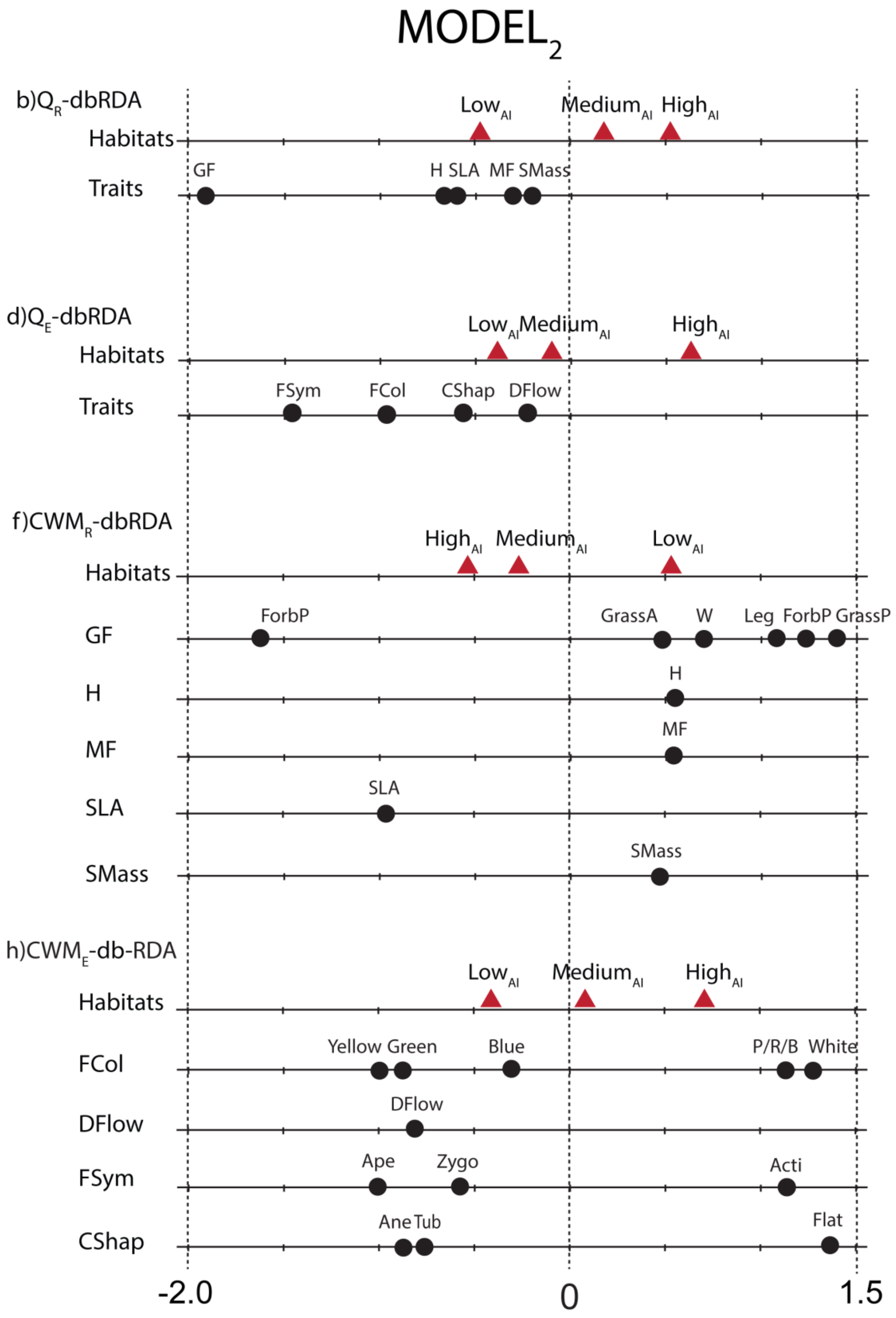

Figure 3 (cont) Mean scores along distance-based redundancy analysis (db-RDA) axis 1 of each single trait value of Rao's Quadratic Entropy (Q) and community weighted-means (CWM), of response (Q_R-db-RDA, CWM_R-db-RDA) and effect traits (Q_E-db-RDA, CWM_E-db-RDA), permuted with the levels of agricultural intensification (AI). Trait abbreviators are given in Table 1.

In terms of CWM, grasses, perennial forbs, woody, legumes and species with late flowering, tall stature and heavy seeds dominated at boundaries, abandoned fields and roadverges (Fig. 3e) as well as at $\mathrm{Low}_{\mathrm{AI}}$ (Fig. 3f), whereas annual forbs with high SLA dominated in edges and inner alfalfa and cereal fields (Fig. 3e) and also at $\mathrm{Medium}_{\mathrm{AI}}$ and $\mathrm{High}_{\mathrm{AI}}$ (Fig. 3f). On the other hand, species with yellow, green and blue flowers, with a long flowering period, apetalous and zygomorphous flowers, in addition to tubular and anemophilous corollas dominated in abandoned fields, roadverges, boundaries, alfalfa edges (Fig. 3g) and at $\mathrm{Low}_{\mathrm{AI}}$ (Fig. 3h). Conversely, edges and inner cereal fields and inner alfalfa fields (Fig. 3g), as well as $\mathrm{Medium}_{\mathrm{AI}}$ and $\mathrm{High}_{\mathrm{AI}}$ (Fig. 3h) were dominated by species with white, pink, red and brown flowers, a short flowering period, actinomorphous flowers and flat corollas. Although there was functional resemblance of Q_R between alfalfa edges and inner alfalfa fields, the Q_E of alfalfa field edges was closer to that of the boundaries than to inner alfalfa fields.

3.2. Additive partitioning of diversity

The additive partitioning comparing the α-diversity and β-diversity components from S and Q are shown in Fig. 4 and Supplementary Appendixes 2 and 3. Regarding habitat diversity (Model_1 Fig. 1), the highest $S\alpha_{\mathrm{patch}}$ was found in roadverges, being significantly higher than $S\alpha_{\mathrm{patch}}$ of boundaries and abandoned fields, as well as $S\alpha_{\mathrm{patch}}$ of alfalfa and cereal field edges (Fig. 4a). The smallest $S\alpha_{\mathrm{patch}}$ was calculated to be between inner alfalfa and cereal fields. The highest $S\beta_{\mathrm{patch}}$ was found in roadverges and significantly decreased in boundaries. $S\beta_{\mathrm{patch}}$ of roadverges and boundaries were significantly higher than $S\beta_{\mathrm{patch}}$ of abandoned fields, alfalfa and cereal edges. The lowest $S\beta_{\mathrm{patch}}$ were found in inner alfalfa and cereal fields, being significantly lower in the latter than in the former.

Abandoned fields, boundaries and roadverges were the habitats with the highest $Q_R\alpha_{\mathrm{patch}}$ (Fig. 4b). Alfalfa and cereal field edges had intermediate $Q_R\alpha_{\mathrm{patch}}$ among the abandoned fields, boundaries and roadverges and inner alfalfa fields. Inner cereal fields had significantly the lowest $Q_R\alpha_{\mathrm{patch}}$. The highest $Q_R\beta_{\mathrm{patch}}$ was quantified in inner alfalfa fields, followed by that of inner cereal fields. Roadverges had significantly the lowest $Q_R\beta_{\mathrm{patch},}$ whereas abandoned fields, boundaries, alfalfa and cereal field edges had a $Q_R\beta_{\mathrm{patch}}$ between those of inner cereal fields and roadverges.

Cereal field edges had significantly more $Q_E\alpha_{patch}$ than abandoned fields and inner cereal fields, whereas the rest of the habitats had intermediate $Q_E\alpha_{patch}$ (Fig. 4c). On the other hand, inner alfalfa and cereal fields had significantly more $Q_E\beta_{patch}$ than abandoned fields, boundaries and roadverges, whereas the rest of the habitats had intermediate $Q_E\beta_{patch.}$

Regarding AI levels, $S\alpha_{patch}$ and $S\beta_{patch}$ were significantly greater in Low_{AI} than in $Medium_{AI}$ and $High_{AI}$ (Fig. 4d). Increasing AI led to a significant decrease of $Q_R\alpha_{patch}$ (Fig. 4e). However, $Q_R\beta_{patch}$ was significantly greater in $Medium_{AI}$ than in Low_{AI} and $High_{AI}$. No differences among AI levels were found in terms of $Q_E\alpha_{patch}$, whereas $Q_E\beta_{patch}$ was significantly greater in $Medium_{AI}$ and $High_{AI}$ than in Low_{AI} (Fig. 4f).

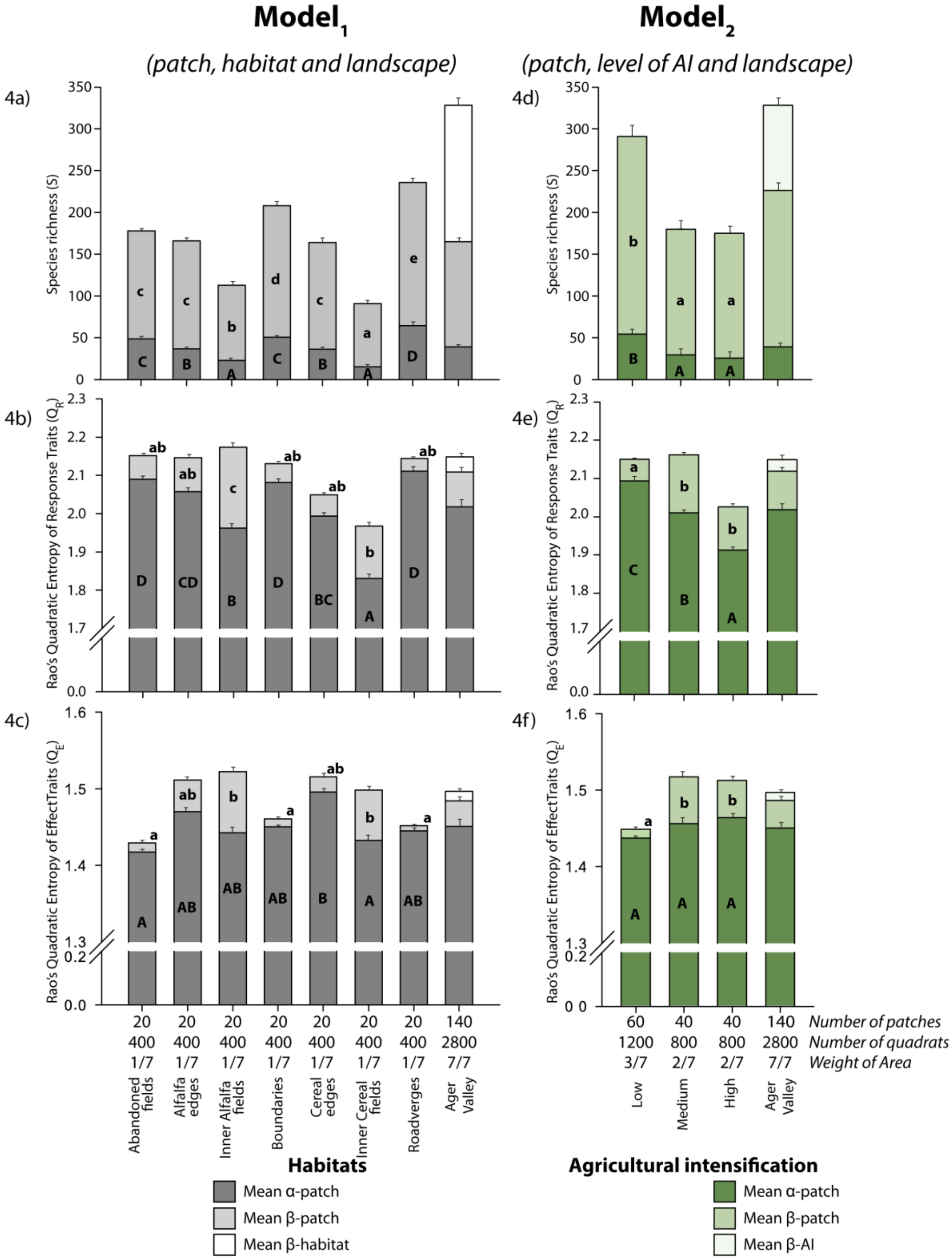

Figure 4. Each column indicates the species richness, Rao's Quadratic Entropy of Response traits (Q_R) and Rao's Quadratic Entropy of Effect Traits (Q_E) from Model$_1$ based on the different habitats within-landscape, and for Model$_2$ based on the different levels of Agricultural Intensification (AI) for the study area (Ager Valley). Diversity is partitioned into patch and habitat diversity components in Model$_1$ and into patch and AI level diversity components in Model$_2$. The height of each column shows the mean value of each diversity component in each habitat, AI level and over the whole area of study. Error bars are ±SE (standard error) of the means.

4.Discussion

4.1. Distribution patterns of species assemblages

The NMDS and the cluster analysis reveal that plant assemblages respond to AI gradients. Although plant assemblages reflect the impact of farming practices at various field positions (Solé-Senan et al., 2014), these compositional differences are downplayed when the habitats and AI gradients are jointly analyzed. However, at AI scale, we observed a higher frequency of species dissimilarity among patches subjected to $\text{Medium}_{\text{AI}}$ than to those subjected Low_{AI} and High_{AI}. This trend may be the result of complementary processes. Firstly, species assemblages at $\text{Medium}_{\text{AI}}$ could harbour more species than habitat patches subjected to High_{AI} and Low_{AI} due to success in the immigration of species from neighbouring habitats. Secondly, subjecting communities to High_{AI} leads to biotic homogenization (Solé-Senan et al., 2014), whereas at Low_{AI}, secondary succession processes are triggered (Kahmen and Poschlod, 2004). Furthermore, in our study area, $\text{Medium}_{\text{AI}}$ is associated with alfalfa fields, and since compositional heterogeneity often influences their historical management (age of the alfalfa and previous crop successions in arable fields) (Meiss et al., 2010), this may lead to the highest variety of species assemblages between similar patches.

4.2. Distribution patterns of trait syndromes

There is the need for examining single-trait values separately in order to quantify the trait abilities and summarize the relationships between plant traits and ecosystem functioning (Ricotta and Moretti, 2011). Our study reveals the simultaneous occurrence of trait-divergence and trait-convergence throughout the habitats within a mosaic landscape based on the AI level that the habitat is subjected to. Indeed, the comparison of the two different models (Fig. 1) indicates that the filtering effect of functional traits is strongly driven by AI rather than the particular environmental factors affecting the habitats within the mosaic landscape. Thus, trait-divergence was associated with a reduction in AI, which corroborates that the increasing AI leads to a strong filtering effect of plants species according to their traits (Pakeman, 2011; Armengot et al., 2016). The increasing trait-divergence was not only found for response traits, but also for effect traits. On the other hand, CWM indicated shifts in mean trait values were due to environmental selection, based on contrasting trait syndromes that are associated with different species responses to AI gradients. Therefore, deterministic process structuring of plant communities leads to trait-convergence towards local conditions. Similarly, this leads to common trait syndromes in response to local conditions, but there are different trade-offs required of plants to acquire and use local resources in contrasted niches caused by differences in AI. Similar trait syndromes found in habitats subjected to the same AI reinforce the idea that the current functional structure of a plant community within a landscape is a legacy from the filtering of the regional species pool.

We found that $\mathrm{Low_{AI}}$ selects for competitive species, whereas increasing AI selects for ruderal species, indicating a trade-off of ecological strategies based on the AI gradient (Grime, 1974; Storkey et al., 2013). The strongest functional resemblance found among habitats subjected to $\mathrm{Low_{AI}}$ may reflect a neighbouring effect and recruitment from the species pool of the adjacent semi-natural habitats (Devlaeminck et al., 2005) followed by a secondary succession stage (Kahmen and Poschlod, 2004). The dominance of perennial species is likely to host few weed species (Solé-Senan et al., 2014). Likewise, relying on the existence of semi-natural habitats at $\mathrm{Low_{AI}}$ entails restoring the presence of legumes, which are less tolerant to fertilization (Van Elsen, 2002). The fact that the tallest plants thrive in habitats at $\mathrm{Low_{AI}}$ rather than in those where AI increases is because plants are taller in the absence of filters such as ploughing and grazing (Lavorel and Garnier, 2002). The decrease in AI results in the accumulation of standing biomass and in the increase in competition for light, which favours perennial plants with traits linked to survival ability such as tall canopies and heavy seeds (Hemrová and Münzbergová, 2015). Late onset flowering observed in such species is a common trait in undisturbed plant communities (Pinke and Gunton, 2014), whereas increasing AI promotes species with early flowering. Indeed, early flowering implies early dispersal, germination and emergence and thus a longer period for available growth, which is expected to be a successful strategy for annual species that need to complete their vital cycle in a short period of time. Conversely, an increase in AI in unshaded habitats entails a resource-rich environment selecting plants with high SLA, which are associated with high growth rate and short life forms. A positive relationship between SLA and nutrient content has been found in other agricultural systems such as in arable fields in Spain (Hernandez Plaza et al., 2015), in the United Kingdom (Storkey et al., 2013) and in grasslands in Sweden (Vandewalle et al., 2014).

Regarding effect traits, habitats arrangements along the first axis of the Q_E-dbRDA analysis suggest that the differences in AI between edges and inner alfalta fields (Medium_{AI}) act as an ecological threshold for pollination services. The differences between edges and inner-fields at Medium_{AI} may be explained by the fact that edges are more susceptible to the colonization by external propagules and thus act as a species reservoir. However, this process would be completely interrupted in High_{AI} since the repeated disturbances compromise the high potential of cereal edges for harbouring species coming from the vicinity. In terms of trait dominance, shifts in CWM trait values of Fdur, FSym, CShap and FCol impact pollination services. Perennials at Low_{AI} increase insect attractiveness by bearing flowers for a long time, which increases insect-foraging time. Conversely, the species pool at Medium_{AI} and in a major extent at High_{AI}, maintains flowers for a shorter period of time due to their short life cycle (Pinke and Gunton, 2014), therefore reducing both insect-attractiveness and insect foraging time. Two different traits syndromes were found at Low_{AI}; first, a trait syndrome characterized by floral traits of a set of perennial *Poaceae* species, which are inaccessible for pollinators; and secondly, a floral trait syndrome characterized by species with zygomorphous and tubular corollas with yellow and blue flowers that are known to be related to insect-body size, proboscis type and insect-attractiveness (Fenster et al., 2004; Ibanez, 2012, Ricou et al., 2014). Conversely, increased AI promoted dominant plant species with trait syndromes characterized by pink, white and actinomorphous flowers as well as flat corollas, which are linked to generalist pollinators (Ricou et al., 2014). Therefore, the presence of such floral traits is expected to trigger the filtering of insect-pollinator syndromes, depending on the accessibility that flowers provide to pollinators.

The shared trait syndrome that provides resources to specialized pollinators in habitats at Low_{AI} suggests a positive plant-plant interaction in community assembly (Rae et al., 2006). The success of one species indirectly enhances pollinator visitation to the neighbours, promoting seed production and the maintenance of species populations whenever disturbance levels do not increase. The trait syndrome that has been uncovered is known to enhance the abundance and richness of prominent ecosystem service-providers such as bees (Holzschuh et al., 2007; Kohler et al., 2007; Nayak et al., 2015), bumblebees and hoverflies (Holland et al., 2015). The plant-plant interaction could therefore explain why trait syndromes of effect traits on alfalfa edges are similar to those found at $\mathrm{Low}_{\mathrm{AI}}$. Alfalfa is generally considered to be a mass flowering crop (Wratten et al., 2012) and bumblebee density is positively related to the availability of highly rewarding mass flowering crops in the landscape (Westphal et al., 2003). Although it is suggested that the benefit of mass-flowering crops on pollinator populations needs to be accompanied by pollinator-supporting practices (Holzschuh et al., 2016), the amount of semi-natural habitats subjected to $\mathrm{Low}_{\mathrm{AI}}$ would enhance habitat attractiveness for pollinators by enhancing plant-plant interaction (Rae et al., 2006). These semi-natural habitats are the favoured places for nesting and hibernating for the major pollinator groups, thus making them an essential element at the landscape scale for effective insect-plant interaction (Batáry et al., 2011). A similar result has been documented in cotton agroecosystems (Cusser et al., 2016), where pollinator abundance and richness were positively correlated with the presence of semi-natural land cover.

4.3. Spatial partitioning of species richness and functional diversity

Our study is the first to analyze S and multi-trait Q_R and Q_E in different habitats subjected to AI gradients. We corroborate that S (Wagner et al., 2000; Flohre et al., 2011) and Q_R (Diaz et al., 1998) are strongly reduced under $\mathrm{High}_{\mathrm{AI}}$. Surprisingly, this trend was not found in terms of Q_E, however, it is worth highlighting that the lowest Q_E found in habitats subjected to $\mathrm{Low}_{\mathrm{AI}}$ may be a driving factor in the dominance of one trait syndrome having important implications in the provisioning of resources to specific pollinators. Despite finding that single-trait values are determined at the AI level, multi-trait values of Q_R and Q_E at the landscape scale did not differ between Model_1 and Model_2. This finding reinforces that traits are determined at AI (Pakeman, 2011) and no further details on field position and habitat environmental characteristics are needed to unravel functional diversity patterns along spatial-scales within a landscape mosaic.

The turnover in S was driven by differences in species pools at larger scales. It is surprising the high turnover was found in inner cereal fields and at $\mathrm{High}_{\mathrm{AI}}$, especially because arable plant communities tend to be homogeneous. However, such variation in species composition proved to be spatially structured between patches, and to have aggregative patterns (in some weeds) (Blanco-Moreno et al., 2006). Indeed, the high $S\beta_{\mathrm{patch}}$ diversity may be due to differences in cropping history and cultural management of the cereal fields. This is just a common pattern of weed communities at larger spatial scales which has been previously observed in annual crop fields such as rice (Pinke et al., 2014), papaver (Pinke et al., 2011) and soybean (Pinke et al., 2016).

The turnover of plant species between AI levels, as well as the concurrent down-shift in terms of functional assemblages of response and in effect traits (Fig. 4), reflect the replacement of species by others with similar traits, thus suggesting a high level of functional redundancy between these habitats. Therefore, shifts in plant assemblages tell us little about functional shifts when trait redundancy is high, as it has been shown in Iberian pastures (de Bello et al., 2009). Furthermore, species turnover at Low_{AI} presented the highest proportion of similar functional features (Fig. 5). The filtering effect of landscape species pool shows asynchronous functional response and a higher niche differentiation when AI increased, which helps maintain system stability during disturbance.

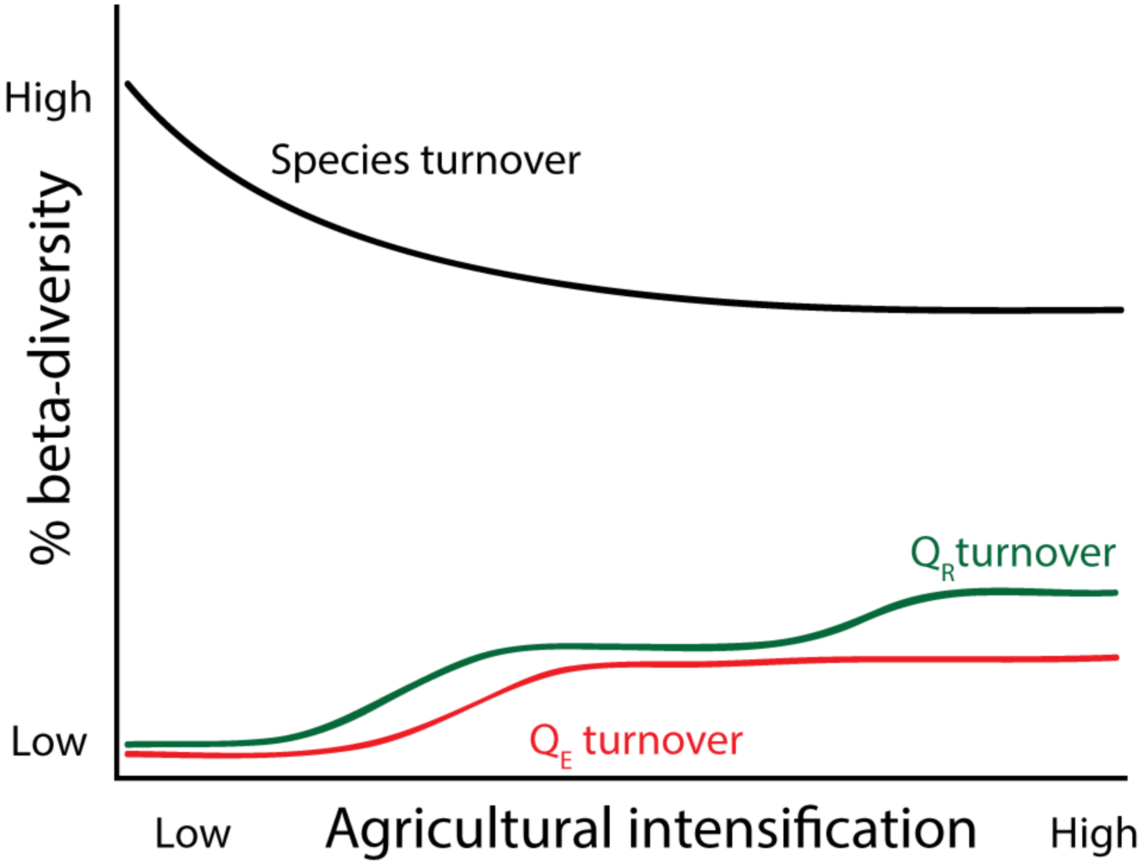

Figure 5. Graph illustrating linkages between the high species turnover and the low functional turnover of the Rao's Quadratic Entropy of Response (Q_R) and Effect traits (Q_E) along gradients of agricultural intensification.

4.4. Implications for management and conservation

Conservation measures in agricultural landscapes are mainly based on the application of agri-environmental schemes (Whittingham et al., 2007). However, nature conservation efforts are currently shifting from managing target species to being based on dynamic ecosystem properties (Bengtsson et al., 2003) and should rely on appropriate knowledge of the functional characteristics of plant communities. Therefore, ecological evaluations must become the foundation of diversity conservation in agricultural landscapes. Even still, further research is needed to fully understand how vegetation should be managed so as to provide specific services.

Our findings reinforce the importance of splitting functional traits in response and effect and how shifts in plant functional assemblages would affect the provision of ecosystem services such as pollination. As functionality encompasses concepts such as trait-convergence and trait-divergence, its study needs to be focused on using a combination of indices involving these concepts, otherwise it may give rise to a wilful misinterpretation of functional diversity patterns.

Finally, management of the provisioning of resources for pollinators should focus on semi-natural vegetation since it is a refuge for plants with valuable trait syndromes that attract and support specialized pollinators. Given that pollinator diversity is important to crop yield, agri-environmental schemes aimed at maintaining such semi-natural habitats at Low_{AI}, rather than increasing local crop heterogeneity, are crucial to preserving plants that offer trophic resources to pollinators. These measures will be highly cost-effective as they do not suppose an extra-managing cost for farmers. Furthermore, such measures may trigger positive ecological and economical impacts by allowing for the maintenance of wild plant diversity, wider ecosystem services stability and crop production (Potts et al., 2010).

5. Conclusions

Our research documents interactions at different spatial scales among plant species and functional assemblages of driver and effect traits across habitats subjected to different levels of AI. We demonstrated how plant functional traits react quickly to changes in AI, and the importance of plant species in semi-natural habitats in providing resources for pollinators due to specialized trait syndromes. Attempts to explain overall diversity patterns need the consideration of the three different indexes: S, Q and CWM, otherwise the study may lead to misinterpretations. β-diversity species richness contributed most to the total species richness, but we did not observe the same trend in terms of functional diversity, which would indicate that the turnover in species richness did not entail a functional turnover. Traits are determined at the AI level and no further details on field position and the diversity of habitats within a mosaic landscape are needed to promote vegetation to support pollinating insects. We suggest maintaining a network of semi-natural areas in mosaic landscapes to ensure functional trait diversity as well as conserving plants with specific floral trait syndromes.

Acknowledgements

We acknowledge the financial support provided by the Universitat de Lleida and the Ministerio de Educación y Ciencia (Projects AGL 2007-60828 and AGL 2010-22084-C02-01). We thank Joel Torra and Aritz Royo for the field assistance and farmers for allowing us to access their fields and Sarah Lade for improving the English.

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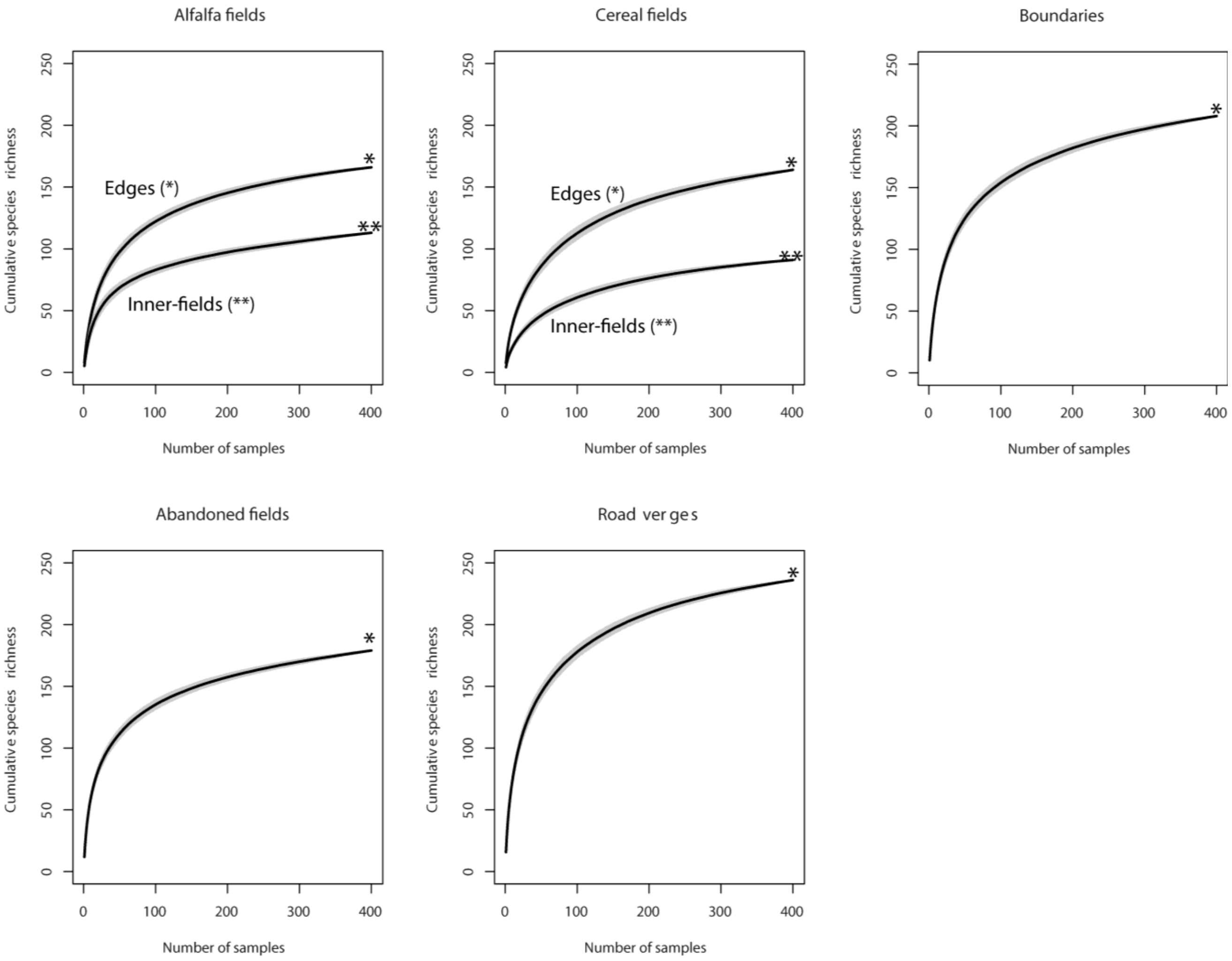

Supplementary Appendix 1. Species accumulation curves at each habitat sampled in the Ager Valley. *, ** First-order jack-knife estimate of total richness

Supplementary Appendix 2. The average and standard error (in parentheses) of the α_{patch} and β_{patch} components of the species richness (S) and the Rao's Quadratic Entropy of response (Q_R) and effect traits (Q_E) among the habitats surveyed in the Ager Valley. Significant differences indicated by different letters within-rows are based on Tukey HSD tests ($p<0.05$).

	Abandoned fields		Alfalfa edges		Alfalfa inner-fields		Boundaries		Cereal edges		Cereal inner-fields		Roadverges	
$S\alpha_{patch}$	48.55(2.196)	c	36.85(2.528)	b	22.75(2.642)	a	50.8(1.639)	c	36.45(1.325)	b	15.4(0.922)	a	64.5(2.859)	d
$S\beta_{patch}$	129.45(2.196)	c	129.15(2.528)	c	90.25(2.642)	b	157.2(1.639)	d	127.55(1.325)	c	75.6(0.922)	a	171.5(2.859)	e
$Q_R\alpha_{patch}$	2.09(0.017)	d	2.057(0.018)	cd	1.962(0.033)	b	2.081(0.012)	d	1.994(0.013)	bc	1.831(0.021)	a	2.111(0.009)	d
$Q_R\beta_{patch}$	0.096(0.016)	ab	0.125(0.018)	ab	0.248(0.033)	c	0.087(0.012)	ab	0.088(0.012)	ab	0.163(0.021)	b	0.071(0.009)	a
$Q_E\alpha_{patch}$	1.418(0.007)	a	1.47(0.015)	ab	1.442(0.019)	ab	1.45(0.011)	ab	1.496(0.012)	b	1.433(0.02)	a	1.445(0.007)	ab
$Q_E\beta_{patch}$	0.042(0.005)	a	0.063(0.012)	ab	0.094(0.017)	b	0.038(0.007)	a	0.053(0.006)	ab	0.089(0.015)	b	0.027(0.004)	a

Supplementary Appendix 3. The average and standard error (in parentheses) of the α_{patch} and β_{patch} components of the species richness (S) and the Rao's Quadratic Entropy of response (Q_R) and effect traits (Q_E) among the three levels of agricultural intensification (Low_{AI}, $Medium_{AI}$ and $High_{AI}$) to which the surveyed habitats in the Ager Valley were subjected. Significant differences indicated by different letters within-rows are based on Tukey HSD tests ($p<0.05$).

	Low_{AI}		$Medium_{AI}$		$High_{AI}$	
$S\alpha_{patch}$	54.617(1.589)	b	29.8(2.129)	a	25.925(1.864)	a
$S\beta_{patch}$	236.383(1.589)	b	150.2(2.129)	a	149.075(1.864)	a
$Q_R\alpha_{patch}$	2.094(0.008)	c	2.01(0.02)	b	1.912(0.018)	a
$Q_R\beta_{patch}$	0.065(0.007)	a	0.153(0.02)	b	0.124(0.016)	b
$Q_E\alpha_{patch}$	1.438(0.005)	a	1.456(0.012)	a	1.464(0.012)	a
$Q_E\beta_{patch}$	0.032(0.003)	a	0.075(0.01)	b	0.072(0.009)	b

Supplementary Appendix 4. Most abundant species per habitat

Abandoned fields		Alfalfa edges		Alfalfa inner-fields		Boundaries	
Medicago minima	58.5	*Anacyclus clavatus*	45	*Arenaria serpyllifolia*	29	*Bromus diandrus*	45
Bromus diandrus	52	*Lolium rigidum*	45	*Polygonum aviculate*	24.25	*Elymus repens*	44
Avena barbata	46	*Bromus diandrus*	35.25	*Hordeum murinum*	23.75	*Avena sterilis*	41.5
Convolvulus arvensis	45.25	*Polygonum aviculare*	29	*Chenopodium album*	21.25	*Dactylis glomerata*	35.25
Cynodon dactylon	45.25	*Hordeum murinum*	28.5	*Capsella bursa-pastoris*	21	*Papaver rhoeas*	33.25
Lolium rigidum	40.5	*Arenaria serpyllifolia*	23.25	*Lolium rigidum*	21	*Anagallis arvensis*	31.75
Crepis vesicaria	32.25	*Papaver rhoeas*	23	*Herniaria cinerea*	19.5	*Convolvulus arvensis*	26
Plantago lanceolata	30.5	*Polygonum convolvulus*	20.75	*Poa annua*	15.5	*Lolium rigidum*	25.75
Hordeum murinum	29.25	*Plantago lanceolata*	20	*Anacyclus clavatus*	14.75	*Centaurea sostitialis*	24.75
Sanguisorba minor	28.75	*Filago pyramidata*	19.75	*Papaver rhoeas*	13	*Avena barbata*	24.5
Medicago rigidula	25	*Capsella bursa-pastoris*	19.5	*Erucastrum nasturtiifolium*	12.25	*Medicago minima*	22.25
Anacyclus clavatus	24.25	*Chenopodium album*	19.5	*Anagallis arvensis*	11.75	*Polygonum convolvulus*	20.75
Chondrilla juncea	23	*Anagallis arvensis*	18.75	*Geranium molle*	11.75	*Brachypodium phoenicoides*	19.25
Pallenis spinosa	20.25	*Koeleria phleoides*	18.75	*Koeleria phleoides*	11.5	*Geranium molle*	18.25
Petrorhagia prolifera	20	*Geranium molle*	18.25	*Bromus diandrus*	11.25	*Polygonum aviculare*	18
Crepis foetida	18.75	*Desmazeria rigida*	13	*Chenopodium vulvaria*	10.75	*Thymus vulgaris*	17.75
Avena sterilis	18.5	*Centaurea sostitialis*	12	*Verbena officinalis*	10.75	*Torilis nodosa*	16
Sonchus oleraceus	18.25	*Bromus hordeaceus*	9.75	*Centaurea aspera*	10	***Caucalis platycarpos***	15
Centaurea sostitialis	17.75	*Herniaria cinerea*	9.5	*Avena sativa*	9.5	***Delphinium pubescens***	14.75
Dactylis glomerata	17.5	*Sonchus oleraceus*	9.5	*Bromus hordeaceus*	9	***Lathyrus aphaca***	14.5

Cereal edges		Cereal inner-fields		Roadverges	
Polygonum aviculare	77	*Polygonum aviculare*	72.75	*Medicago minima*	58.5
Polygonum convulvulus	58.75	*Polygonum convolvulus*	50.5	*Bromus diandrus*	52
Papaver rhoeas	58	*Papaver rhoeas*	34.5	*Avena barbata*	46
Lolium rigidum	43.5	*Avena sterilis*	28.5	*Convolvulus arvensis*	45.25
Anagallis arvensis	36.5	*Anagallis arvensis*	25.25	*Cynodon dactylon*	45.25
Fumaria officinalis	28.25	*Fumaria officinalis*	23.25	*Lolium rigidum*	40.5
Avena sterilis	25.25	*Lolium rigidum*	20.75	*Crepis vesicaria*	32.25
Chenopodium album	20	*Chenopodium album*	16.25	*Plantago lanceolata*	30.5
Anacyclus clavatus	17.75	*Convolvulus arvensis*	10.5	*Hordeum murinum*	29.25
Bromus diandrus	17	*Centaurea sostitialis*	7	*Sanguisorba minor*	28.75
Caucalis platycarpos	17	***Delphinium pubescens***	7	*Medicago rigidula*	25
Centaurea sostitialis	16.5	*Silene vulgaris*	6.75	*Anacyclus clavatus*	24.25
Hypecoum procumbens	15.5	***Adonis flammea***	6.25	*Chondrilla juncea*	23
Polycnemum majus	15	***Hypecoum procumbens***	5.5	*Pallenis spinosa*	20.25
Lathyrus aphaca	13	*Fumaria parviflora*	5.25	*Petrorhagia prolifera*	20
Silene vulgaris	13	*Cynodon dactylon*	5	*Crepis foetida*	18.75
Adonis flammea	12	*Galium parisiense*	5	*Avena sterilis*	18.5
Convolvulus arvensis	12	*Lithospermum arvensis*	5	*Sonchus oleraceus*	18.25
Coronilla scorpioides	10.25	*Erucastrum nasturtiifolium*	4.5	*Centaurea sostitialis*	17.75
Delphinum pubescens	9.5	*Xanthium strumarium*	4.5	*Dactylis glomerata*	17.5

CHAPTER 4

Plant diversity in Mediterranean cereal fields: Unravelling the effect of landscape complexity on rare arable plants

Published in *Agriculture, Ecosystems and Environment*, 185: 221-230.

Plant diversity in Mediterranean cereal fields: unraveling the effect of landscape complexity on rare arable plants

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Abstract

Landscape complexity is thought to increase plant diversity in Mediterranean dryland cereal fields, although this assumption has not been tested specifically for rare arable plants (RAP). Standardized landscape metrics may help elucidate efforts to enhance RAP conservation. Our paper evaluates the impact of the surrounding landscape on the plant diversity and species composition for both total species and rare arable plants (RAP) at three contrasted field positions (boundary –first metre of non-cultivated habitat surrounding a field-, edge –first metre of cultivated habitat adjacent to the boundary- and centre) in 90 conventional cereal fields in 45 landscapes (2 fields per landscape) over three regions in the NE Iberian Peninsula (15 landscapes per region). Total species richness (S) and Shannon diversity (H’) were partitioned into α- and β-components. β-components accounted the maximum contribution to the total diversity. $S\alpha_{landscape}$ –species richness within-landscape- and $H'\alpha_{landscape}$ –Shannon diversity within-landscape- of total species and $S\alpha_{landscape}$ of RAP were higher in structurally complex landscapes than in simple ones. The positive effect of landscape complexity on the $\alpha_{landscape}$ diversity was highest at the boundary for total species but at the edge for RAP. Two subsets of RAP, G1 and G2, were identified according to their response to landscape metrics gradients. G1 and G2 were assembled in complex and simplified landscapes, respectively. Landscape metrics explained the highest variation in species composition at the boundary and the edge for total species and exclusively at the edge for RAP. Moreover, the variation in species composition explained by landscape metrics was higher for RAP than for total species. Thus, RAP assemblages in arable fields are greatly influenced by processes operating at the landscape scale which may filter plant species. Our study provided a formal framework to help policy makers identify landscape configurations that most benefit plant conservation policies. As a depleted species pool may prevent the re-assembly of RAP, agri-environmental schemes targeting landscapes with useful structural elements supporting diversity may increase populations of RAP. Low-input farming practices at the edge of the arable fields in complex landscapes are expected to be the best cost-effective methods for enhancing RAP.

Keywords: α-diversity, boundary, community assembly, conservation measures, edge, structural elements.

1. Introduction

Arable plants are among the most endangered plant species in Europe (Storkey et al., 2012) as a result of increased land-use intensity and decreased landscape complexity in agricultural landscapes over the last few decades (Tscharntke et al., 2005; Van Calster et al., 2008). In particular, a set of arable plants which tend to be less tolerant to fertilizer and herbicides has become extremely rare and threatened (Kleijn and vanderVoort, 1997; Fried et al., 2009 and Storkey et al., 2012). The conservation status of these rare arable plants (RAP) is increasingly raising concerns in Europe and, as a consequence, the number of RAP included in conservation polices has therefore increased (Aboucaya et al., 2000; Byfield and Wilson, 2005).

To counteract impacts of farming practices on agricultural landscapes, the European Union has developed the Agri-environmental schemes (AES). The effectiveness of AES on the conservation of plant diversity in the Mediterranean area has been constrained by the shared effects of landscape complexity and land-use intensity (Concepcion et al., 2008). Landscape complexity plays a crucial role in dryland Mediterranean cereal areas, which harbor high levels of plant diversity (Holzer and Immonen, 1982) and large populations of RAP of European conservation concern (Kleijn et al., 2011), and are characterized by low rainfall (<500 mm/year) and low crop yields (<3000 kg/ha). Farming practices are mainly conventional, based on the use of herbicides and fertilizers (Lopez-Bellido, 1992). In this scenario, landscape complexity is expected to play a preeminent role in supporting RAP because their persistence will depend on their ability to colonize a suitable habitat in the surrounding landscape.

The relationship between species diversity and landscape complexity is controversial. Complex landscapes have been reported to benefit plant diversity because they offer more habitat heterogeneity than simple landscapes (Gabriel et al., 2005; Roschewitz et al., 2005; Concepción et al., 2012). However, some authors have pointed out that the effect of the surrounding landscape on plant diversity occurs only at local scale, within a radius of 500 m (Marshall, 2009; Gaba et al., 2010). Many studies have shown that the degree of landscape complexity affects exclusively the outer positions of the field, i.e. boundaries and edges, with no effects in the centre (Weibull et al., 2003; José-Maria et al., 2010). Additionally, complex landscapes contain higher perimeter-area ratios of patches and therefore more boundaries and sharp edges to provide refuge for plants

(Gabriel et al., 2005; Gaba et al., 2010; Bassa et al., 2011), especially those most sensitive to conventional farming practices (Smart et al., 2002; Fried et al., 2009). Therefore, fields surrounded by structurally complex landscapes are expected to harbor plant communities with a higher diversity of RAP than simplified ones.

Although some studies on the relationship of plant diversity and landscape complexity in Mediterranean systems have been conducted recently (Concepcion et al., 2008; José-Maria et al., 2010; Armengot et al., 2011; Bassa et al., 2011; Concepcion et al., 2012), they have not focused on RAP. Identifying sites where RAP remain is essential to ensure their conservation through sustainable management. We hypothesize that RAP are more abundant at boundaries and edges of the fields and that landscape complexity provides safe havens for species of conservation concern. Structural complexity is expected to sustain plant populations and reduce their risk of local extinction. Thus, the use of landscape structure indicators such as the presence of arable lands, fields with sharp edges, and linear features of natural vegetation may help to elucidate the effect of landscape complexity on species diversity and community composition at boundaries, edges and the centres of the fields and to estimate, particularly, their importance for the maintenance of RAP. We used the additive diversity partitioning method (Lande, 1996), such that $\gamma = \alpha + \beta$, to divide the diversity in α-diversity within-landscape ($\alpha_{landscape}$), between-landscape β-diversity ($\beta_{landscape}$) and between-region β-diversity (β_{region}) for each location in field (boundary, edge and field centre) and for two diversity measures: species richness (S) and Shannon diversity (H’). Additionally, as diversity measures are usually large invariant to changes in species composition, we also focused on species assemblages. Our aims were to (i) examine whether changes occurred in the α- and β-components of S and H’ of total species and RAP depended on the field position (boundary, edge and field centre) at two spatial scales (landscape and region) (ii), to analyse the effect of landscape complexity on the within-landscape component ($\alpha_{landscape}$) of S and H’ of total species and RAP from the boundary to the field centre and (iii) to determine whether total species and RAP assemblages are equally affected by a gradient of landscape complexity. This information is essential to allow policy makers to develop guidelines for conserving plant diversity and particularly enhance RAP in the Mediterranean area.

2. Materials and methods

2.1 Study area and landscape structure characterization

The study was conducted in 2008 in three regions (Noguera, Segarra and Pallars Jussà) within a dryland area of the eastern Ebro Valley, in Catalonia, in the NE Iberian Peninsula. We have chosen these three regions because of three main reasons, namely; (1) they are representative of the traditional management of cereal in dry-land areas, (2) they provide a gradient of landscape complexity and (3) they have not suffered any relevant landscape transformation in the last century. Regional environmental characteristics and farming practices applied in the fields are summarized in Table A.1. Landscape is characterized by mosaics of small arable fields, almond and olive groves interspersed with patches of natural vegetation. In each region, we selected 15 localities along a gradient of complexity ranging from simple landscapes with a high percentage of arable land (95%) to complex landscapes with a low percentage of arable land (5%). All landscapes were at least 5 km (from centre to centre) away from each other. At each locality two fields which were representative of the landscape (i.e. as similar as possible in terms of shape and area to that of most of the fields within the locality or landscape) were randomly selected. The two fields were not adjacent but were close in proximity to ensure similar abiotic conditions. Georeferenced aerial photographs (ICC, 2008) were digitalized and classified as natural vegetation or arable patches in a circular buffer area of 1-km radius around the two focal fields using a geographical information System (ESRI, 2006). Natural vegetation included forestry and shrubby patches and linear elements such as hedgerows. Arable patches included cereal fields, almond groves and olive groves, and man-made structures. There was no east–west or north–south gradient of landscape complexity, as XY-coordinates of the localities do not correlate with landscape context (X-coordinates vs. percentage of natural vegetation: $\rho = 0.03$, $P = 0.83$; Y-coordinates vs. percentage of natural vegetation: $\rho = 0.15$, $P = 0.32$). Afterwards, landscape structure was characterized by a set of landscape metrics widely used in landscape ecology (McGarigal and Marks, 1994) which are summarized in Table A.2:

Percentage of natural vegetation (hereafter PER_{NV}).

Total length of perimeter of arable patches (TLAP), which is the sum of the lengths of the perimeters of all of the arable patches.

Perimeter-area ratios of the natural vegetation (PA_{NV}) *and arable* (PA_{ARA}) *patches*, which are the weighted perimeter-area ratios of each patch for each type (natural vegetation or arable lands).

Shape index of natural vegetation (SI_{NV}) *and arable* (SI_{ARA}) *patches*, which reflect the compactness of each patch. The minimum value is 1 and the index increases as the shape of the patch becomes more convoluted and dendritic. The shape index is computed as follows:

$$SI_{patch} = p/(2(\pi a)^{-1/2})$$

where p is the length of the perimeter and a is the area of one patch of each type. The SI of each local landscape was calculated as follows:

$$SI_{NV/ARA} = \Sigma_{ij} SI_{patch\ i}/(a_i/Ai)$$

where a_i is the area of one patch and A_i is the sum of the areas of all of the patches.

2.2 .Plant data sampling

Plant surveys were conducted before harvest, between May and July 2008. As plants are not homogenously distributed over the field (Wilson and Aebischer, 1995), the surveys were performed at three different positions: a) the boundary, which is the first metre of non-cultivated habitat surrounding a field, b) the edge, which encompasses the metre of cultivated habitat that is adjacent to the boundary, and c) the field centre, 50 m from the edge. At each position, surveys were conducted by one transect of five plots (1 x 5 m) that ran parallel to the edge of the field at 10-m intervals. Plant nomenclature followed de Bolòs et al. (2005). The six-point scale of Braun-Blanquet (1979) was used to quantify species abundance. The sampling effort was evaluated by species richness estimators (Incidence-based Coverage Estimator – ICE) using R (R Development Core Team, 2008) with package Fossil (Vavrek, 2011).

2.3 Rare arable plants

Due to the absence of legal instruments such as decrees or red lists identifying RAP in Spain, we used three criteria for the selection of RAP. Firstly, we followed the Plan national d'action pour la conservation des plantes messicoles (Aboucaya et al., 2000), which is based on rates of decline according to surveys of expert botanists in France. We made an a posteriori comparison of the species recorded with the French list because the French list may include species on the southern edge of its range that are uncommon in Spain and may not include species that are common in Spain. Moreover, some species that are rare and threatened in France are common in Spain. Secondly, we identified the species of our check-list included in the syntaxonomical order Secalietalia cerealis according to the local flora (De Bolòs et al., 2005). Only those species categorized with a status of rarity in the study area according to De Bolòs et al. (2005) – R, rare; RR, very rare; RRR, extremely rare- were chosen. Thirdly, an expert local botanist advised us on the selection of the set of RAP according to his criterion and experience based on the study of the evolution of weed communities in the study area for more than 30 years (unpublished data).

2.4 Diversity partitioning

Diversity partitioning of the total diversity observed (γ_{obs}) (Lande, 1996) for both total species and RAP into α- and β-components allows to compare the relevance of each component at various spatial scales (Wagner et al., 2000). The total diversity observed (γ_{obs}) depending on the field position was partitioned as:

$$\gamma_{obs} = \alpha_{landscape} + \beta_{landscape} + \beta_{region}$$

where $\alpha_{landscape}$ is the mean diversity per landscape, $\beta_{landscape}$ is the mean between-landscape β-diversity, and β_{region} is the mean between-region β-diversity. These values were obtained as follows:

$$\alpha_{landscape} = \frac{1}{n}\sum_{ij} \alpha_{ij}$$

$$\beta_{landscape} = \frac{1}{n}\sum_{ij} (\gamma_j - \alpha_{ij})$$

$$\beta_{region} = \frac{1}{N}\sum_{ijk} (\gamma_{obs} - \alpha_j)$$

where n is the total number of landscapes (45), N is the total number of regions (3), i is the identifier landscape within region (15) and j the identifier for each region (3).

To compare the relevance of each diversity component to the total diversity observed for both total species and RAP (γobs) at multiple spatial scales, we used the effective number of species derived from the species richness (S) and the Shannon entropy index (H) (so-called Hill numbers), which represent the true diversity (Jost, 2007). Species richness $\alpha_{\text{landscape}}$ was obtained by pooling all the species found in the two fields surveyed in each landscape. Mean $\alpha_{\text{landscape}}$ was obtained by averaging the 15 $\alpha_{\text{landscape}}$ per region, whereas total α_{region} diversity is obtained by pooling all the species found within each region. Shannon's diversity (H') is presented as H'=exp(H) to allow comparison with species richness (Hill, 1973). Transforming species diversity or entropies to effective number of species produces a stable, easily interpreted, sensitive general similarity measure (Jost, 2006).

Shannon entropy index (H) is a function of the proportional abundance π_i of species i in n:

$$H = -\sum_{i}^{n} \pi_{in} * ln\, \pi_{in}$$

The proportional abundance π_{il} of species i in the landscape l is obtained by dividing the total cover plant species of i in l (f_{il}) by the total cover in l (f_l):

$$\pi_{il} = \frac{f_{il}}{f_l}$$

The proportional abundance π_{ij} of species i in the region j is obtained by dividing the cover plant species of i in j (f_{ij}) by the total cover in j (f_j):

$$\pi_{ij} = \frac{f_{ij}}{f_j}$$

The proportional abundance π_{ia} of species $_i$ in the total study area a is obtained by dividing the cover plant species of i in s (fia) by the total cover in s (fs):

$$\pi_{ia} = \frac{f_{ia}}{f_a}$$

Thus, when considering a hierarchical scale, α-diversity components in terms of Shannon diversity (H') were analysed by the following formula (Jost, 2007):

$$H'\alpha = e^{H} = e^{\left[-\frac{1}{N}(\sum_{i=1}^{S}(\pi_{i1}\, ln\pi_{i1}) + \sum_{i=1}^{S}(\pi_{i2}\, ln\pi_{i2}) + \cdots + \sum_{i=1}^{S}(\pi_{in}\, ln\pi_{in})\right]}$$

where *N* is the total number of observation for each hierarchical scale and π_{ik} are the proportional abundances of the specie *i* in the scale *k*.

2.5 Statistical analysis

The effect of landscape complexity on $S\alpha_{\text{landscape}}$ and $H'\alpha_{\text{landscape}}$ for both total species and RAP was tested with linear mixed-effects models (Pinheiro and Bates 2000), which account for non-independent errors due to hierarchically nested sampling design. The landscape metrics PER_{NV}, PA_{ARA} and SI_{ARA} were included in the models because they were not correlated (PER_{NV}-PA_{ARA}: ρ = 0.14, P=0.10; PER_{NV}-SI_{ARA}: ρ=0.12, P = 0.14; PA_{ARA}-SI_{ARA}: ρ=0.17, P = 0.16). Landscape metrics, which were standardized to compare their effect and their interaction with field position, were included as fixed factors, whereas locality and region were used as random factors to account for the nested design. Localities were nested to the regions. Orthogonal contrasts were used to compare the outer positions (edge and boundary) against the field centre (E&BvsC), and the edge against the boundary (EvsB). Data exploration and model assumptions were confirmed following Zuur et al. (2010).

We performed a model selection procedure based on the information-theoretic approach and Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). Competing models were ranked in relation to the difference between their Akaike scores and the score of the best model (Δi), which has the lowest AICc. We considered models with ΔAICc<2 as the best fitted models for each predictive variable (Johnson and Omland, 2004). We used the multi-model inference method, which averages the estimates and standard errors of the parameters in the different models weighted by the Akaike weights to calculate relative importance of each variable (Johnson and Omland, 2004). We also calculated the direction and the 95% confidence interval of the effect size of the variables in the models with ΔAICc<2 to determine the relationship between the response and the explanatory variables.

Species composition of each locality was analyzed by non-metric multidimensional scaling (NMDS), which is the most robust unconstrained ordination method in community ecology (Leps and Smilauer, 2003). To calculate the resemblance matrix among sites (15 landscapes x 3 regions x 3 positions=135 sites), we used the Bray-Curtis dissimilarity distance. The Monte Carlo test was used to identify the overall pattern of dispersion in the species composition with respect to the landscape metrics gradients and the field position. Smooth surfaces of the key variables identified by Monte Carlo tests were generated on the NMDS plot by fitting thin plane splines using general additive models from the ordisurf function in R and interpolating the fitted values in the unconstrained ordination diagrams (Oksanen et al., 2011). Species that were not considered as RAP and only occurred in one locality were excluded because their presence could be accidental. Only RAP were projected on the NMDS.

To quantify how the gradients landscape complexity affects species composition at each position, we used a permutational multivariate analysis of variance (PERMANOVA) for both total species and RAP. Distance matrices were based on the Bray-Curtis dissimilarity index. All landscape metrics were used and non RAP species that occurred in a unique position and locality were excluded from the analyses. Statistical analyses were performed using R (R Development Core Team, 2008) with packages LME4 (Bates et al., 2008) for mixed models and VEGAN (Oksanen et al., 2011) for NMDS, Monte Carlo test and PERMANOVA.

3. Results

3.1 Spatial partitioning of diversity

A total of 435 species were recorded throughout the study area, representing 96.3% of the total estimated species richness. Our proposed list of RAP contained 42 species (Table A.3), which were recorded throughout the study area, representing 95.7% of the total estimated species richness. These results show that the sampling size of the plant survey was enough to detect species richness. The highest species diversity was found at the boundary and decreased progressively through the edge and to the centre of the fields (Fig. 1a,b,c). A deviation of this pattern was observed in the overall H' of RAP, whose value was slightly higher at the edge (12.88) than it was at the boundary (12.33) (Fig. 1d).

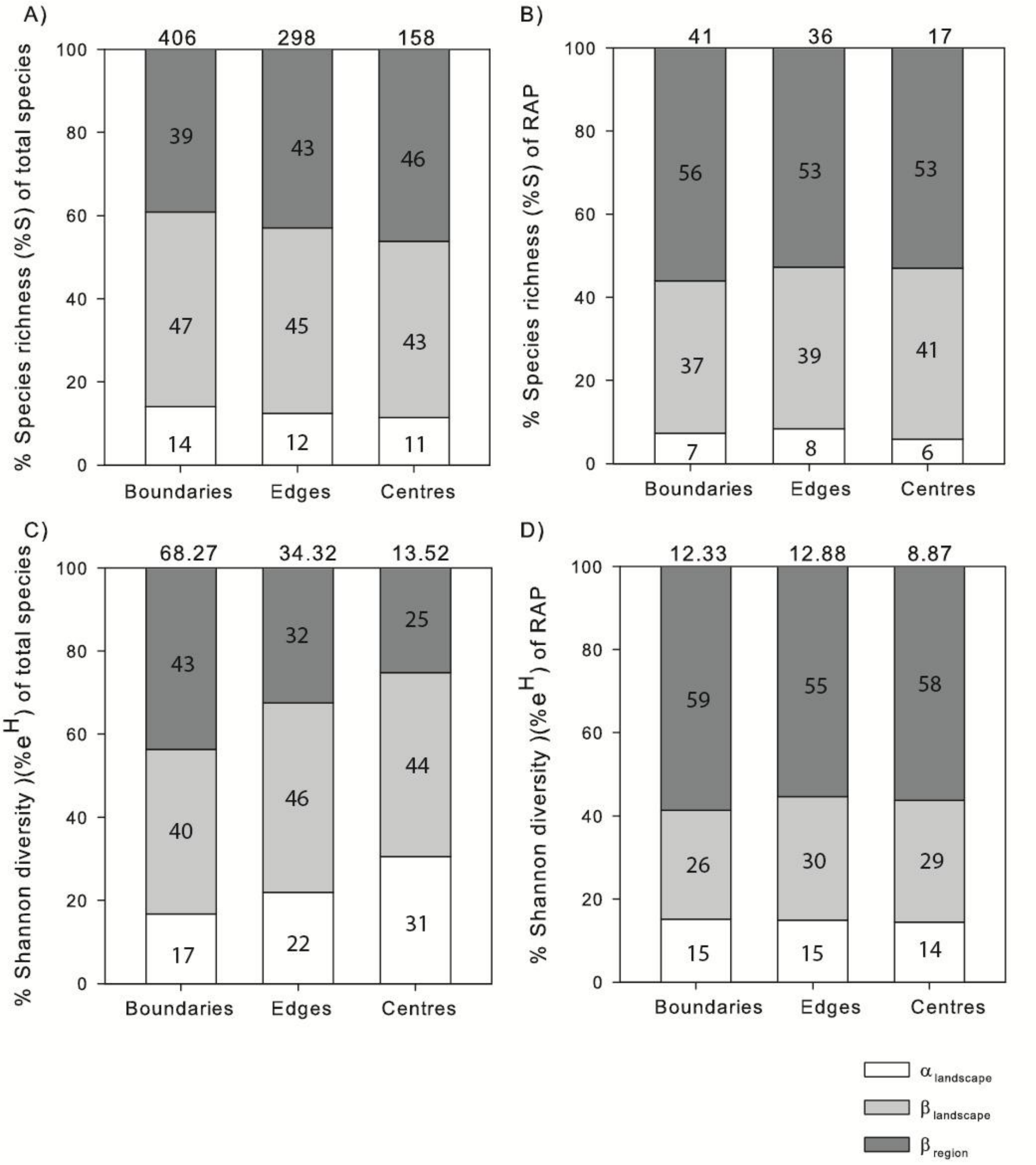

Figure 1. Relative contribution of $\alpha_{landscape}$ and $\beta_{landscape}$ components to overall species richness (S) of total species (a) and rare arable plants (RAP) (b) and Shannon diversity (H') of total species (c) and rare arable plants (RAP) (d) depending on the field position in Mediterranean barley fields. Absolute values are showed above each column.

$S\alpha_{landscape}$ of total species ranged from 11% to 14% of observed total S ($S\gamma_{obs}$) (Fig. 1a). β-diversity accounted for the bulk of $S\gamma_{obs}$ of total species richness, which is divided roughly equally between $\beta_{landscapes}$ (averaged contribution between positions of 45%) and βregion (43%). $S\alpha_{landscape}$ of RAP ranged from 6% to 8% (Fig. 1b). β-diversity accounted for the bulk of $S\gamma_{obs}$ of RAP in which βregion is higher than $\beta_{landscape}$

(averaged contribution between positions of 54% against 39% respectively (Fig. 1b)).

$H'\alpha_{landscape}$ of total species ranged from 17% to 31%. Relative $H'\alpha_{landscape}$ was the highest in the field centres (31%), followed by the edges (22%) and finally by the boundaries (17%) (Fig. 1c). β-diversity accounted for the bulk of $H\gamma_{obs}$ of total species, which is slightly higher for $\beta_{landscapes}$ (averaged contribution between positions of 43%) than for β_{region} (34%). Mean $H'\alpha_{landscape}$ of RAP was between about 15% in all the three positions (Fig. 1d). $H'\beta_{region}$ was higher than $H'\beta_{landscape}$ (averaged contribution between positions of 57% against 28% respectively (Fig. 1d)).

3.2 Effects of landscape complexity and field position on $\alpha_{landscape}$ diversity

Confidence sets of fitted models to $S\alpha_{landscape}$ and $H'\alpha_{landscape}$ of total species and RAP are summarized in Table 1. Both $S\alpha_{landscape}$ and $H'\alpha_{landscape}$ of total species and RAP were influenced by the field position and the gradient of landscape complexity, as indicated by the magnitude of their effects, the relative importance of the estimator and the confidence intervals, which do not include 0 (Table 2). Diversity index values both for $S\alpha_{landscape}$ and $H'\alpha_{landscape}$ of total species were highest at the boundaries. In contrast, $S\alpha_{landscape}$ of RAP was highest at the edge whereas $H'\alpha_{landscape}$ of RAP were higher in the outer field positions than in the field centre.

Table 1. Model selections for $\alpha_{landscape}$ component of the diversity measures for total species and rare arable plants (RAP). Only models which $\Delta i<2$ are showed.

	Models	*K*	AICc	Δi	*Wi*
a) $S\alpha_{landscape}$					
Total species	$Pos\cdot PER_{NV}$	5	1045.13	0	0.76
RAP	$Pos\cdot PER_{NV}$	5	541.51	0	0.54
	$Pos\cdot(PER_{NV}+PA_{ARA})$	7	543.42	1.91	0.21
b)$H'\alpha_{landscape}$					
Total species	$Pos\cdot PER_{NV}$	5	810.914	0	0.88
RAP	$Pos\cdot(PER_{NV}+PA_{ARA})$	7	389.48	0	0.72

K, number of parameters; AICc, Akaike's information criterion corrected for small sample size; Δ_i, the AICc differences compared with the most parsimonious model; w_i, Akaike weights; S; Species richness, H'; Shannon diversity; Pos, field position -boundary, edge and centre-; PER_{NV}, Percentage of natural vegetation; PA_{ARA}, Perimeter–area ratio of arable land patches.

Complex landscapes support more $S\alpha_{landscape}$ than simple ones both for total species (PER_{NV} effect size (with UnSE): 3.32 (0.16)) and for RAP (PER_{NV}: 0.36 (0.06); PA_{ARA}: 0.09 (0.04)) (Table 2a). For the $S\alpha_{landscape}$ of total species, the strong interaction between PER_{NV} and field position indicates that landscape effect was concentrated in the outer field positions (E&BvsC·PER_{NV}: -9.54 (0.27)); with the maximum at the boundary (EvsB·PER_{NV}; $S\alpha_{landscape}$: 3.16 (0.16)) (Table 2a). In contrast, the highest positive effects of landscape complexity on the $S\alpha_{landscape}$ of RAP were observed at the edge (EvsB·PER_{NV}: -0.29 (0.05); E&BvsC·PER_{NV}: -0.78 (0.08)). Moreover, PA_{ARA} effect on $S\alpha_{landscape}$ of RAP did not differ between outer positions but it increased in the field centre (E&BvsC·PA_{ARA}: 0.06 (0.03) (Table 2a).

The patterns observed for the $H'\alpha_{landscape}$ of total species did not differ from the ones observed for the $S\alpha_{landscape}$. Landscapes with high values of PER_{NV} support higher $H'\alpha_{landscape}$ than simple ones both for total species (PER_{NV} effect size (with UnSE); 0.88 (0.08)) and RAP (PER_{NV}: 0.14 (0.03) (Table 2b). However, an increase of the PA_{ARA} value implied a reduction on the overall $H'\alpha_{landscape}$ of RAP (-0.21 (0.04)). The interaction between PER_{NV} and field position indicates that for the $H'\alpha_{landscape}$ of total species the landscape effect was concentrated in the outer field positions (E&BvsC·PER_{NV}: -3.10 (0.16)); with the maximum at the boundary (EvsB·PER_{NV}: 1.42 (0.12)) (Table 2b). In contrast, the highest positive effects of landscape complexity on the $H'\alpha_{landscape}$ of RAP was observed at the edge (EvsB·PER_{NV}: -0.12 (0.04), E&BvsC·PER_{NV}: -0.44 (0.06)). Exclusively for $H'\alpha_{landscape}$ of RAP, PA_{ARA} effect did not differ between outer positions but it increased in the field centre (0.50 (0.06)) (Table 2b).

Table 2. Model-averaged estimated, unconditional standard error of the estimate (UnSE), relative importance (RI) and confidence interval (CI, α=0.95) of the predictor variables and their interaction for the diversity measures both for total species and rare arable plants (RAP). In bold predictors with substancial support.

	Total species					RAP				
	Estimated	UnSE	RI	CI		Estimated	UnSE	RI	CI	
a) Species richness (S)										
Intercep	**28.54**	**0.46**	**1**	**27.63**	**29.44**	**1.65**	**0.11**	**1**	**1.43**	**1.87**
EvsB	**14.84**	**0.33**	**1**	**14.19**	**15.49**	**-0.14**	**0.04**	**1**	**-0.22**	**-0.05**
E&BvsC	**-44.88**	**0.58**	**1**	**-46.01**	**-43.75**	**-2.49**	**0.14**	**1**	**-2.76**	**-2.22**
PER_{NV}	**3.32**	**0.16**	**0.99**	**3**	**3.63**	**0.36**	**0.06**	**0.87**	**0.25**	**0.47**
PA_{ARA}						**0.09**	**0.04**	**0.23**	**0.01**	**0.16**
EvsB·PER_{NV}	**3.16**	**0.16**	**0.99**	**2.84**	**3.47**	**-0.29**	**0.05**	**0.87**	**-0.39**	**-0.19**
E&BvsC·PER_{NV}	**-9.54**	**0.27**	**0.99**	**-10.07**	**-9.01**	**-0.78**	**0.08**	**0.87**	**-0.93**	**-0.62**
EvsB·PA_{ARA}						0.02	0.04	0.23	-0.05	0.09
E&BvsC·PA_{ARA}						**0.06**	**0.03**	**0.23**	**0.01**	**0.11**
b)Shannon diversity (H')										
Intercep	**6.77**	**22**	**1**	**6.33**	**7.12**	**1.22**	**0.1**	**1**	**1.03**	**1.41**
EvsB	**3.42**	**0.16**	**1**	**3.11**	**3.74**	-0.04	0.03	1	-0.1	0.02
E&BvsC	**-9.4**	**0.16**	**1**	**-9.91**	**-8.88**	**-0.88**	**0.08**	**1**	**-1.04**	**-0.72**
PER_{NV}	**0.88**	**0.08**	**0.99**	**0.72**	**1.05**	**0.14**	**0.03**	**0.77**	**0.07**	**0.21**
PA_{ARA}						**-0.21**	**0.04**	**0.94**	**-0.29**	**-0.13**
EvsB·PER_{NV}	**1.42**	**0.12**	**0.99**	**1.42**	**1.87**	**-0.12**	**0.04**	**0.77**	**-0.19**	**-0.05**
E&BvsC·PER_{NV}	**-3.1**	**0.16**	**0.99**	**-3.41**	**-2.79**	**-0.44**	**0.06**	**0.77**	**-0.56**	**-0.32**
EvsB·PA_{ARA}						0.04	0.03	0.94	-0.09	0.03
E&BvsC·PA_{ARA}						**0.5**	**0.06**	**0.94**	**0.37**	**0.62**

B&EvsC Boundary and edge against centre, BvsE Boundary against edge, PER_{NV} Percentage of natural vegetation, PA_{ARA} Perimeter –area ratio of arable land patches.

3.3 Effects of landscape complexity and field position on species composition

The NMDS analysis showed differences in plant species composition between field positions (Fig. 2). Field position ($F = 7.57$, $P < 0.001$), PER_{NV} ($F = 3.09$, $P < 0.001$), TLAP ($F = 1.3$, $P < 0.05$), PA_{NV} ($F = 1.84$, $P < 0.001$), PA_{ARA} ($F = 1.62$, $P < 0.01$), and SI_{NV} ($F = 1.68$, $P < 0.001$) significantly influenced the variation in the overall species composition according to the Monte Carlo test. The surface fitted onto the NMDS analysis (see r^2 and p-values of the averages obtained after fitting each factor onto the ordination in Fig. 3) represents graphically how plant species are related to the gradients of those landscape metrics. RAP were mainly assembled in the outer positions of the fields. Two subsets of RAP (G1 and G2) were observed (Fig. 3). Species in G1 were likely to be more strongly related to complex landscape than species in G2. RAP of G1 were mainly assembled in landscapes characterized by high PER_{NV} (Fig. 3b), low TLAP (Fig. 3c), low PA_{NV} (Fig. 3d) and high PA_{ARA} (Fig. 3e). By contrast, RAP of G2 were assembled in landscapes characterized by low PER_{NV} (Fig. 3b), high TLAP (Fig. 3c), high PA_{NV} (Fig. 3d) and low PA_{ARA} (Fig. 3e). RAP of neither G1 nor G2 showed any pattern of preference for SI_{NV} gradients (Fig. 3f).

The PERMANOVA test indicated that PER_{NV}, TLAP, PA_{NV}, PA_{ARA} and SI_{NV} explained a significant variation in the species composition at different field positions (Fig. 4). PER_{NV} explained the higher variation in total species assemblages regardless of the field position. Overall, the total variation explained by the landscape metrics for RAP doubled the total variation explained for total species regardless of the position. At the edge, landscape metrics reached the highest value of the total variation in RAP assemblages (30.44%), followed by the boundary (25.93%) and the field centre (19.65%).

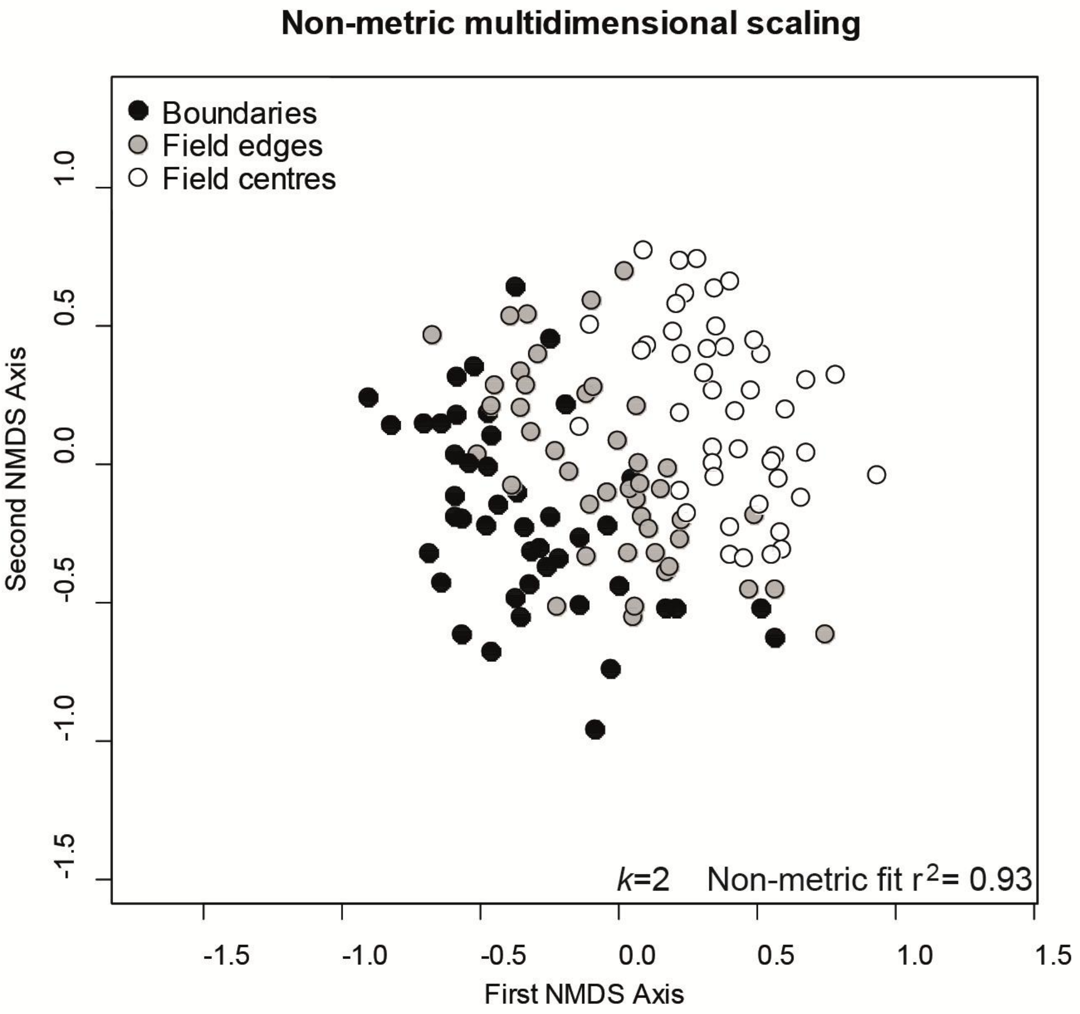

Figure 2. Non-metric multidimensional scaling ordination based on the floristic similarities depending on the field position in the barley fields of 45 landscapes. k; number of parameters; r^2, non-metric fit value according the ordination (P<0.0001).

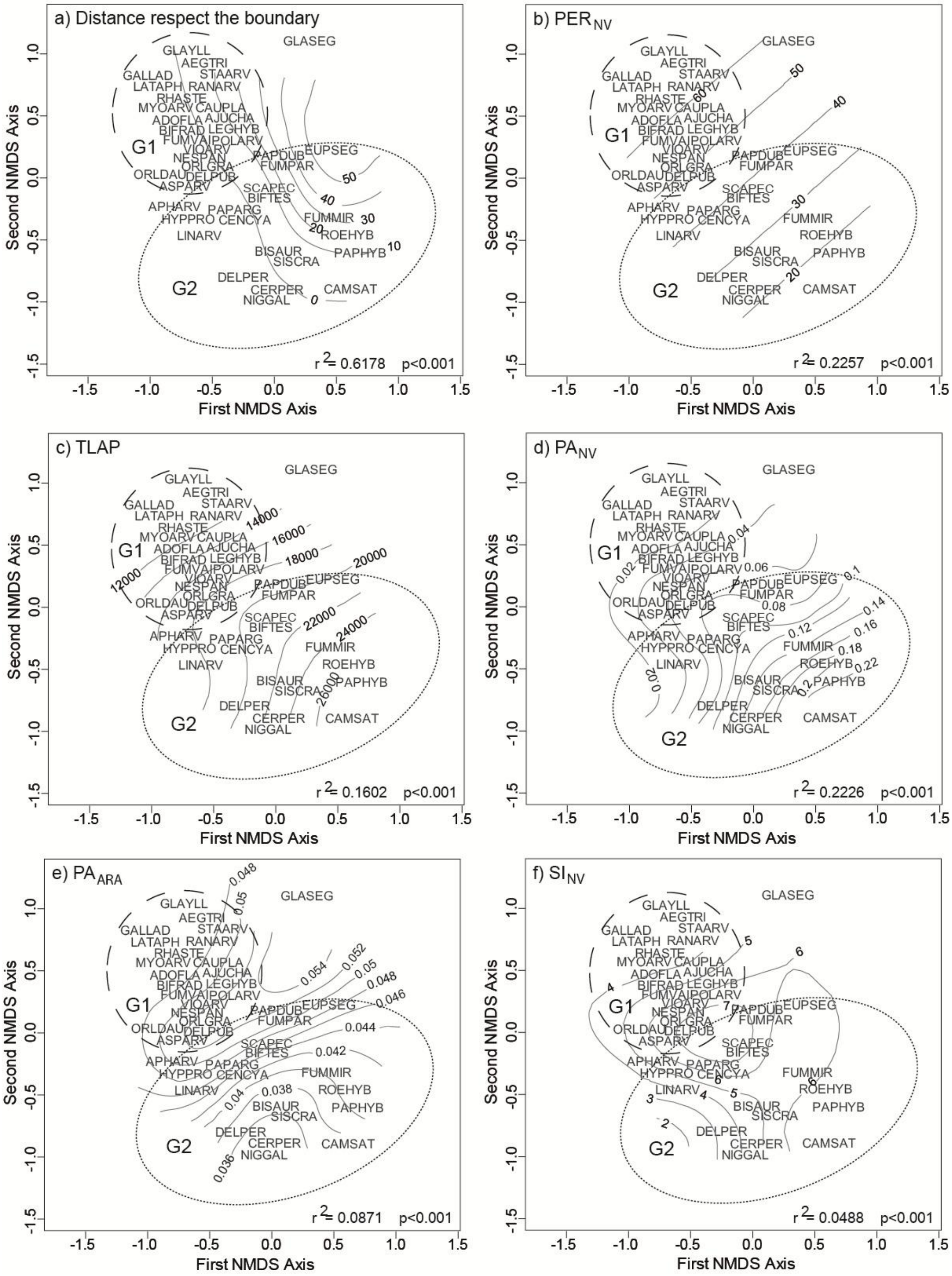

Figure 3. Non-metric multidimensional scaling ordination showing RAP and ordination axes with respect to the field position and landscape metrics. Species codes are included in Table A2. r^2 and p-values correspond to the averages. Smooth surface (contours) representing values of a) field position (m), b) Percentage of natural vegetation, c) Total length of the perimeter of arable patches, d) Perimeter-area ratio of natural vegetation patches, e) Perimeter-area ratios of arable land patches, f) Shape index of natural vegetation patches.

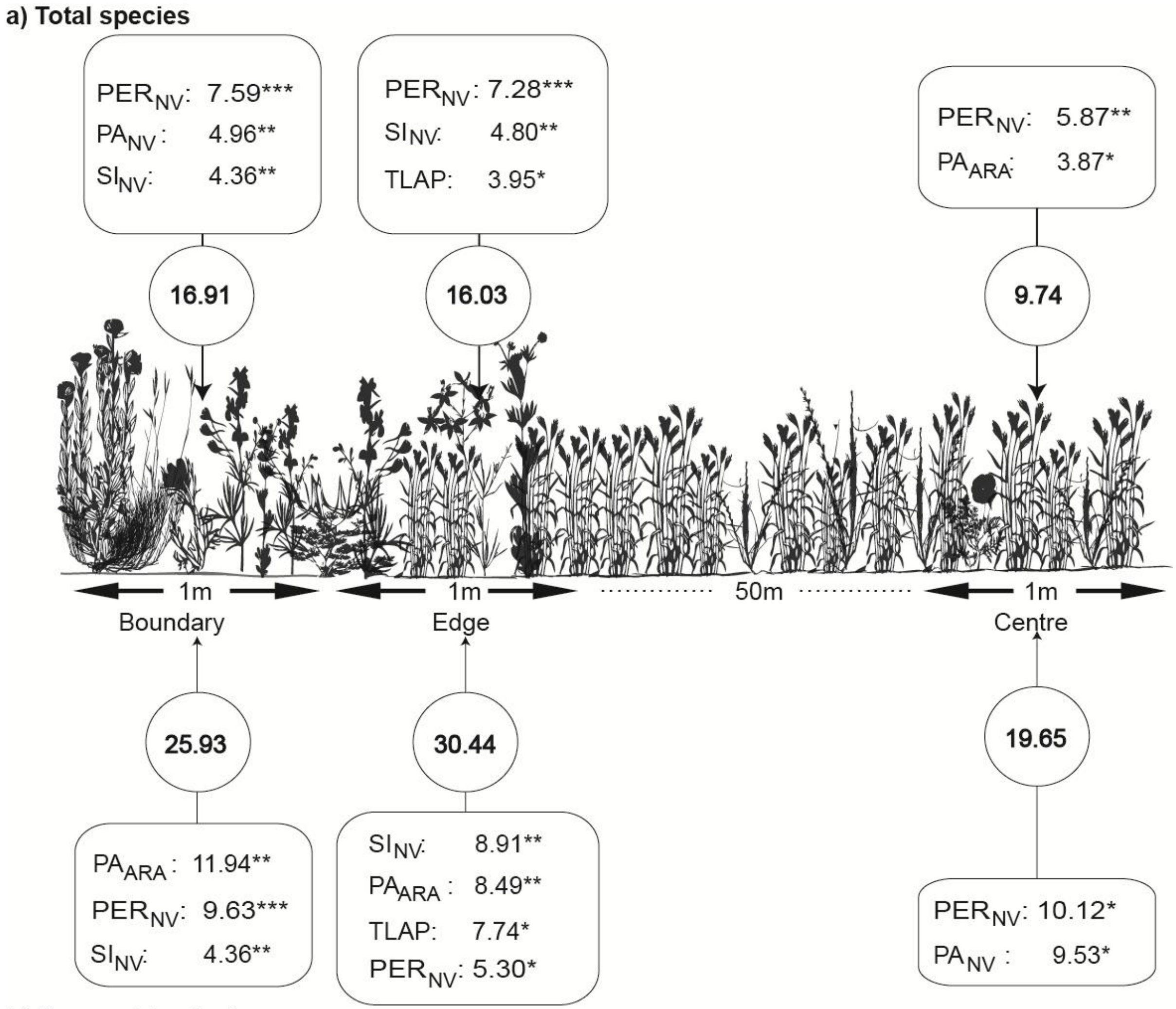

Figure 4. Percentage of Variation explained (%VE) by landscape metrics in species assemblages for both total species and rare arable plants depending on the field position. Levels of significance (*** $p<0.001$; ** $p<0.01$; * $p<0.05$). PER_{NV}, Percentage of natural vegetation; TLAP, Total length of perimeter of arable patches; PA_{NV}, Perimeter-area ratios of the natural vegetation patches; PA_{ARA}, Perimeter-area ratios of arable land patches, SI_{NV} Shape index of natural vegetation patches.

4. Discussion

4.1. Spatial partitioning of diversity

The comparison of the overall species richness (S) and Shannon diversity (H’) showed very similar patterns in the relevance of the additive diversity components as affected by the field position. For all the diversity measures and irrespective of the set of the species, β-components made the greatest contribution to the total diversity. This indicates that spatial diversity patterns mainly result from a change in species composition rather than from variation in species abundance. Substantial differences in the plant species composition occurred between regions and landscapes. Differences in the local species pool are a consequence of the increase in environmental heterogeneity both between landscapes and between regions (Lososova et al., 2004).

S is completely insensitive to species frequencies (Jost, 2006) and it is inflated by generalist species that occur in most of the landscapes. The averaged contribution of the β-components to the overall S of total species between positions was seven times higher than the averaged contribution of the $\alpha_{\text{landscape}}$ component whereas for RAP it was thirteen times higher. The higher relevance of the β-component in the overall S of RAP in comparison to the one observed for the total species indicate that RAP show sparse and fragmented distributions reflecting their potential threatened status throughout the agricultural landscapes. Specifically for S of RAP, the results of our study are comparable with those of Gabriel et al. (2006) in that we also found β_{region} to be the most relevant contributor to the total S.

The conversion of the Shannon entropy index (H) to the true Shannon diversity (H’) (effective numbers of species) produces an intuitive measure of diversity which is always measured in units of number of species (Jost, 2006). Moreover, H’ measures both the effect of species richness and abundance (Pielou, 1969). The contribution of the Shannon diversity components of total species at both landscape scale and regional scales showed that β-components contributed most in the outer positions of the field than in the field centre. This finding indicated that substantial differences in the presence and abundance in the plant community composition occurred between landscapes and regions and additionally, between field positions. The increasing relevance of the $H'\alpha_{\text{landscape}}$ encountered in the field centres can be attributed to the higher efficacy of farming practises at the field centre compared with the edges and the boundaries. Thus, field edges undergo a medium level of soil disturbance, which is maximum in the centres and minimum on the boundaries (Wilson and Aebischer, 1995). Similarly, the higher efficacy of farming practices such as fertilization and weed control in the field centre than in the edge (Kleijn and van der Voort 1997) favours a set of tolerant species which are less strongly affected by farming practices and can become increasingly dominant. Therefore, the arable plant communities in fragmented landscapes can undergo either declines (floristic homogenization) or increases (floristic differentiation) in $H'\beta_{diversity}$ depending on the spatial scale and on the field position where plant communities are examined. In contrast, the averaged value of $H'\alpha_{landscape}$ of RAP between positions (15%, Fig. 1d) is lower than the one of total species (23%, Fig. 1c) and additionally constant between positions (Fig. 1d). These findings support the idea that RAP are encountered more frequently at the largest scales despite their low abundance at landscape and regional scale compared to the total species.

4.2 Effects of landscape complexity and field position on $\alpha_{landscape}$ diversity

The effect of landscape complexity on the $\alpha_{landscape}$ diversity differs between field positions and plant species (total species and RAP). Diversity of total species increased with the increase of PER_{NV} (Table 2a), as was expected (Gabriel et al., 2005; Roschewitz et al., 2005; José-María et al., 2010). In overall, landscape effect is greatest at the boundary and decreases progressively to the field centre. The absence of landscape effect in the field centre is consistent with the findings of Marshall (2009), Gaba et al. (2010) and Armengot et al. (2011), indicating that inhibition of plant diversity is a consequence of the negative impact of farming practices in the field centre (Wilson and Aebischer, 1995).

Bassa et al. (2011) found that landscape complexity was the most important factor affecting boundary plant diversity. Moreover, Fernández et al. (2002) suggested that boundary networks can benefit from the emerged flora at the edges due to their role as a transitory habitat and due to the ecological edge effect between the two outer field positions. The surrounding landscape can provide seeds at short distance due to the neighbouring effect from adjacent habitats (Devlaeminck et al., 2005), which is inhibited in field centres (Marshall, 2009). By contrast, landscape simplification promotes an increase of arable lands which, in turn, favours wind-dispersed species (long distance seed dispersal) (Marshall, 2009; José-María et al., 2011). Therefore, at the boundary and at the edge, our findings support those of Tscharntke et al. (2005), who suggest that landscape complexity compensates for the negative effects of farming intensification.

Regarding RAP, complex landscapes characterized by high PER_{NV} and the presence of arable fields with high PA_{ARA} harbour higher $S\alpha_{landscape}$ than structurally simpler ones. Additionally, the PER_{NV} effect was greatest at the edge whereas the PA_{ARA} effect was greatest at the field centre (Table 2b). The increase of PA_{ARA} implies a reduction of $H'\alpha_{landscape}$ of RAP. Therefore, our results suggest differences on the effect of PA_{ARA} on RAP diversity depending on the diversity index measured. These differences are consequence of the different mean of each diversity measure. As H' is affected by species richness and plant abundance, our results suggest that the increase in PA_{ARA} may benefit the success of perennial species at the boundary hampering the colonization and spread of annual species as RAP. Indeed, boundary vegetation is mainly characterized by the dominance of perennial species which hinder the colonization and spread of RAP (Kleijn and Van der Vort, 1997; Marshall, 2009). Although we expected boundaries and edges of fields in complex landscapes to have more RAP species than field centres, our results indicate that the maximum effect of the PA_{ARA} for RAP was at the field centres. Arable fields with complex shapes have a greater number of species because the increase in perimeter in relation to area provides more safe havens for RAP at the field edge. These fields tend to be elongated with edges close to the field centres, and therefore favour arable plants spread at short distance (Benvenuti, 2007). Thus, we found an effect of the field shape as there was a higher diversity of RAP in the centre than in the edges if the distances between the edge and the centre are shorter.

4.3 Landscape complexity on species composition

Differences on species composition depending on the field position are well-documented (Marshall, 2009; José-María et al., 2010, Poggio et al., 2012). According to the Monte Carlo test and NMDS analyses (Fig. 2), the major differences in overall floristic composition were found between the boundaries and the two inner field positions. Boundaries present environmental conditions that are relatively more stable than the inner field positions. This relative stability favours the spread and the colonization of species from the surrounding whereas soil disturbance in the inner field positions renders difficult the colonization of some species such as perennial species.

On the contrary, a simplification of the landscape complexity impacts on plant assemblages at the boundaries, which favours the colonization of the species in the positions inner the field (José-Maria et al., 2011; Bassa et al., 2011). Moreover, our results showed that the landscape metrics related with the shape of the patches affect species composition. Irregular shaped fields with higher perimeter-area ratio than regular shaped ones provide a higher amount of potential source habitat for arable weeds (Gabriel et al., 2005), enhancing therefore the spread of those species over the field. On the contrary, regular shaped fields are located in most simplified landscapes where those potential habitats are less frequent. Thus, a complex landscape may contain a larger species pool than a homogeneous landscape, thereby enhancing migration of plant species into the fields (Devlaeminck et al., 2005). Landscape complexity might point to a functional scale at which the existence of potential source habitats and ecological process promotes two subsets of RAP assemblages (Fig.3). Species integrated in G1 (Fig. 3) assembled in structurally complex landscapes whereas species integrated in G2 assembled in structurally simple landscapes that still maintained linear patches of natural vegetation interspersed between fields (Fig. 3d). The existence of the two subsets of RAP may be a consequence of various phenomena.

Firstly, landscape complexity provides safe havens characterized by low inputs and low productivity that can act as a local pool for species of G1. The presence of these havens increases as landscape complexity increases; fields are more elongated and convoluted, with dendritic edges. Thus, the loss of natural corridors and road verges, boundary networks and the land consolidation of the fields reduce the availability of potential refuges for arable plants (Kleijn and Verbeek, 2000). Moreover, in disturbed landscapes, nitrophilous species replace RAP at the boundary and at the edge, where the former species are favoured by the high proportion of arable land (Bassa et al., 2011, José-María et al., 2011). Our observations follow the findings of Smart et al. (2002) in British grasslands, suggesting that a local increase in the field productivity implies that some species will become uncommon or absent at the adjacent boundaries, whether or not they are able to colonize the suitable edge. Secondly, RAP may be separated into two groups because of differences in the ecological requirements between the subsets of RAP (e.g. soil pH, water). However, these physical and ecological variables are constant throughout the study area. All soils in the study area are calcareous and, additionally, sowing periods and management (e.g. lack of crop rotation, external inputs) are similar among the surveyed fields. Thirdly, biological reasons may allow the two subsets of RAP to be discriminated. Gunton et al. (2011) and Petit and Fried (2012) pointed out that arable plants are likely to be associated with local management practices that select species according to their biological traits. Additionaly, Jose-María et al. (2011) reported that landscape structure selects plant communities according to their functional traits in dryland Mediterranean cereal fields. Specifically, landscape complexity has been found to affect the influence of insect pollinator diversity (Cranmer et al., 2012; Power et al., 2012), which is required for successful reproduction in many arable plants (Gabriel and Tscharntke 2006). Thus, pollination traits may disentangle the differences between the species in G1 and G2 as a consequence of the parallel declines reported in insect-pollinated plants and their pollinators (Biesmeijer et al., 2006). Similarly, Gibson et al. (2006) found that in the UK, RAP were linked to other plant species in the community by shared pollinators, for which they were often the primary food sources. However, more research is needed on the relationship between insect-pollinators and plants because such data are still lacking in most plant trait databases of the Mediterranean area.

The variation in species assemblages explained by the set of landscape metrics was two times higher for RAP than for total species. Our study only partly supports the general opinion that the decline of RAP is caused by intensive agricultural practices at field scale and the decrease in landscape complexity (Roschewitz et al., 2005). The differences between the variance explained by the gradients of the landscape metrics among total species and RAP (Fig. 4) suggest that farming practices affect more negatively the total species than RAP because of the probable selection of species by their traits. For example, perennial species from the boundary are inhibited in the field centre (Marshall, 2009). On the other hand, the low range of seed dispersal of many arable weeds (Benvenuti, 2007) would explain the effects of the landscape indicators on the RAP assemblages at all three positions in the field. The edge is the most relevant position and acts as a pool for RAP, suggesting that it provides a platform for short-distance seed spreading of species restricted to the periphery of the fields. Short-distance seed dispersal of RAP from the edge to the centre may be favoured by irregular patches of natural vegetation that allow the seeds to colonize the centre of elongated fields (Fig. 4). However, more research is needed on this topic. Functional plant-trait analysis may help to elucidate these processes (Gunton et al., 2011.).

5. Conclusions

As Storkey et al. (2012) suggested, there is an urgent need to implement successful conservation strategies of arable plants to prevent the decline of this threatened component of the European flora. To our knowledge, our study is the first focusing on the effects of landscape complexity on RAP in the Mediterranean area. As there is increasing concern in Europe about the conservation of these species, our study illustrates the importance of the landscape structure in promoting and enhancing populations of RAP even when conventional farming practices are common. Landscape simplification is a threat to RAP populations, although simplified landscapes can also include some RAP. Thus, the general view that the decline of rare species is caused by intensive agricultural practices at field scale and decreasing landscape complexity is partially supported.

Conservation measures to counteract the loss of biodiversity in the agricultural landscapes in the European Union are based on the AES, whose effectiveness has been questioned (Whittingham, 2006). Our results suggest that AES in the Mediterranean area should be based on targeting those landscape structures in which species pools of RAP are not expected to be depleted. The use of a set of landscape metrics may help to determine the structures on which policy makers should focus. Moreover, our results indicate that a 1-m-wide strip is enough to enhance RAP. Therefore, it is crucial to focus low-intensity farming practices at the edges of the fields in complex landscapes. The most cost-effective measure for enhancing RAP is to reduce the intensity of farming practices at the edge of the fields. These measures are expected to benefit RAP assemblages and strengthen their role as species pools to spread over the surrounding landscape. Our results confirm that low-intensity farming practices at the field edges may enhance plant diversity of RAP, irrespective of the landscape complexity. However, it is expected that these schemes could be more efficient in increasing RAP diversity in the most complex landscapes compared to the most simplified ones.

Acknowledgements

We acknowledge the financial support provided by the Universitat de Lleida and the Ministerio de Educación y Ciencia (Projects AGL 2007-60828 and AGL 2010-22084-C02-01). We thank two anonymous referees for valuable comments on the manuscript. We thank J. Pedrol from the Flora Iberica project for his help in selecting RAP, J. Conde for statistical advice, C. Cantero and J.M. Montull for providing information on management, and the landowners for allowing us to access their fields.

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Table Appendix 1 (Table A1). Summary of the environmental characteristics and farming practices on the cereal fields of the three studied areas. Altitudinal range (AR), mean annual temperature (T), mean annual precipitation (P), potential evapotranspiration (PE), accumulated precipitation during the cropping period of the study (Ps-m), potential vegetation (PV), sowing density (SD), seed provenance (SP), rotational scheme (RS), pre-emergence weed control for broad-leaves and grass-leave (Pre.E.B&G), post-emergence to control *Bromus diandrus* (Post.Bro), post-emergence to control broad-leaves species (Post.B), post-emergence to control *Lolium rigidum* (Post.L), post-emergence to control *Avena sterilis* (Post.A).

	La Noguera	La Segarra	El Pallars Jussà
AR (m)	247-586	453-852	408-940
T (ºC)	14.9	13.2	13.7
P (mm)	419	462	521
PE (mm)	816.3	745	774
Ps-m (mm)	233.1	234.4	317.6
PV	*Quercetum rotundifoliae* Br.-Bl. & O. Bolòs in Vives 1956 *Buxo sempervirentis-Quercetum Rotundifoliae* Gruber 1974	*Quercetum rotundifoliae* Br.-Bl. & O. Bolòs in Vives 1956 *Violo willkommii-Quercetum fagineae* Br.-Bl. & O. Bolòs 1950 corr. Rivas-Martínez 1972	*Violo willkommii-Quercetum fagineae* Br.-Bl. & O. Bolòs 1950 corr. Rivas-Martínez 1972
SD(kg·ha^{-1})	180-200	180-200	180-200
SP	Re-use of own cereal seed after cleaning		
RS	Cereal monoculture for more than 10 years		
Fertilization	*Autumn base fertilization*		
	N:P:K (15-15-15), (8-15-15), (12-8-15). (250-350 kg·ha^{-1})		
	Pig slurry (20-50 m^{3}·ha^{-1})		
	Spring top-dressed fertilization		
	N32. (150-250 kg·ha^{-1})		
	Pig slurry (5-20 m^{3}·ha^{-1})		
Weed control			
Pre.E.B&G	Clortoluron 1.25 kg·ha^{-1}		
Post.Bro	Iodosulfuron 3 + mesosulfuron 15		
Post.B	Tribenuron 0.015 kg·ha^{-1} or 2,4-D 0.6 kg·ha^{-1}		
Post.L	Diclofop 540		
Post.A	Tralkoxidim 400		

Table Appendix 2 (Table A2). Values of landscape metrics for each local landscape

Locality	X-long	Y-lat	PER$_{\mathrm{NV}}$	TLAP	PA$_{\mathrm{NV}}$	PA$_{\mathrm{ARA}}$	SI$_{\mathrm{NV}}$	SI$_{\mathrm{ARA}}$
N1	300125	4637043	55.49	16271	0.006	0.047	1.776	2.195
N2	303246	4637641	33.32	14378	0.007	0.027	1.817	2.145
N3	311152	4631218	74.28	9484	0.003	0.047	1.444	2.025
N4	299611	4633673	58.51	10523	0.032	0.047	4.156	1.719
N5	306328	4637591	34.33	17695	0.043	0.034	2.832	2.645
N6	306049	4634398	18.77	14181	0.076	0.022	3.978	1.988
N7	309172	4634353	34.58	12438	0.036	0.024	3.011	1.582
N8	314551	4628341	51.31	14922	0.029	0.039	2.169	1.972
N9	312384	4634383	30.54	21928	0.028	0.04	1.506	1.588
N10	305546	4637459	9.26	38729	0.285	0.056	5.056	2.754
N11	308789	4640855	9.02	25935	0.269	0.037	10.792	2.164
N12	313434	4631418	24.48	27026	0.025	0.046	1.595	1.854
N13	317138	4631234	48.67	13692	0.009	0.034	1.761	2.848
N14	314634	4637372	14.87	16665	0.129	0.025	5.066	1.689
N15	311602	4631198	51.39	13927	0.006	0.036	1.593	1.991
S1	350159	4624351	19.33	28861	0.191	0.047	8.167	1.494
S2	360738	4624037	23.59	20762	0.102	0.035	7.201	1.044
S3	354372	4627717	32.79	16763	0.058	0.032	6.676	1.849
S4	354283	4642147	17.45	22129	0.153	0.034	6.405	2.389
S5	363921	4638337	18.91	22309	0.126	0.036	6.508	1.877
S6	357869	4629017	17.37	28938	0.226	0.046	11.622	1.928
S7	357645	4624082	24.91	27356	0.161	0.049	6.315	1.452
S8	360917	4627224	20.23	30838	0.185	0.049	16.293	1.829
S9	351772	4630941	45.95	20413	0.058	0.048	4.993	2.891
S10	361679	4623768	75.74	17362	0.049	0.097	4.507	2.286
S11	364145	4627000	34.77	25405	0.086	0.05	9.86	1.556
S12	361634	4624216	76.76	13025	0.036	0.071	3.641	2.327
S13	369883	4641210	50.44	30640	0.082	0.079	8.009	2.897
S14	365445	4638117	54.68	20760	0.056	0.058	8.364	2.046
S15	365893	4634437	20.23	30838	0.185	0.049	16.293	1.829
P1	341961	4658988	77.33	8962	0.016	0.047	3.615	2.201
P2	338931	4657442	83.85	7194	0.015	0.035	3.367	1.928
P3	343566	4661638	58.16	15207	0.035	0.032	5.944	2.455
P4	341485	4657717	65.34	9959	0.027	0.034	3.726	1.821
P5	338144	4660199	57.83	13254	0.034	0.036	4.552	1.492
P6	334418	4660840	48.83	11559	0.033	0.046	5.375	1.908
P7	332248	4663383	54.74	14950	0.035	0.049	5.615	1.69
P8	328075	4663109	35.33	19955	0.065	0.049	9.57	1.625
P9	329889	4658848	80.47	9299	0.017	0.048	3.696	1.88
P10	329365	4666193	27.69	22223	0.095	0.097	12.463	1.337
P11	333340	4664944	33.6	16172	0.056	0.05	7.667	1.537
P12	337348	4663817	25.48	18758	0.088	0.071	7.241	2.941

P13	340631	4667706	21.67	19697	0.064	0.079	2.39	2.321
P14	336734	4667477	34.98	16448	0.051	0.058	7.068	1.817
P15	328178	4669127	30.52	21075	0.075	0.049	7.871	1.831

X-Long Longitude; Y-Lat Latitude; PER_{NV}, Percentage of natural vegetation (%); *TLAP*, Total length of the perimeter of arable patches (m); PA_{NV} Perimeter-area ratios of patches of the natural vegetation; PA_{ARA}, Perimeter-area ratios of arable land patches; SI_{NV}, Shape index of natural vegetation patches; SI_{ARA}, Shape index of arable land patches

Table Appendix .3 (Table A.3). List of rare arable plants found depending on the field position. The *X* in the columns Aboucaya et al. (2000) indicates the inclusion in the French List. *R* –rare-, *RR* –very rare-, *RRR* –extremely rare- in the study area according De Bolòs et al. (2005). The *X* in the column LBC indicates the inclusion of the species according the criteria of the local expert botanist.

	CODE NMDS	B	E	C	TOTAL	Family	Aboucaya et al. (2000)	De Bolòs et al (2005)	LBC
Myosotis arvensis (L.) Hill	MYOARV	2	1	0	3	*Boraginaceae*			*X*
Legousia hybrida (L.) Delarbre	LEGHYB	5	5	2	12	*Campanulaceae*	*X*	*R*	*X*
Cerastium perfoliatum L.	CERPER	1	0	0	1	*Caryophyllaceae*		*RRR*	*X*
Polycnemum arvense L.	POLARV	5	7	2	14	*Chenopodiaceae*	*X*	*RR*	*X*
Centaurea cyanus L.	CENCYA	1	1	0	2	*Compositae*	*X*		*X*
Hedypnois rhagadioloides (L.) F.W. Schmidt	HEDRAG	1	0	0	1	*Compositae*		*R*	*X*
Rhagadiolus stellatus (L.) Gaertn.	RHASTE	2	1	0	3	*Compositae*		*R*	*X*
Biscutella auriculata L.	BISAUR	3	2	1	6	*Cruciferae*		*R*	*X*
Camelina sativa (L.) Crantz	CAMSAT	2	2	0	4	*Cruciferae*	*X*	*RRR*	*X*
Neslia paniculata (L.) Desv.	NESPAN	1	1	0	2	*Cruciferae*	*X*		
Sisymbrium crassifolium Cav.	SISCRA	1	1	0	2	*Cruciferae*		*RR*	*X*
Euphorbia segetalis L.	EUPSEG	1	2	2	5	*Euphorbiaceae*			*X*
Aegilops triuncialis L.	AEGTRI	1	1	0	2	*Gramineae*			*X*
Gladiolus illyricus Koch	GLAYLL	1	0	0	1	*Iridaceae*	*X*	*RR*	*X*
Gladiolus italicus Mill.	GLAITA	1	1	2	3	*Iridaceae*	*X*	*R*	
Ajuga chamaepitys (L.) Schreb.	AJUCHA	6	5	3	14	*Labiatae*	*X*		
Galeopsis ladanum subsp. *angustifolia* (Ehrh. ex Hoffm.) Celak	GALLAD	1	1	0	2	*Labiatae*		*R*	
Stachys arvensis (L.) L.	STAARV	2	2	2	6	*Labiatae*			*X*
Lathyrus aphaca L.	LATAPH	3	3	0	6	*Leguminosae*		*RRR*	*X*
Fumaria mirabilis var. *faurei* Pugsley	FUMMIR	2	4	3	9	*Papaveraceae*		*RRR*	
Fumaria parviflora Lam.	FUMPAR	10	13	6	29	*Papaveraceae*			*X*
Fumaria vaillantii Loisel.	FUMVAI	3	1	0	4	*Papaveraceae*			*X*
Hypecoum procumbens L.	HYPPRO	16	2	0	18	*Papaveraceae*	*X*		*X*

	CODE NMDS	B	E	C	TOTAL	Family	Aboucaya et al. (2000)	De Bolòs et al (2005)	LBC
Papaver argemone L	PAPARG	4	0	1	5	*Papaveraceae*	*X*	*R*	*X*
Papaver dubium L.	PAPDUB	0	2	0	2	*Papaveraceae*		*R*	*X*
Papaver hybridum L.	PAPHYB	6	10	6	22	*Papaveraceae*	*X*	*R*	
Roemeria hybrida (L.) DC.	ROEHYB	5	8	6	19	*Papaveraceae*	*X*	*R*	*X*
Adonis flammea Jacq.	ADOFLA	2	1	0	3	*Ranunculaceae*	*X*	*R*	*X*
Delphinium peregrinum subsp. *verdunense* (Balb.) Cout	DELPER	1	1	0	2	*Ranunculaceae*	*X*	*R*	*X*
Delphinium pubescens DC	DELPUB	5	3	1	9	*Ranunculaceae*	*X*		*X*
Nigella gallica Jord.	NIGGAL	1	1	0	2	*Ranunculaceae*		*RR*	*X*
Ranunculus arvensis L.	RANARV	3	5	1	9	*Ranunculaceae*	*X*		*X*
Aphanes arvensis L.	APHARV	2	1	0	3	*Rosaceae*	*X*	*RRR*	*X*
Asperula arvensis L.	ASPARV	1	0	0	1	*Rubiaceae*	*X*	*R*	*X*
Linaria arvensis (L.) Desf.	LINARV	2	1	0	3	*Scrophulariaceae*		*R*	*X*
Bifora radians M. Bieb.	BIFRAD	1	1	0	2	*Umbelliferae*	*X*		*X*
Bifora testiculata (L.) Spreng.	BIFTES	1	3	0	4	*Umbelliferae*	*X*	*R*	*X*
Caucalis platycarpos L.	CAUPLA	9	11	2	22	*Umbelliferae*	*X*		*X*
Orlaya daucoides (L.) Greuter	ORLDAU	1	0	0	1	*Umbelliferae*	*X*		*X*
Orlaya grandiflora (L.) Hoffm.	ORLGRA	2	2	0	4	*Umbelliferae*	*X*	*RR*	*X*
Scandix pecten-veneris L.	SCAPEC	16	15	4	35	*Umbelliferae*	*X*		*X*
Viola arvensis Murray	VIOARV	4	1	1	6	*Violaceae*	*X*		*X*

B, Boundaries; E, edges; C, Field centres.

CHAPTER 5

Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services of Mediterranean arable plants

Published in *Agriculture, Ecosystems and Environment*, 247: 255-264

Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services by Mediterranean arable plants

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Keywords: Field position, landscape heterogeneity, Rao quadratic entropy index, Community-weighted means, pollination, biodiversity.

Abstract

Agricultural intensification structures arable plant communities, including shifts in species assemblages and trait distributions, which affect the provision of ecosystem services. We used a response-effect trait framework to characterize the impact of agricultural intensification on two ecosystem services delivered by arable plants to pollinator and non-pollinator insects and birds. Agricultural intensification was characterized by field position as a gradient of the impact of crop management at field scale and the surrounding landscape heterogeneity, which can be divided into compositional and configurational heterogenenity. Shifts in functional assemblages of response and effect traits were analyzed by multivariate analyses, whereas changes in single trait metrics were analyzed by mixed-model effects. At field scale, we found a trade-off between ruderal and competitive species. The contrasting disturbance regime from boundaries to inner-fields overflows the potential shifts in functional assemblages both for response and effect traits due to the gradient of landscape heterogeneity.

Conversely, some response and effect single trait metrics changed along gradients of landscape heterogeneity. We thus propose a response-effect trait framework to capture functional relationships along different trophic levels. Compositional heterogeneity affected traits linked to the provision of suitable habitat for insects and birds, whereas configurational heterogeneity affected traits linked to pollination. Incorporating this framework into decision-making processes may help to focus conservation efforts on maintaining the delivery of ecosystem services.

Abbreviations:

Bl/Pur: Blue and/or purple flowers
CShap; Corola shape
CWM: Community-weighted means
DFlow: Duration of flowering
DRs: Driver response traits
ESs: Ecosystem services
FCol: Flower colour
FSym: Flower symmetry
FEs: Functional effect traits
H: Plant height
LF&Leg: Life form and legume
OF: Onset of flowering
NWood: Non-woody perennial species
PA_{ARA}: Perimeter-area ratio of arable patches
PER_{NV}: Percentage of natural vegetation
P/R/B: Pink, red and/or brown flowers
Q: Rao's quadratic entropy
SLA: Specific leaf area
SMass: Seed mass
TEs: Trophic effect trait
TRs: Trophic response trait
Wood: Woody perennial species
In the text, the functional metric of the different traits appears beside the name of each trait
$Trait_{Q}$; $Trait_{CWM}$

1. Introduction

Agricultural intensification is causing species loss across many trophic groups with potential effects on the provision of ecosystem services within agroecosystems (hereafter ESs) (Storkey et al., 2013). Causes of such phenomenon are increasing land-use disturbance regimes from boundaries to inner-fields (José-María et al., 2010), as well as the decline of landscape heterogeneity (Tscharntke et al., 2005). Landscape heterogeneity is influenced by the presence of patches of semi-natural and agricultural habitats (referred to as compositional heterogeneity), and their arrangement and shape (better known as configurational heterogeneity) (Fahrig et al., 2011). Increased compositional heterogeneity promotes more niches to support more species, whereas increased configurational heterogeneity promotes connectivity between patches, edge and mass effects for biodiversity along boundary networks (Fahrig et al., 2011). Studies focusing on compositional (José-María et al., 2010; Solé-Senan et al., 2014) and configurational heterogeneity in agricultural areas (Solé-Senan et al., 2014; Fahrig et al., 2015; Rotchés-Ribalta et al., 2015) suggest that landscape heterogeneity increases species richness and diversity in arable plant communities and promotes species persistence. Moreover, its positive effects on plant community composition are higher at boundaries than in inner-fields (José-María et al., 2010; Solé-Senan et al., 2014).

Plant community composition stems from the responses of plant functional traits to environmental filters here considered as abiotic factors, which are abiotic factors that prevent species establishment or persistence in a particular location (Violle et al., 2007). Environmental filters include land-use changes, field size increase and the increase of nitrogen and pesticide inputs, which may affect the structure and composition of arable plant communities differently. The use of plant traits has been demonstrated as useful in disentangling the delivery of ESs (Lavorel et al., 2013; Storkey et al., 2013; Robleño et al., 2017), increasing awareness of the negative impacts of diversity loss on the ecosystem functioning, stability and sustainability (Wood et al., 2015). Therefore, nature conservation vision has shifted from targeting species to focusing on ecosystem properties. In this scenario, shifts in functional trait distributions of arable plants caused by the increasing use of nitrogen and pesticides and landscape simplification need to be quantified (Lavorel et al., 2013). Such quantification can be addressed using two metrics (Ricotta and Moretti, 2011): (1) functional diversity using Rao's quadratic entropy (hereafter Q); and (2) community-weighted mean (hereafter CWM). Q is used to test the complementary resource use hypothesis (Tilman et al., 1996) and with a higher Q among species within a community reflects higher diversity of resource strategies, and consequently, a more complete exploitation of resources than in less functionally diverse communities, thus improving ecosystem functioning. Q reveals patterns of trait over- or under-dispersion, compared to a random expectation. On the other hand, CWM is used to test the mass ratio hypothesis (Grime, 1998), assuming that the dominant traits in a community exert the greatest effect on ecosystem functions.

Agricultural intensification has promoted a decline in pollinators (Holzschuh et al., 2006; Bretagnolle and Gaba, 2015; Holland et al., 2015; Martins et al., 2015; Nayak et al., 2015; Perovic et al., 2015), non-pollinator arthropods (Kormann et al., 2015; Rouabah et al., 2015) and bird populations (Diaz et al., 1990). Likewise, it has been demonstrated that linkages among plant traits to those species (Ricou et al., 2014; Moretti et al., 2013; Diaz, 1990) are responsible for the delivery of ESs. In this context, the response-effect trait framework has been identified as a useful tool for predicting the impact of environmental changes on ecosystem services delivery in multi-trophic systems (Lavorel et al., 2013). This framework integrates plant traits, divided into driver response traits (DRs) that govern how plants respond to different environmental filters, and trophic effect traits (TEs) that determine how plants affect their environment (Lavorel and Garnier, 2002). There is agreement that TEs influence other trophic levels linked to trophic response traits (TRs) (e.g. floral traits to pollinator traits, seed traits to bird traits). Finally, the framework identifies functional effect traits (FEs) of the consumer community that drive ESs. The functional trait approach has been successfully used in studies focusing on grasslands under different management regimes to quantify trade-offs and synergies between plant traits and grasshopper traits (Moretti et al., 2013), as well as in arable communities to quantify relationships between crop management, plant and invertebrate traits that can potentially provide ESs to farmland birds (Storkey et al., 2013). However, neither Moretti et al. (2013) nor Storkey et al. (2013) have focused on the role of landscape heterogeneity in modulating plant functional traits. Concurrently, it has been suggested that agricultural intensification in the Mediterranean area increases the dominance of some response traits of non-woody (Armengot et al., 2016) and wind-pollinated species (José-María et al., 2011), promotes for tall, heavy-seeded and early-flowering species (Guerrero et al., 2014), and enhances plants with high SLA (Hernandez Plaza et al., 2014). Conversely, Fried et al. (2012)

found that under recurrent disturbances, short plants with small seeds are promoted. Yet, these studies have not focused on a functional trait approach aimed at disentangling the impact of shifts of these response traits to other trophic levels.

Our study represents the first attempt to analyze the effect of agricultural intensification on ESs, both at field and landscape-scale in the Mediterranean area, by integrating plant functional traits in a response-trait framework. By using functional traits, we address the recent call of Wood et al. (2015) for the application of functional approaches in agriculture to investigate the impact of agricultural intensification on ESs. Considering the different levels of disturbance regimes within an arable field along pre-defined field positions, we hypothesized that landscape heterogeneity may help to counteract the negative impact of such disturbances on the functional composition of arable plant communities. Furthermore, we expect functional diversity of plant communities to display different responses to compositional and configurational landscape heterogeneity. Increasing compositional heterogeneity is expected to provide suitable habitats for biodiversity since it may offer more resources to specialized organisms. In contrast, increasing configurational heterogeneity is expected to enhance pollination as semi-natural habitats acting as boundaries benefit pollinator populations. The study was based on two measures of landscape heterogeneity and three different positions at field scale –boundaries, inner-edges and inner-fields- to evaluate their effects on (i) functional diversity (using Rao's quadratic entropy) and (ii) functional dominance on Mediterranean arable plants (using the community-weighted mean). Our research was aimed at identifying trade-offs in functional traits of arable plant communities which could suggest different ecological strategies, analyzing the extent to which functional assemblages and single trait metrics of DRs and TEs vary along environmental gradients (landscape heterogeneity and field positions), and proposing a response-effect trait framework for mapping the impact of agricultural intensification on pollination and the provision of suitable habitat for farmland biodiversity at field and landscape scales.

2. Materials and methods

2.1. Study area

The study was conducted in a dryland cereal area in Catalonia, in the northeastern Iberian peninsula (41º35'-42º11'N; 0º35'-1º21'E) of 4500 km^2. Study sites were composed of rain-fed barley fields interspersed with patches of Mediterranean woodlands of *Quercus ilex* L. and *Quercus faginea* Lam. We selected forty-five localities, defined by a circular buffer area of 1-km radius, along a gradient of landscape heterogeneity ranging from very simple landscapes with a high percentage of arable lands (95%), to complex landscapes with a lower percentage of arable lands (5%). A strong relationship between landscape heterogeneity and plant species richness and diversity in a 1km buffer area has been previously highlighted (Solé-Senan et al., 2014). Landscapes were at a distance of at least 5 km (centre to centre) from each other. Two fields of barley with similar size and shape were selected at each landscape as study sites, since field size is known to affect weed richness and diversity (Gaba et al., 2010). Environmental characteristics and farming practices applied in the fields are described in Supplementary Appendix A.

2.2. Landscape heterogeneity

At each locality, compositional landscape heterogeneity was characterized by the percentage of natural vegetation (PER_{NV}) (José-Maria et al., 2010), whereas configurational landscape heterogeneity was characterized by the perimeter-area ratio of arable patches (PA_{ARA}) (Perović et al., 2015). While PER_{NV} was computed by summing the proportion of areas not devoted to agriculture, PA_{ARA} was calculated as follows:

$$PA_{ARA} = \sum_{i=1}^{m} P_i \Big/ \sum_{i=1}^{m} A_i$$

where *P* is the perimeter, *A* is the arable patch area, *i* the patch number and *m* the number of patches in the landscape buffer. The two metrics presented a wide range of values along localities (Spearman's Correlation coefficient of mean values: PER_{NV}–PA_{ARA}: $\rho = 0.14$; $p>0.05$). Landscape metrics were calculated using GIS-Software (ArcGIS^{TM} 9.2, ESRI).

2.2. Plant surveys

Plant surveys were carried out between May and July 2008. As plants are not homogeneously distributed over fields (Solé-Senan et al., 2014), the surveys were performed at three different positions: a) boundary, which is the first meter of non-cultivated habitat surrounding a field, b) inner-edge, which encompasses the first meter of cultivated habitat that is adjacent to the boundary, and c) inner-field, located 50 m away from the edge. At each position, surveys were conducted in one transect of five plots (1 m x 5 m) that ran parallel to the field edge at 10 m intervals. Species nomenclature follows de Bolòs and Vigo (2011) and plant species abundance was quantified using Braun-Blanquet's (1979), in which the cover-abundance of each species is assigned a value between + (sparse and covering a small area) and 5 (covering more than 75% of the area). Those values were transformed into the median value of percent cover range in each cover class (+ = 0.01%; 1 = 5%, 2 = 17.5%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). To obtain a species abundance matrix, we calculated the plant abundance of each species per position within a landscape by dividing the total plant cover estimated by Braun-Blanquet data cover by the total number of plots per position (2 fields x 5 plots/position =10 plots/position per landscape).

2.3. Response and effect traits

We selected five driver response traits (DRs) to screen the ongoing functional response to agricultural intensification, and four trophic effects traits (TEs) with an effect on ecosystem services (ESs). Plant traits were compiled from scientific literature (Table 1). Regarding DRs, the classification into types of life-forms is based on the publication of Storkey et al. (2013): annuals; herbaceous perennials; rhizomatous perennials and woody perennials. Due to the small number of rhizomatous perennials encountered, life-forms were secondarily regrouped into three broader but still meaningful categories: annuals, non-woody perennial (herbaceous perennials and rhizomatous perennials), and woody perennials. Furthermore, as leguminous species can be used to identify the response of plant species to agricultural intensification practises such as fertilization (Van Elsen, 2000; Lavorel et al., 2013), annual legumes, non-woody perennial legumes and woody legumes were regrouped in a broad category referenced as legumes (see José-Maria et al., 2011); hence, this trait was called life-form and legume (LF&Leg). DRs such as plant height (H), onset of flowering (OF), specific leaf area (SLA) and seed mass (SMass) are associated with agricultural intensification (José-Maria et al., 2011; Fried et al., 2012; Juarez-Escario et al., 2013; Storkey et al., 2013; Fontana et al., 2014; Guerrero et al., 2014), whereas TEs such as corolla shape (CShap), duration of flowering (DFlow), flower colour (FCol) and flower symmetry (FSym) trigger a trophic response on other organisms (Lavorel et al., 2013; Ricou et al., 2014) (Table 1). All SMass values were log-transformed. Regarding flower colours (FCol), “Pink” and “Red and Brown” were secondarily regrouped into a broad, but still meaningful, group called “Pink, Red and Brown” (P/R/B) based on their similar range of values of attractiveness proposed by Ricou et al. (2014). FCol was encoded as a “fuzzy” variable. The sum of the values of all the variables coding a fuzzy trait must sum to 1. In these cases, we gave values larger than 0.0 and less than 1.0 for each colour, which represented the probability of each colour to be encountered. The same occurred for the classification of the corolla shape and the flower symmetry in most of the *Asteraceae* species.

2.4. *Identifying trade-offs in functional traits of arable plant communities*

The species abundance matrix and the nine traits (Table 1) were used to perform a principal coordinate analysis (hereafter PCoA) (Gower, 1971) to identify whether the ordination axes represented a spectrum of plant ecological strategies (trade-off). The ordination was based on a generalization of Gower’s distance, which is suitable for the treatment of both continuous and categorical variables (Pavoine et al., 2009). This analysis was performed using CANOCO 5.0 (ter Braak and Smilauer, 2012).

2.5. Trait metrics

Two complementary approaches were used to characterize community trait composition: 1) functional diversity of each trait (Q) and 2) dominant attributes of each trait (CWM). Q and CWM trait values of both DRs (Q_{DR} and CWM_{DR}) and TEs (Q_{TE} and CWM_{TE}) (Table 1) were calculated by using the species abundance matrix. A principal coordinates analysis based on the Gower distance was used to obtain the Q values for dummy and fuzzy traits and get a PCoA scores matrix of that trait. The PCoA scores represent the same information as the original traits values, but with the added dimension of being on a fully quantitative scale (Smilauer and Leps, 2014). These matrices were then used to calculate functional diversity based on Q. For quantitative trait Q was quantified using the Euclidean distance. For dummy and fuzzy traits, CWM trait values corresponded to the proportion of the different levels of the factor. These values were calculated using CANOCO 5.0 (ter Braak and Smilauer, 2012).

Table 1. Driver response (DRs) and trophic effect (TEs) traits used in the analyses.

Plant	Functional trait	Acronyms	Type, classes (abreviations)	References
DR	Life-form and legume	LF&Leg	Dummy: Annual, legume, non-woody perennial (NWood), woody perennial (Wood)	a
	Height	H	Quantitative (cm)	a
	Onset of flowering	OF	Quantitative (1 to 12)	a
	Specific leaf area	SLA	Quantitative ($mm^2 \cdot mg^{-1}$)	e, f
	Seed mass	SMass	Quantitative (g)	d
TE	Corolla shape	CShap	Fuzzy: Anemophilous, flat, tubular	a
	Duration of flowering	DFlow	Quantitative (1 to 12)	a
	Flower colour	FCol	Fuzzy: Blue & purple (Bl/Pur), green, pink, red & brown (P/R/B), white, yellow	a
	Flower symmetry	FSym	Fuzzy: Actinomorphous, apetalous, zygomorphous	a

*List of references a) De Bolòs & Vigo (2011), b) Klimešová J. & Klimeš (2008), c) Klimešová & de Bello (2009), d) Royal Botanic Gardens Kew (2015), e) Kleyer et al. (2008), f) Storkey et al. (2013)

2.6 Functional assemblages and shifts of DR and TE trait values along environmental gradients

To examine relationships between functional assemblages, landscape heterogeneity and field positions, we conducted a distance-based redundancy analysis (dbRDA), which is the most useful community-based analysis to reveal to what extent functional community composition changes along environmental gradients (Kleyer et al., 2012). Matrices including Q_{DR}, CWM_{DR}, Q_{TE} and CWM_{TE} trait values per landscape were used as response variables, which were constrained to PER_{NV}, PA_{ARA} and field positions (hereafter Q_{DR}-dbRDA, CWM_{DR}-dbRDA, Q_{TE}-dbRDA and CWM_{TE}-dbRDA) and a Monte Carlo Permutation test (9999 permutations of samples) was conducted to test the significance of PER_{NV}, PA_{ARA} and field positions for each dbRDA. Trait values were always centered and standardized. These analyses were performed using CANOCO 5.0 (ter Braak and Smilauer, 2012).

We analyzed the variability of trait metrics using mixed-effects models, which account for non-independent errors that may occur due to hierarchically nested designs. The effect of PER_{NV}, PA_{ARA} and field position (POS) -boundaries (B), inner-edges (E) and inner-fields (IF)- and their interactions were tested as fixed factors. Locality was included as a random factor to account for the nested design, whereas PER_{NV} and PA_{ARA} were previously standardized to compare their effect and their interaction with field position. Orthogonal contrasts used to compare the different levels of the factor position were fixed and considered *a priori,* so as to compare inner-edges and boundaries with inner-fields (E&BvsIF) and inner-edges with boundaries (EvsB). Models adequacy was checked by confirming the normality and homoscedasticity of the residuals, as well as correlations between the observed and fitted values for the confidence sets of models following the protocol provided by Zuur et al. (2010).

The identification of the best predictive model from our data set was obtained using the methods described by Burnham and Anderson (2002). The approach compares the fit of a suite of models using Akaike's Information Criterion (AIC). For each Q and CWM trait metric, four models with all possible combination of the selected explanatory variables were evaluated. The AICc, which includes a correction for small sample sizes, and Akaike weights (w) were calculated for each model. We ranked the competing models according to their AICc value and subsequently estimated their Akaike differences (Δi) with respect to the best model (lowest AICc) and the Akaike weight (w_i) of each model. We considered models with $\Delta i<2$ as the best-fitted models for each predictive variable (Johnson and Omland, 2004). The effect of each variable was inferred on the set of models with $\Delta i<2$ using the model averaging procedure, which weights the estimated values and the standard errors of the explanatory variables by the Akaike weights (wi). Finally, to evaluate the significance of the explanatory variables throughout the model averaging procedure, we computed their 95% confidence intervals. Explanatory variables in which the confidence interval included 0 were dismissed from inference making. These analyses were conducted using the *lmer* function in the lme4 package (Bates et al., 2008) in R (R Development Core Team, 2008).

3. Results

3.1. Identifying trade-offs in functional traits of arable plant communities

The PCoA analysis revealed a spectrum of ecological strategies among the plant species encountered (Fig. 1). The first PCoA axis explained 26.53% of the total trait variation and was mainly associated with LF&Leg, SMass, H, SLA, OF, DFlow and floral traits. This axis reflected a gradient from tall, non-annual species with late and long flowering periods, heavy seeds and low SLA; to short, annual species with early and short flowering periods, light seeds and high SLA. Non-annual species were linked to being zygomorphous, and having tubular corollas as well as yellow and blue flowers. In contrast, annual species typically had flat corollas with actinomorphous white flowers. The second axis explained 19.25% of the total trait variation and was associated with floral traits that reflect a gradient from grass to non-grass species. We did not find any strong correlation between qualitative traits or between qualitative and quantitative traits ($\rho<0.6$) (Graham, 2003).

3.2 Functional assemblages and shifts in DRs trait values along environmental gradients

According to the Monte Carlo permutation test, functional assemblages of Q_{DR}-dbRDA varied along field positions (B: $F=18.3$, $p<0.01$; IF: $F=11.8$, $p<0.01$; E: $F=3.0$, $p<0.05$) but did not vary along gradients of landscape heterogeneity (PER_{NV}: $F=1.5$, $p=0.20$;

PA_{ARA}: F=0.3, p=0.94). Field positions explained 17.0 % of the variation in the Q_{DR}-dbRDA, of which 83.1% and 13.3% were accounted for in the first two axes, respectively. The arrangement of study sites along Q_{DR}-dbRDA axis 1 (Fig. 2a) showed that all Q_{DR} trait metrics over-dispersed at boundaries, whereas there was functional resemblance of species thriving in inner-fields and inner-edges.

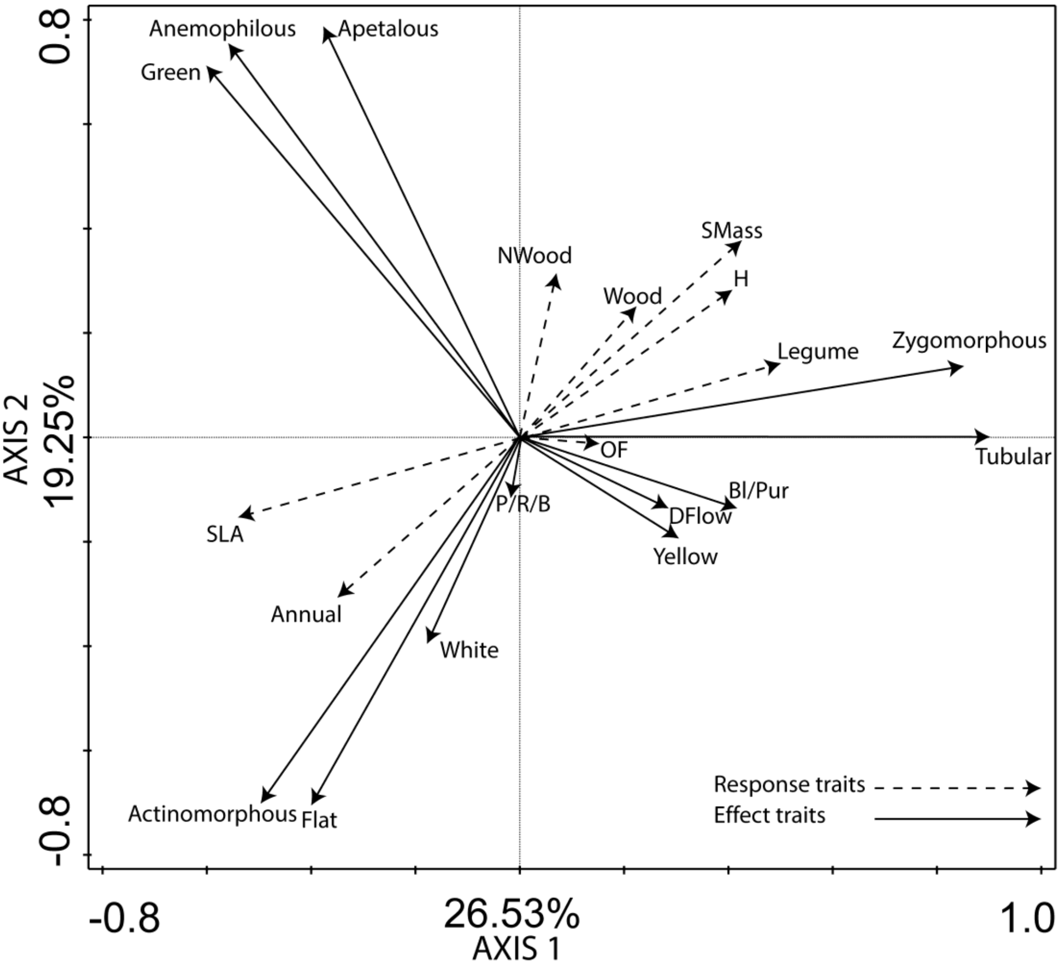

Figure 1. Principal coordinates analysis (PCoA) based on the response and effect traits of the plant species sampled. Ordination based on the response and effects traits of 425 species. The percentage of explained variance of each axis is given. Trait data were standardized and centered. Dashed arrows represent DRs. Solid arrows represent TEs. Trait abbreviations are given in Table 1

The averaged model (Table 2a) highlighted that all Q_{DR} decreased from boundaries to inner-fields, although SLA_Q and $SMass_Q$ did not vary between boundaries and inner-edges. OF_Q was positively affected by configurational heterogeneity (PA_{ARA}), but the effect of PA_{ARA} decrease from boundaries to inner-fields.

According to the Monte Carlo permutation test, functional assemblages of CWM_{DR}-dbRDA varied along field positions (B: F=21.9, p<0.01; IF: F=6.0, p<0.01; E: F=4.0, p<0.01) but did not vary along gradients of landscape heterogeneity (PER_{NV}: F=0.9, p=0.45; PA_{ARA}: F=0.8, p=0.57). Field positions explained 19.8% of the variation in the CWM_{DR}-dbRDA, of which 89.8% and 7.8% were respectively accounted for in the first and the second axes (Fig. 2b). The arrangement of POS along axis 1 showed functional resemblance of dominant species in inner-fields and inner-edges, which were different to those at boundaries. Species were characterized as annual, short in stature, early flowering, with high SLA but low SMass dominated in inner-edges and inner-fields; whereas dominant plant species at boundaries were characterized as perennial and legumes tall in stature, late flowering, low SLA but high SMass

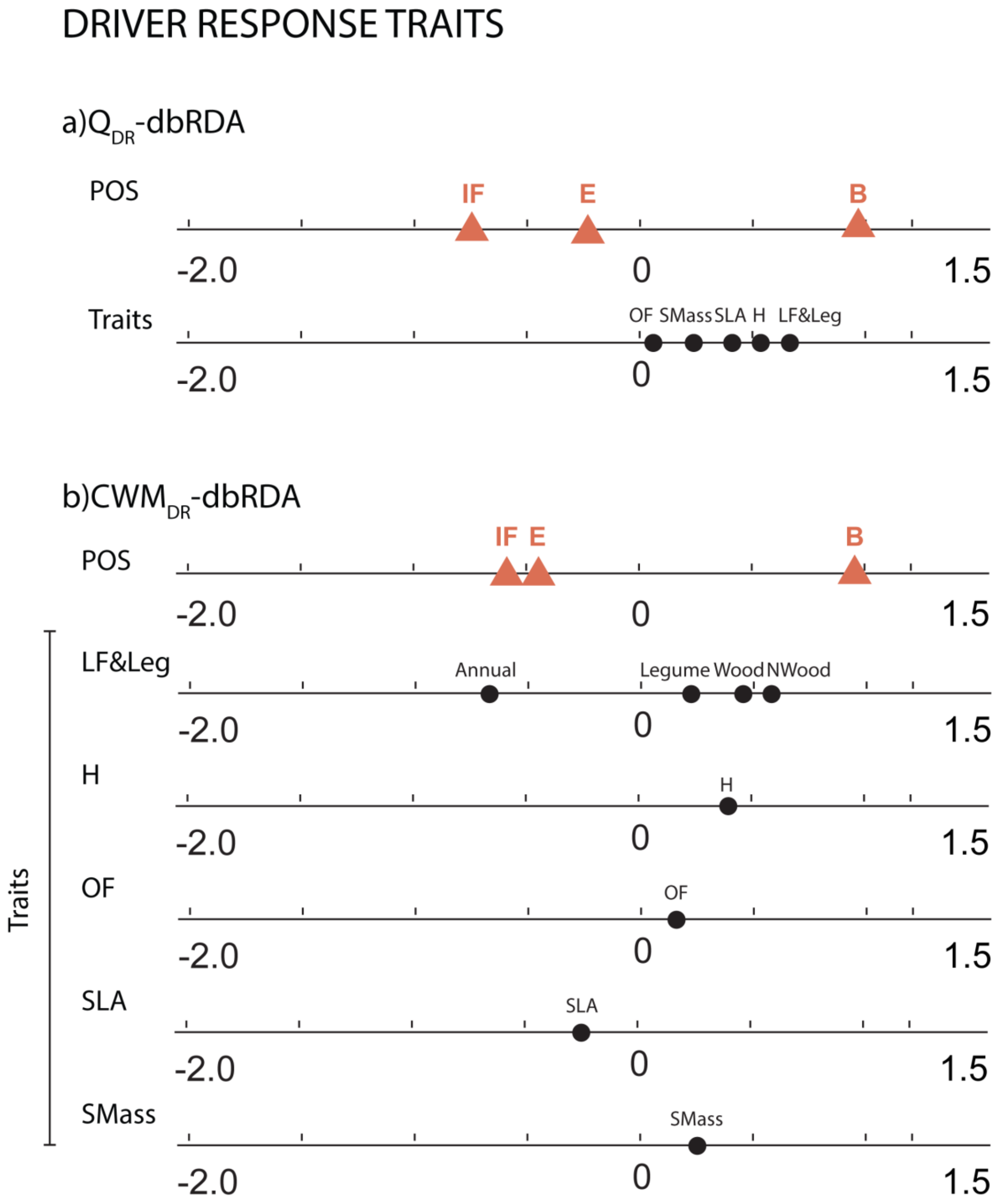

Figure 2. Mean scores along RDA axis 1 of (a) Q of DRs, (b) CWMs of DRs. Triangular symbols represent the arrangement of field positions (POS) along axis 1. B= Boundaries, E= Edges, IF= Inner-fields. Circles represent the arrangement of traits and trait classes along axis 1. Trait abbreviations are given in Table 1.

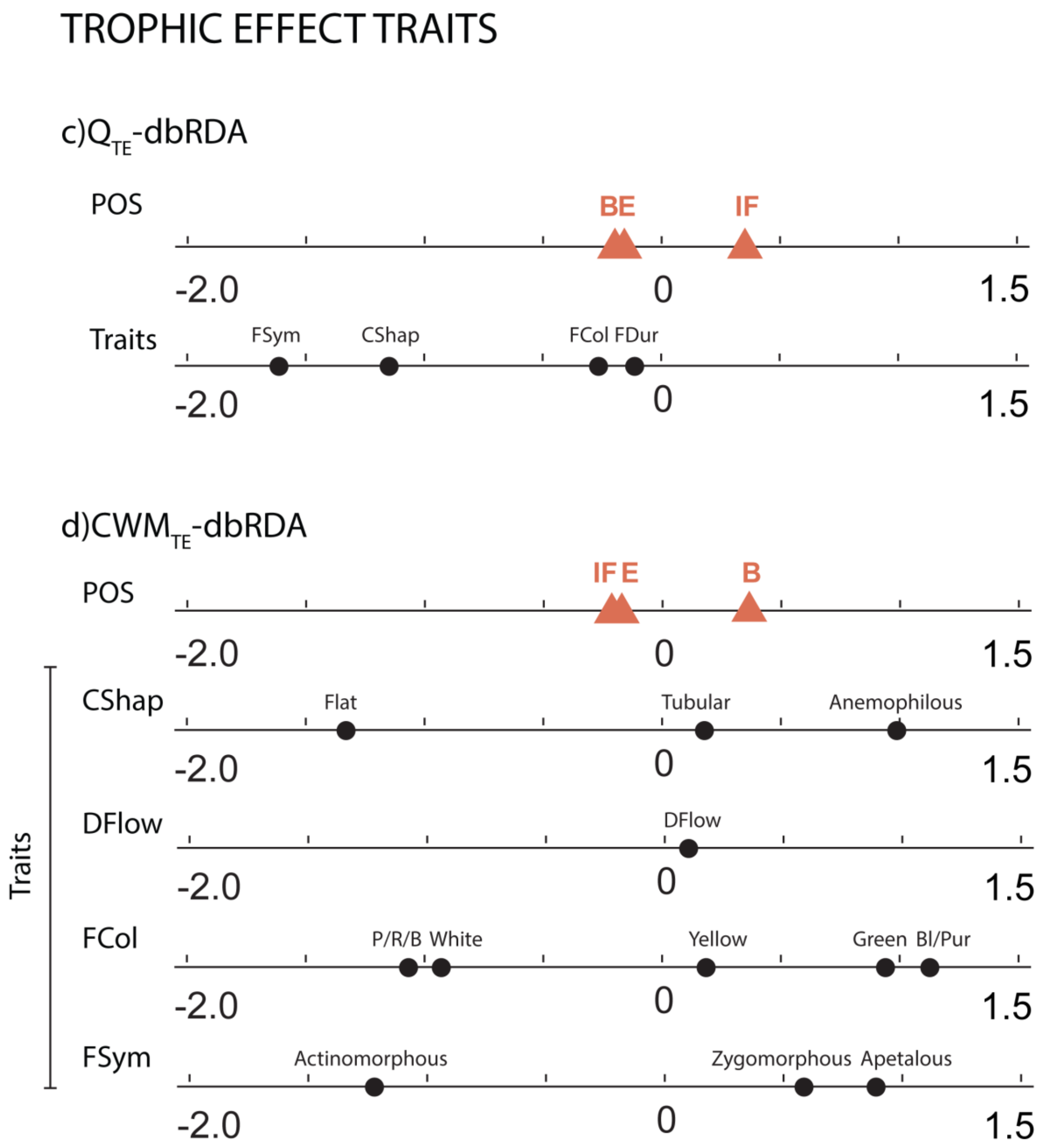

Figure 2 (cont). Mean scores along RDA axis 1 of (c) Q of TEs, (d) CWMs of TEs. Triangular symbols represent the arrangement of field positions (POS) along axis 1. B= Boundaries, E= Edges, IF= Inner-fields. Circles represent the arrangement of traits and trait classes along axis 1. Trait abbreviations are given in Table 1.

The averaged model (Table 2a) highlighted that all Q_{DR} decreased from boundaries to inner-fields, although SLA_Q and $SMass_Q$ did not vary between boundaries and inner-edges. OF_Q was positively affected by configurational heterogeneity (PA_{ARA}), but the effect of PA_{ARA} decrease from boundaries to inner-fields.

According to the Monte Carlo permutation test, functional assemblages of CWM_{DR}-dbRDA varied along field positions (B: F=21.9, $p<0.01$; IF: F=6.0, $p<0.01$; E: F=4.0, $p<0.01$) but did not vary along gradients of landscape heterogeneity (PER_{NV}: F=0.9, p=0.45; PA_{ARA}: F=0.8, p=0.57). Field positions explained 19.8% of the variation in the CWM_{DR}-dbRDA, of which 89.8% and 7.8% were respectively accounted for in the first and the second axes (Fig. 2b). The arrangement of POS along axis 1 showed functional resemblance of dominant species in inner-fields and inner-edges, which were different to those at boundaries. Species were characterized as annual, short in stature, early flowering, with high SLA but low SMass dominated in inner-edges and inner-fields; whereas dominant plant species at boundaries were characterized as perennial and legumes tall in stature, late flowering, low SLA but high SMass.

Table 2. Averaged model estimations (and standard errors) of the predictors obtained from the mixed-effect models of DR trait values a) Rao quadratic entropy index (Q) and that of b) Community-weighted means values (CMW) in relation to field position (E&BvsIF, boundaries and inner-edges against inner-field; EvsB, boundaries against inner-edges), percentage of natural vegetation (PER_{NV}) and perimeter-area ratio of arable patches (PA_{ARA}) and their interactions. Trait names are given in Table 1. x = estimated predictors that were dismissed from inference making as 0 was included in their confidence interval.

Measure			**Intercep**	**EvsB**	**E&BvsIF**	**PER_{NV}**	**PER_{NV}·EvsB**	**PER_{NV}·E&BvsIF**	**PA_{ARA}**	**PA_{ARA}·EvsB**	**PA_{ARA}·E&BvsIF**
a)Q	$LF\&Leg_Q$		1.18(0.09)	0.27(0.04)	-0.46(0.06)	x	x	x			
	H_Q		0.45(0.05)	0.06(0.02)	-0.44(0.05)	x	x	x	x	x	x
	OF_Q		1.08(0.08)	0.09(0.02)	-0.15(0.03)	x	x	x	0.26(0.04)	0.43(0.06)	-0.88(0.08)
	SLA_Q		0.97(0.08)	x	-0.07(0.02)						
	$SMass_Q$		1.5(0.08)	x	-0.04(0.02)	x	x	x			
b)CWM	$LF\&Leg_{CWM}$	$Annual_{CWM}$	0.67(0.07)	-0.30(0.04)	0.39(0.05)						
		$Legume_{CWM}$	0.04(0.01)	0.33(0.05)	-0.06(0.02)						
		$NWood_{CWM}$	0.13(0.03)	0.12(0.03)	-0.13(0.03)	x	x	x			
		$Wood_{CWM}$	0.05(0.02)	0.12(0.03)	-0.14(0.03)						
	H_{CWM}		81.67(0.78)	44.22(0.60)	-45.58(0.64)	0.25(0.04)	0.36(0.05)	-0.38(0.06)	x	x	x
	OF_{CWM}		4.01(0.17)	0.67(0.07)	-0.26(0.06)	x	x	x	6.23(0.22)	6.43(0.24)	-2.29(0.25)
	SLA_{CWM}		24.26(0.43)	-0.83(0.08)	x	x	x	x			
	$SMass_{CWM}$		0.61(0.07)	0.24(0.04)	-0.62(0.07)						

The averaged model (Table 2b) indicated that values of $\mathrm{Leg}_{\mathrm{CWM}}$, $\mathrm{NWood}_{\mathrm{CWM}}$ and $\mathrm{Wood}_{\mathrm{CWM}}$ decreased gradually from boundaries to inner-fields, whereas $\mathrm{Annual}_{\mathrm{CWM}}$ showed the opposite pattern. $\mathrm{H}_{\mathrm{CWM}}$, $\mathrm{OF}_{\mathrm{CWM}}$, and $\mathrm{SMass}_{\mathrm{CWM}}$ decreased gradually from boundaries to inner-fields, while $\mathrm{SLA}_{\mathrm{CWM}}$ was higher in inner-edges than at boundaries, but it did not vary between the outer positions and inner-fields. $\mathrm{PER}_{\mathrm{NV}}$ had a positive effect on $\mathrm{H}_{\mathrm{CWM}}$ and $\mathrm{PA}_{\mathrm{ARA}}$ had a positive effect on $\mathrm{OF}_{\mathrm{CWM}}$. The relevance of landscape heterogeneity decreased progressively from boundaries to inner-fields in both measures.

Although landscape heterogeneity appeared in the confidence sets of the most of the fitted models of Q_{DR} and $\mathrm{CWM}_{\mathrm{DR}}$ trait values (Supplementary Appendix B), with the exception of $\mathrm{OF}_{\mathrm{FD}}$, $\mathrm{H}_{\mathrm{CWM}}$, and $\mathrm{OF}_{\mathrm{CWM}}$ (Table 2), the remaining model-averaged estimators were dismissed from inference making since 0 was included in their confidence interval.

3.3. Functional assemblages and shifts in TE trait values along environmental gradients

Functional assemblages of Q_{TE}-dbRDA varied along field positions but not along gradients of landscape heterogeneity ($\mathrm{PER}_{\mathrm{NV}}$: F=1.5, p=0.21; $\mathrm{PA}_{\mathrm{ARA}}$: F=1.1, p=0.35). Field positions (IF: F=8.3, $p<0.01$, B: F=4.3, $p<0.01$ and E: F=4.1, $p<0.01$ according to the Monte-Carlo Test) explained 10.5% of the variation in the Q_{TE}-dbRDA, of which 66.5% and 26.5% were respectively accounted for in the first and the second axes. All the trait metrics were over-dispersed at boundaries and inner-edges (Fig. 2c). The arrangement of POS along axis 1 showed functional resemblance of species in inner-edges and boundaries, which were different from those in inner-fields.

The averaged model indicated changes in Q_{TE} trait values between boundaries and inner-edges (Table 3a). $\mathrm{CShap}_{\mathrm{Q}}$ and $\mathrm{FCol}_{\mathrm{Q}}$ were higher in inner-edges than in boundaries, whereas $\mathrm{FSym}_{\mathrm{Q}}$ was higher at boundaries than in inner-edges. $\mathrm{DFlow}_{\mathrm{Q}}$ did not vary between boundaries and inner-edges but decreased towards inner-fields. No Q_{TE} trait metric varied along gradients of landscape heterogeneity.

Table 3. Averaged model estimations (and standard errors) of the predictors obtained from the mixed-effect models of TE trait values a) Rao quadratic entropy index (Q) and that of b) Community-weighted means values (CMW) in relation to field position (E&BvsIF, boundaries and inner-edges against the inner-fields; EvsB, boundaries against inner-edges), percentage of natural vegetation (PER$_{NV}$) and perimeter-area ratio of arable patches (PA$_{ARA}$) and their interactions. Trait names are given in Table 1. x = estimated predictors that were dismissed from inference making as 0 was included in their confidence interval.

Measure			**Intercep**	**EvsB**	**E&BvsIF**	**PER$_{NV}$**	**PER$_{NV}$·EvsB**	**PER$_{NV}$·E&BvsIF**	**PA$_{ARA}$**	**PA$_{ARA}$·EvsB**	**PA$_{ARA}$·E&BvsIF**
a)Q	CShap$_{Q}$		1.41(0.10)	-0.08(0.02)	-0.43(0.05)						
	DFlow$_{Q}$		0.90(0.08)	x	-0.12(0.03)	x	x	x			
	FCol$_{Q}$		1.49(0.10)	-0.19(0.03)	-0.14(0.03)						
	FSym$_{Q}$		1.41(0.10)	0.12(0.03)	-0.57(0.06)						
b)CWM	CShap$_{CWM}$	Anemophilous$_{CWM}$	0.44(0.05)	0.20(0.03)	x						
		Flat$_{CWM}$	0.26(0.04)	-0.13(0.03)	0.36(0.05)				-0.27(0.06)	-0.33(0.08)	-3.38(0.16)
		Tubular$_{CWM}$	0.19(0.03)	-0.09(0.03)	-0.49(0.06)				0.82(0.10)	x	x
	DFlow$_{CWM}$		0.90(0.08)	x	-0.11(0.03)	x	x	x			
	FCol$_{CWM}$	Bl/Pur$_{CWM}$	0.05(0.02)	0.05(0.02)	-0.07(0.02)	x	x	x			
		Green$_{CWM}$	0.42(0.05)	0.17(0.02)	x						
		P/R/B$_{CWM}$	0.10(0.03)	-0.10(0.03)	0.15(0.04)						
		White$_{CWM}$	0.14(0.03)	x	0.18(0.03)				-0.35(0.05)	-1.00(0.09)	-1.68(0.12)
		Yellow$_{CWM}$	0.14(0.03)	-0.08(0.02)	-0.08(0.02)	x	x	x	0.56(0.06)	0.17(0.05)	-0.19(0.06)
	FSym$_{CWM}$	Actinomorphous$_{CWM}$	0.36(0.05)	-0.15(0.03)	0.12(0.03)						
		Apetalous$_{CWM}$	0.35(0.025)	0.14(0.03)	x						
		Zygomorphous$_{CWM}$	0.09(0.02)	x	-0.10(0.03)						

Functional assemblages of CWM_{TE}-dbRDA did not vary along gradients of landscape heterogeneity (PER_{NV}: F=1.8, p=0.12; PA_{ARA}: F=1.1, p=0.35). Meanwhile, POS (B: F=9.4, p<0.01; IF: F=5.7, p<0.01 and E: F=5.3, p<0.01 according to the Monte-Carlo test) explained 14.8% of the variation in the CWM_{TE}-dbRDA, of which 63.5% and 25.3% were respectively accounted for the first and the second axes (Fig. 2d). The arrangement of POS along axis 1 showed functional resemblance of dominant species in inner-fields and inner-edges, which were different from those at boundaries. Plant species with flat corollas, a short flowering duration, pink, red, brown and white petals and actinomorphous flowers dominated in inner-fields and in inner-edges, whereas dominant species in boundaries had anemophilous and tubular corollas, long flowering periods, yellow, green, blue and purple flowers which were zygomorphous or apetalous (Fig. 2d).

The averaged model (Table 3b) indicated that $Anemophilous_{CWM}$, $Green_{CWM}$ and $Apetalous_{CWM}$ values were higher at boundaries than in inner-edges but their values did not vary from the outer positions to inner-fields. $White_{CWM}$ did not vary between boundaries and inner-edges but increased to inner-fields. While $Flat_{CWM}$, $P/R/B_{CWM}$ and $Actinomorphous_{CWM}$ decreased from boundaries to inner-fields, Bl/Pur_{CWM} showed the opposite pattern. $Tubular_{CWM}$ and $Yellow_{CWM}$ were higher in inner-edges than at boundaries and in inner-fields. $DFlow_{CWM}$, $White_{CWM}$ and $Zygomorphous_{CWM}$ did not vary between inner-edges and boundaries. $White_{CWM}$ increased from the outer positions to inner-fields, whereas $DFlow_{CWM}$ and $Zygomorphous_{CWM}$ decreased.

Regarding landscape heterogeneity (Table 3b), $Tubular_{CWM}$ and $Yellow_{CWM}$ were positively related to PA_{ARA}, while $Flat_{CWM}$ and $White_{CWM}$ showed the opposite trend. Variations in PA_{ARA} values along field positions did not imply shifts in values of $Tubular_{CWM}$. Conversely, the effect of PA_{ARA} on $Flat_{CWM}$ and $White_{CWM}$ was higher in inner-edges than at boundaries and in inner-fields, while that of $Yellow_{CWM}$ decreased from boundaries to inner-fields.

Although most of confidence sets of fitted models suggested that some Q_{TE} and CWM_{TE} trait metrics varied along gradients of landscape heterogeneity (Supplementary Appendix C), PER_{NV} was dismissed from all the models in terms of inference making since 0 was included in the confidence interval of their estimates.

4. Discussion

4.1. Trade-off between species traits

Two different ecological strategies were highlighted based on the multivariate analysis. A set of species with traits such as an annual life cycle, high SLA, short height and early onset of flowering allow species to grow rapidly and complete their life cycle in a short period, which is a crucial characteristic of long-term survival in disturbed habitats. This strategy was defined by Grime (1974) as ruderal. Conversely, non-annual species with low SLA, late onset flowering and taller height acquired resources more slowly, suggesting abilities for competitive dominance (Grime, 1974). The trade-off observed between ruderal and competitive species' adaptability may be caused by the contrasting disturbance regimes from the regularly cultivated inner-fields to the perennial boundaries (Poggio et al., 2013; Solé-Senan et al., 2014) as well as reflecting the lower efficacy of fertilization and weed control at boundaries compared with the inner-fields and the competition with crop (José-Maria et al., 2010; Fried et al., 2012). Our results reinforce the idea that trade-offs in Mediterranean arable communities are the result of competitive abilities like in Northern European arable communities (Storkey et al., 2013), Mediterranean dryland areas (Gross et al., 2013) and Mediterranean riparian areas surrounded by agricultural fields (Juarez-Escario et al., 2016). Additionally, ruderal species exhibited floral traits linked to generalist pollinators (Ricou et al., 2014), whereas competitive species had traits linked to specialist pollinators such as yellow, blue and purple flowers, tubular corollas or zygomorphous flowers (Ricou et al., 2014; Villalobos and Vamosi, 2016). This finding is consistent with Lososova et al. (2006) who found that specialist insect-pollinated plants are more abundant in perennial plant communities than in disturbed habitats, such as arable fields, since disturbance filters perennial species that are more likely to be insect-pollinated.

4.2. Functional assemblages and trait values along gradients of agricultural intensification

Our results revealed that the similarities between functional assemblages and shifts in trait values respond to the different locations within a field, following the same pattern as described by Perronne et al. (2014). Thereby, DRs are linked to competitive species that are dominant at boundaries; whereas DRs are linked to ruderality, dominant in inner-edges and inner-fields. Furthermore, DRs are over-dispersed at boundaries but under-dispersed in inner-edges and inner-fields. This pattern can be attributed to the contrasting disturbance regime, as disturbance constrains the number of successful ecological strategies, which are defined by their combination of traits (Diaz et al., 1998).

Although DR assemblages did not vary along gradients of landscape complexity, landscape complexity indicators proved to be important explanatory variables for explaining shifts in single trait values of OF_{Q}, H_{CWM}, OF_{CWM}, $CShap_{CWM}$ and $FCol_{CWM}$. This difference suggests an antagonistic effect of traits on plant resources use and trait dominance. Despite that field positions and landscape heterogeneity have been found to affect plant DRs in Mediterranean agricultural fields (José-Maria et al., 2011), our results highlight that concurrent shifts in trait values along gradients of landscape heterogeneity will depend on a single trait. This is in strong contrast to Guerrero et al. (2014), who found no influence of landscape heterogeneity on single trait values. However, Guerrero et al. (2014) exclusively focused on inner-field positions where decreasing plant diversity was a function of the impact of crop management and the lower probability of seed arrival from boundaries, leading to community homogenization through trait filtering (Armengot et al., 2016). Our results demonstrate that landscape heterogeneity may buffer in-field management intensification, favors spill-over and filters the species pool regarding species traits, thus supporting the landscape-moderated traits selection hypothesis (Tscharntke et al., 2012).

We found antagonistic trends between functional assemblages of DRs and trophic effect traits (TEs). Field positions shaped a functional resemblance in terms of Q_{DR} and CWM_{DR} among plant species thriving in inner-fields and inner-edges. Boundaries and inner-edges showed a functional resemblance in terms of Q_{TE}, whereas CWM_{TE} indicated functional resemblance of plant species thriving in inner-fields and inner-edges, differing from those at boundaries. This finding highlights for the first time that although the increasing disturbance regime from boundaries to inner-field leads to the dominance of the same TEs in inner-fields and inner-edges, plants thriving at boundaries and inner-edges can potentially provide similar ESs since plant communities in those positions converge in a similar structure. Therefore, species from boundaries are replaced by other species with similar traits. The high level of functional redundancy in terms of Q_{TE} between the outer-field positions indicates that shifts in species assemblages as well as species turnover little tell us about functional shifts when trait redundancy is high.

4.3. Response-effect framework as a tool to explain the delivery of ecosystem services.

We have developed a pilot proposal of the response-effect framework in Mediterranean agricultural landscapes according to shifts in trait metrics of plant species (Fig. 3). Agricultural intensification affects DRs (DR_0 in Fig. 3), which can be linked to TEs (TE_0 in Fig. 3). In turn, TEs trigger trophic responses (TRs) in higher trophic levels entailing functional effects (FEs) that then trigger the delivery of ESs.

Shifts in trait metrics of LF&Leg and OF (DR_{1a} and DR_{1b}) along field positions may trigger a trophic effect (TE_1) (Fig.3) on pollinators since LF&Leg are related with DFlow, FSym, CShap and FCol (DR_{1a}~TE_{1a}). Perennial plants may increase insect-attractiveness (TR_1) by bearing flowers with a long DFlow as well as polycarpy ability and thus increasing insect-foraging time (FE_1) (TR_1~FE_1), whereas annual plants bear flowers in a short period of time due to their short life cycle (Pinke and Gunton, 2014). Regarding FSym, most of the species with zygomorphous flowers surveyed at boundaries are *Fabaceae* (e.g. Legumes Fig. 2b, Table 2b) and *Lamiaceae* species (Supplementary Appendix D). These species can be encountered within patches of natural vegetation surrounding the fields, which may reflect the neighboring effect of the adjacent habitats at boundaries (Devlaeminck et al., 2005). Meanwhile, the reduction of the likelihood of fertilizer drift from inner-fields to boundaries is functional in restoring plant species less tolerant to fertilizer than legumes (Van Elsen, 2002) at the outer positions. Most of these legumes and *Lamiaceae* species have flowers with blue and yellow petals and tubular corollas (CShap). These traits are known to increase the attraction of specialized insects (TR_1) (Ricou et al., 2014). On the contrary, grasses will have a direct effect on TE_{1a} since they include plant species without interest for pollinators due to the anemophilous corollas, green and apetalous flowers (Ricou et al., 2014). The presence of grasses at boundaries is consequence of the dominance of a subset of perennial boundary-dwelling *Poaceae* species (Supplementary Appendix D) that cannot colonize inner-field positions since their perennial form cannot face within-field disturbances.

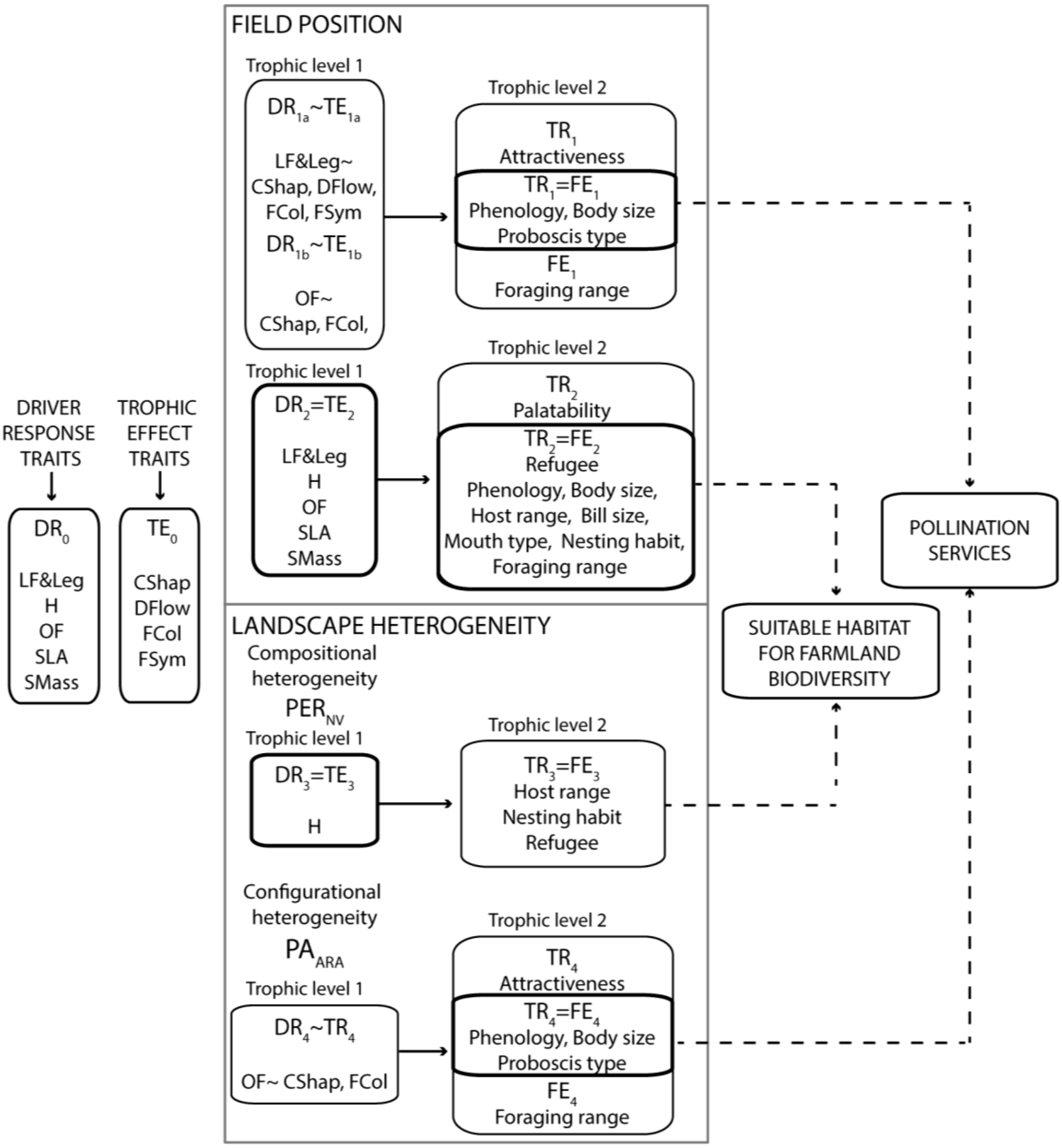

Figure 3. Theorical multitrophic response-effect trait framework to predict changes in ecosystem functioning. The framework splits field position from landscape heterogeneity. Traits abbreviations are given in Table 1. DR_0 and TE_0 represent respectively the set of driver response traits and trophic effect traits considered in this study. DR_{1a}, DR_{1b}, DR_2, DR_3 and DR_4 represent the set of traits that respond to the environmental driver of interest (field position, PER_{NV} and PA_{ARA}). TE_{1a}, TE_{1b}, TE_2, TE_3 and TE_4 represent the trophic effect trait of a lower trophic level which affect the next trophic level up (TR_1, TR_2, TR_3 and TR_4 as trophic response traits of upper trophic levels). FE_1, FE_2, FE_3 and FE_4 identify functional effect traits that determine the efficiency of the service delivery. Linkages between driver and effect traits at each trophic level can occur through direct overlap (response trait = effect trait) or through association (indicated by ~). Trophic level 1: Plant species. Trophic level 2: Pollinator and non-pollinators insects and birds. Boxes in bold highlight direct overlap of trophic and effect traits. Arrows between trophic levels indicate the direction of the linkages. Dashed arrows indicate linkages between trophic levels and ecosystem services.

Correlations between flowering periods and pollinator phenology (Isaacs et al., 2009) reveal that species with late OF affect pollinator abundance and diversity, in addition to pollination success (DR_{1b}~TE_{1b}) (Kremen et al., 2007). Concurrently, late OF is a competitive trait linked to others like CShap and FCol, that are related with specialist pollinators (Ricou et al., 2014). Thus, the trophic response (TR_1) of pollinators to TE_{1a} and TE_{1b} will depend on their phenology, body size and proboscis type (Ricou et al., 2014), raising the pollinators' foraging range (FE_1). Species with such traits are located at the outer-field positions where there is a greater diversity of insect-pollinated species (Holzschuh et al., 2006, Nayak et al., 2015). This highlights the importance of the surrounding natural vegetation patches from the retention of specialized pollinator assemblages in agroecosystems (Kohler et al., 2007). Conversely, the increasing occurrence of species with flat corollas could provide an advantage for non-specialized pollinators in inner-fields. Results thus highlight the importance of boundaries and inner-edges in the provision of pollination services for specialized pollinators, confirming that the availability of floral resources in agricultural landscapes with such traits may support and enhance the abundance and richness of prominent ecosystem service-providers such as bees, bumble-bees and hoverflies (Holland et al., 2015).

Increasing configurational landscape heterogeneity (PA_{ARA}) may also increase pollination services since pollinator species such as butterflies and bees are known to be negatively affected by reduced configurational landscape heterogeneity (Holland et al., 2015; Perovic et al., 2015). Similarly to DR_{1b}, heterogeneous landscapes shelter species with late OF will trigger changes in trait values of CShap and FCol (DR_4~TR_4). Specialized pollinators are linked to species with tubular corollas, which provide nectar and copious amounts of pollen attracting (TR_4) a wide range of bee species and butterflies (Ricou et al., 2014; Perovic et al., 2015). Furthermore, it has been reported that in intensive agricultural landscapes, boundaries with remnant high-quality habitats sustain more pollinators and insect-pollinated species than the surrounding countryside (Kohler et al., 2007), possibly explaining the presence of plants species with tubular corollas (TE_4 and TR_4, TR_4=FE_4, FE_4) due to the presence of adequate pollinators at outer-field positions. The effectiveness of floral resource enhancement for pollinators depends not only on the density and diversity of flowers, but also on the ecological contrast that management creates. High plant diversity induced by reduced herbicide usage (Hardman et al., 2016), proximity of natural plant communities (Martins et al., 2015), presence of non-crop areas (Hardman et al., 2016) and creation of sown flower strips (Holland et al., 2015) have all been found to enhance pollination services in the local vicinity.

Regarding the provision of a suitable habitat for insects and birds by delivering trophic resources and refuge, within-field high disturbances promote the germination of species characterized by ruderal traits (Grime, 1974) such as early flowering time (Pinke and Gunton, 2014), high SLA (Armengot et al., 2016) and low seed mass (Guerrero et al., 2014) (DR_2). The later has been related to greater seed production (Moles et al., 2004) and seed-bank persistence (Hernandez Plaza et al., 2015), an essential characteristic for maintaining species population in the long term. So, these DR_2 will have a direct trophic effect, providing suitable habitat for farmland biodiversity (DR_2=TE_2). The decrease in disturbance intensity results in the accumulation of standing biomass and an increase in competition for light-favoring perennial plants with traits linked to survival ability such as tall canopies and heavy seeds (Hemrová and Münzbergová, 2015), and late flowering at boundaries. It has been suggested that complex plant canopies of perennial species act as a refuge (TR_2) for predator beetles such as *Coccinellidae*, *Staphylinidae* and *Carabidae* (Woodcock et al., 2005), which have been reported to be important in the foraging range of steppe-bird species by potentially increasing chick survival (TR_2=FE_2) (Jiguet, 2001). Likewise, the reduction of the proportion of grasses has been associated with a lower number of these predator beetles but a higher number of farmland birds (Henderson et al., 2007).

The reduction of plant height due to increasing disturbance described in this study will benefit those birds that prefer foraging or nesting in more open areas; whereas those that prefer closed areas for refuge will benefit from taller plants at boundaries (TR_2=FE_2). In this sense, short vegetation height is reported to be the optimal nesting and foraging habitat for steppe-birds species, whose main breeding and winter populations are found in the Iberian peninsula (Brotons et al., 2004).

High SLA can make plants more palatable to herbivores (TR_2) (Mattson, 1980), providing resources for animals with varying mouth type. The SMass preferred by different farmland birds (Diaz, 1990), however, suggests that functional diversity will increase for a larger range of birds, enhancing the foraging range with varying bill sizes (TR_2=FE_2). Therefore, the variation of DR_2 such as H, SLA or SMass along field positions may offer suitable habitat sites both for breeding and foraging, depending on bird traits (Butler and Norris, 2013). The importance of each position for the provision of suitable habitat will thus depend on the particular requirement of the species they rely on. We found that high H values were concurrent with high compositional heterogeneity (PER_{NV}) values. This suggests that tall plants from patches of natural vegetation may be successful at colonizing new environments and dispersing further than short species do (Thomson et al., 2011). Plants thriving in non-disturbed habitats like boundaries are subsets of the landscape-wide species pool (Tscharntke et al., 2012) able to embed into such positions through dispersal as a function of the neighborhood effect (Devlaeminck et al., 2005). As it was previously mentioned, the higher range of H (DR_3=TE_3) will lead to host a wider range of predators, which can in turn provide resources for birds by varying their host range, nesting habit and refuge (TR_3=FE_3).

4. Conclusions

We have successfully identified trade-offs between functional traits in Mediterranean arable plant communities due to species' adaptability to the gradients of agricultural intensification at field scale. Our study shows that agricultural intensification, both at field and landscape scale, leads to shifts in the functional structure of arable plant communities. Such shifts are bound to entail impacts on the ability of communities to provide ESs. In terms of functional assemblages, agricultural intensification leads to convergence and trait dominance of DRs in inner-edges and inner-fields such as annual species with short stature and light seeds, which differs from those that are at boundaries. However, boundaries and inner-edges may deliver similar ESs due to the similar exploitation of resources, although the traits of the dominant plant species vary between boundaries and inner-edges. Therefore, conservation efforts aimed at increasing such traits should be applied to inner-edges, which represent an intermediate level of intensification. On the other hand, our study reinforces that shifts in trait values along gradients of landscape heterogeneity are mainly masked by the high impact of agricultural intensification at field scale. Even still, the use of trait values in a response-effect framework allows us to unravel the importance of compositional heterogeneity, so as to provide suitable habitats for insects such as predators and birds; this is in contrast to configurational heterogeneity which would affect trait values linked to pollination services. Our work highlights the usefulness of a response-effect framework in the study of Mediterranean arable farmlands across multiple trophic levels to predict the evolution of each ecosystem service.

Acknowledgements

We acknowledge the financial support provided to X.O. Solé-Senan by the Universitat de Lleida (UdL PhD grants), A. Juarez-Escario by the Generalitat de Catalunya (FI PhD grants), I. Robleño by Ministerio de Economia y Competitividad (FPI PhD grants) and the Ministerio de Educación y Ciencia (Projects AGL 2007-60828 and AGL 2010-22084-C02-01). We thank two anonymous reviewers for constructive comments on the manuscript. We thank all collaborating fieldworkers and farmers for allowing us to access their fields as well as Sarah Lade for improving the English in this paper.

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Supplementary Appendix A. Summary of the environmental characteristics and farming practices on the cereal fields of the sample area. Altitudinal range (AR), mean annual temperature (T), mean annual precipitation (P), potential evapotranspiration (PE), accumulated precipitation during the cropping period of the study (Ps-m), potential vegetation (PV), sowing density (SD), seed provenance (SP), rotational scheme (RS), pre-emergence weed control for broad-leaves and grass-leave (Pre.E.B&G), post-emergence to control *Bromus diandrus* (Post.Bro), post-emergence to control broad-leaves species (Post.B), post-emergence to control *Lolium rigidum* (Post.L), post-emergence to control *Avena sterilis* (Post.A).

AR (m)	250-900		
T (ºC)	13.2-14.9		
P (mm)	419-521		
PE (mm)	745-816		
Ps-m (mm)	233-317		
PV	*Quercetum rotundifoliae* Br.-Bl. & O. Bolòs in Vives 1956	*Buxo sempervirentis-Quercetum Rotundifoliae* Gruber 1974	*Violo willkommii-Quercetum fagineae* Br.-Bl. & O. Bolòs 1950 corr. Rivas-Martínez 1972
SD($kg\cdot ha^{-1}$)	180-200		
SP	Re-use of own cereal seed after cleaning		
RS	Cereal monoculture for more than 10 years		
Fertilization (MIN-MAX)	*Autumn base fertilization* N:P:K (15-15-15), (8-15-15), (12-8-15). (250-350 $kg\cdot ha^{-1}$) Pig slurry (20-50 $m^3\cdot ha^{-1}$) *Spring top-dressed fertilization* N32. (150-250 $kg\cdot ha^{-1}$) Pig slurry (5-20 $m^3\cdot ha^{-1}$)		
Weed control			
Pre.E.B&G	Clortoluron 1.25 $kg\cdot ha^{-1}$		
Post.Bro	Iodosulfuron 3 + mesosulfuron 15		
Post.B	Tribenuron 0.015 $kg\cdot ha^{-1}$ or 2,4-D 0.6 $kg\cdot ha^{-1}$		
Post.L	Diclofop 540		
Post.A	Tralkoxidim 400		

Supplementary Appendix B. Summary of the models describing variation in the response traits values of a) Rao Quadratic entropy index (Q) and that of b) Community-weighted means values (CMW) in relation to field position (POS) and its interaction between the percentage of natural vegetation (PER$_{NV}$) and perimeter-area ratio of arable patches (PA$_{ARA}$). k, number of parameters; AICc, Akaike's information criteria corrected for small sample size; Δi, the AICc differences of each model compared with the most parsimonious and Wi, Akaike weights. Only models with Δi<2 are showed. Traits names are given in table 1.

Explanatory traits and classes			Models	K	AICc	Δi	Wi
a)	LF&Leg$_{Q}$		POS·PER$_{NV}$	4	73.17	0	0.49
			POS	3	73.52	0.35	0.41
	H$_{Q}$		POS·(PER$_{NV}$+PA$_{ARA}$)	5	-514.88	0	0.49
			POS·PER$_{NV}$	4	-513.84	1.04	0.29
			POS	3	-513.12	1.76	0.2
	MF$_{Q}$		POS	3	-237	0	0.5
			POS·PER$_{NV}$	4	-235.4	1.59	0.23
			POS·(PER$_{NV}$+PA$_{ARA}$)	5	-235.38	1.62	0.22
	SLA$_{Q}$		POS	3	-437.35	0	0.88
	SMass$_{Q}$		POS	3	-424.71	0	0.51
			POS·PER$_{NV}$	4	-424.35	0.36	0.43
b)	LF&Leg$_{CWM}$	Annual$_{CWM}$	POS	3	-35.83	0	0.89
		Legume$_{CWM}$	POS	3	-346.92	0	0.89
		NWood$_{CWM}$	POS	3	-120.36	0	0.57
			POS·PER$_{NV}$	4	-199.48	0.89	0.37
		Wood$_{CWM}$	POS	3	-126.14	0	0.82
	H$_{CWM}$		POS	3	1473.33	0	0.5
			POS·PER$_{NV}$	4	1474.62	1.29	0.26
			POS·(PER$_{NV}$+PA$_{ARA}$)	5	1475.11	1.79	0.2
	MF$_{CWM}$		POS	3	339.4	0	0.35
			POS·PA$_{ARA}$	4	339.63	0.24	0.31
			POS·PER$_{NV}$	4	340.4	1.01	0.21
			POS·(PER$_{NV}$+PA$_{ARA}$)	5	341.26	1.87	0.14
	SLA$_{CWM}$		POS	3	671.33	0	0.6
	SMass$_{CWM}$		POS	3	385.09	0	0.72

Supplementary Appendix C. Summary of the models describing variation in the effects traits values of a) Rao Quadratic entropy index (Q) and that of b) Community-weighted means values (CMW) in relation to field position (POS) and its interaction between the percentatge of natural vegetation (PER$_{\mathrm{NV}}$) and perimeter-area ratio of arable patches (PA$_{\mathrm{ARA}}$). k, number of parameters; AICc, Akaike's information criteria corrected for small sample size; Δi, the AICc differences of each model compared with the most parsimonious and Wi, Akaike weights. Only models with Δi<2 are showed. Traits names are given in table 1

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	Explanatory traits and classes		Biological Models	K	AICc	Δi	Wi
a)	CShap$_{\mathrm{Q}}$		POS	3	178.80	0.00	0.74
	DFlow$_{\mathrm{Q}}$		POS·PER$_{\mathrm{NV}}$	4	-174.52	0.00	0.74
	FCol$_{\mathrm{Q}}$		POS	3	128.10	0.00	0.85
	FSym$_{\mathrm{Q}}$		POS	3	147.09	0.00	0.81
b)	CShap$_{\mathrm{CWM}}$	Anemophylous$_{\mathrm{CWM}}$	POS	3	26.57	0.00	0.86
		Flat$_{\mathrm{CWM}}$	POS	3	-27.44	0.00	0.55
			POS·PA$_{\mathrm{ARA}}$	4	-26.37	1.07	0.32
		Tubular$_{\mathrm{CWM}}$	POS·PA$_{\mathrm{ARA}}$	4	-79.51	0.00	0.56
			POS	3	-78.49	0.00	0.34
	DFlow$_{\mathrm{CWM}}$		POS	3	371.85	0.00	0.64
			POS·PER$_{\mathrm{NV}}$	4	373.69	1.84	0.25
	FCol$_{\mathrm{CWM}}$	Bl/Pur$_{\mathrm{CWM}}$	POS	3	-260.31	0.00	0.53
			POS·PER$_{\mathrm{NV}}$	4	-259.73	0.58	0.40
		Green$_{\mathrm{CWM}}$	POS	3	23.32	0.00	0.79
		P/R/B$_{\mathrm{CWM}}$	POS	3	-88.51	0.00	0.79
		White$_{\mathrm{CWM}}$	POS	3	-107.09	0.00	0.60
			POS·PA$_{\mathrm{ARA}}$	4	-105.83	1.26	0.32
		Yellow$_{\mathrm{CWM}}$	POS·PER$_{\mathrm{NV}}$	4	156.53	0.00	0.36
			POS	3	-156.45	0.08	0.35
			POS·PA$_{\mathrm{ARA}}$	4	-155.53	1.00	0.22
	FSym$_{\mathrm{CWM}}$	Actinomorphous$_{\mathrm{CWM}}$	POS	3	26.52	0.00	0.79
		Apetalous$_{\mathrm{CWM}}$	POS	3	41.76	0.00	0.82
		Zygomorphous$_{\mathrm{CWM}}$	POS	3	-219.43	0.00	0.80

CHAPTER 6

General discussion and main conclusions

GENERAL DISCUSSION

The experimental work included in this thesis allows to improve insights into how the diversity of arable plants varies throughout spatial scales such as at within-field scale –comparing field boundaries to their respective field edges and inner-fields-, within-local landscape scale –from patch, habitat, up to landscape- and between landscapes from a regional perspective. Besides, changes in plant diversity at different spatial scales are expected to drive shifts on the delivery of ecosystem services of arable plant communities. Understanding and predicting how agriculture intensification modulates plant diversity and thus the potential provision of ecosystem services is expected to be a breakthrough to achieve healthier agro-ecosystems. Therefore, our findings can be applied to develop further management practices aimed at achieving the quality of agro-ecosystems, which is nowadays a raising concern in our society.

Overall perspective in plant richness

The total number of species encountered throughout the study sites included in this thesis highlights how diverse are Mediterranean arable plant communities compared to those from northern and central Europe. A total of 208, 170 and 405 species have been respectively found along the boundaries and the inner-fields of Andalucia, Aragon and Catalonia (Chapter 2). The prospection in the local landscape of the Ager Valley (Chapter 3) has allow to find 328 plant species. On the other hand, in the prospection throughout 90 arable fields in Catalonia (Chapters 4 and 5) 435 species have been found, of which 42 species (9.6%) were considered as rare arable plants, following Aboucaya et al. (2000) and de Bolós et al. (2005). The most abundant weeds were *Lolium rigidum* Gaudin, *Bromus diandrus* Roth, *Avena sterilis* L., *Papaver rhoeas* L. and Convolvulus arvensis L. (Chapters 2, 3, 4 and 5), whereas the most abundant perennial species were *Salsola vermiculata* L. (Chapters 2, 4 and 5), *Brachypodium phoenicoides* (L.) Roem & Schult. (Chapters 3, 4 and 5), *Dactylis glomerata* L. (Chapters 2, 3, 4 and 5) and *Elymus repens* (L.) Gould (Chapter 3).

Plant communities at field scale

The structural heterogeneity of the boundaries of arable fields has been observed throughout a wide prospection across three regions in the Iberian Peninsula (Andalucia, Aragon and Catalonia), where dryland arable crops dominate the agricultural landscape

(Chapter 2). Disentangle how this boundary heterogeneity affects arable plant communities is an important issue in agro-ecology. This importance lies behind the fact that boundaries reduce the negative effects of run-off and soil erosion and provide semi-natural habitats for biodiversity, which include pollinators for crops but also harmful weeds, predators and agricultural pests. The traditional idea that boundaries act as a structure from where weeds can spread into inner-fields has been supported by some studies in northern Europe (Marshall and Arnold, 1995; Kleijn and Verbeek, 2000; Mante and Gerowitt, 2009), and our study partially supports this fact too.

On the other hand, this thesis points out that the heterogeneity of species composition and shifts in dominant species in the plant communities thriving at the boundaries of arable fields can be explained by using a set of structural descriptors that can be easily obtained (Chapter 2). Accordingly, we have described up to five types of boundaries regarding their physical structure, which may be a refuge for a wide variety of plant species, ranging from those species from forests, shrubs, dry-grasslands to weeds. Differences in the percentage of perennial species at the boundary, the boundary width and slope as well as the presence of stone-walls lead to changes on species assemblages and affect the role of boundaries in hosting harmful weeds. Likewise, rare arable plants are also affected by boundary structure. In the context of rarity and species with conservation value, Bassa et al. (2011) found that these species are more likely to be found in wide boundaries. However, these species were mainly perennial rather than annual.

Boundaries dominated by perennial species not only exclude undesirable weeds by light and niche competition as Critchley et al. (2006) suggested, but also impact negatively on rare arable plants for the same reasons, which is consistent with Marshall (2009) due to the dependence of rare arable plants on regular disturbances.

Increasing boundary width reduces harmful weeds abundance, avoiding therefore the role of boundaries as a potential reservoir of these weeds. Furthermore, width provides an opportunity for plant species to escape from herbicides and pesticides loads, as well as species richness is increased with the increasing area (Aavik and Lira, 2010). These results confirm that plant diversity is positive related to the boundary width (Schippers and Joenje, 2005). Conversely, the impact of herbicides and fertilizers of the adjacent fields in the narrowest boundaries may negatively affect the abundance of perennial species, thus increasing the abundance of harmful weeds, leading to a higher risk of infestation in the inner-fields. However, rare arable plants do not find a safe site to growth as these species are highly sensitive to agricultural intensification that takes place in the narrowest boundaries.

Furthermore, an increasing slope in boundaries avoids vegetation disturbance because agricultural machinery cannot reach them, thus triggering process of plant secondary succession (Aavik and Lira, 2010) and promoting perennial species that compete with the annuals (Marshall, 2009). A similar trend is observed in those boundaries with stone-walls where the fallen stones make agricultural disturbance more difficult.

Species diversity at landscape scale

We have studied patterns of diversity components at different levels of agricultural intensification among habitats (Chapter 3) and among field positions (Chapter 4). At local landscape scale, agricultural intensification, which was characterized as a proxy of the most common land-use practices (see Chapter 3), was proved to be the most important diversity driver in agricultural landscapes. In a similar fashion to most of the European studies, our results point out that species richness is reduced under high-intensity management practices (Kleijn et al., 2009; Flohre et al., 2011). Likewise, species assemblages change from habitats subjected to low agricultural intensification to those subjected to high intensification (José-María et al., 2010). High intensification (fertilization, weed control, below-ground disturbance and vegetation removal) limits species establishment and survival, leading to poorer communities (Kleijn and van der Voort, 1997), whereas reduced pesticide and fertilizer inputs benefit plant species richness (Gabriel et al., 2006; Romero et al., 2008). These results were also observed at field scale along three different positions within arable fields –i.e boundary, edge and centre-, both for total plant species and for rare arable plants (Chapter 4). Strong differences were found between the total plant diversity at edges and inner-fields, probably because edges are less subjected to management than inner-fields (Kleijn and van de Voort, 1997; Romero et al., 2008; Gabriel et al., 2009; José-Maria et al., 2010), but also because they are close to boundaries, which allows more spill-over and neighbourhood effect (Devlaeminck et al., 2005).

Regarding rare arable plants, these species were encountered mainly in the outer positions of the fields (Chapter 4). Although we found more rare species at boundaries than in edges, the Shannon diversity of rare arable plants was slightly higher in edges than at boundaries. This result, which is concordant with José-María et al. (2010) indicate that the medium level of disturbance that undergoes in edges enhances rare arable plants rather than the absence of disturbance in boundaries, which lead to the dominance of perennial species (Chapter 5) (Fried et al., 2008; Marshall, 2009).

Regarding the components of diversity, β-diversity at higher spatial scales contributed the most to total species richness (Chapters 3 and 4) and Shannon diversity (Chapter 4), highlighting the importance of heterogeneity at higher scales due to differences in species pools (Wagner et al., 2000; Clough et al., 2007). β-diversity component among levels of agricultural intensification was remarkable (over 30% of the total) (Chapter 3). This reflect that plant communities subjected to different levels of agricultural intensification show independent trajectories, thus confirming that different management practices associated to each habitat create particular conditions that provide specific ecological niches.

We found a strong positive effect of landscape heterogeneity in the total plant species diversity at boundaries of cereal fields, whereas for rare arable plants this effect was higher in edges. As all the study sites were subjected to conventional farming practices, our results support that landscape heterogeneity counteracts the negative effect of those farming practices, in particular for rare arable plants (Tscharntke et al., 2005). The positive effects of landscape heterogeneity in plant communities at boundaries are probably due to the fact that heterogeneity support more habitats with specific species pool that can disperse at short and medium distance (Devlaeminck et al., 2005; Bassa et al., 2011). The decrease of its influence from boundaries to inner-fields has been attributed firstly to differences in the agricultural impact (José-Maria et al., 2010) and secondly to limited seed dispersal (Devlaeminck et al., 2005) from boundaries up to inner-fields. Although landscape heterogeneity has been generally reported to increase the diversity of arable plants (Weibull et al., 2003; Gabriel et al., 2005; Roschewitz et al., 2005), some studies (Marshall, 2009; Armengot et al., 2011) did not found this relationship since they exclusively focused on inner-fields, were the major intensity of agricultural intensification take place and seed dispersal from adjacent habitats is limited, as it has been previously mentioned.

Higher landscape heterogeneity may represent higher compositional or configurational heterogeneity (Fahrig et al., 2011). Although we found that compositional heterogeneity (represented by the percentage of natural vegetation) affected positively to total and rare arable plants richness and diversity, configurational heterogeneity (represented by perimeter-area ratio of arable fields) benefit exclusively rare arable plants richness (Chapter 4) but affects negatively their Shannon diversity. In this sense, Rotchés-Ribalta et al. (2015) found no effect of the perimeter-area ratio on rare arable plants. However, their study was assessed using the presence of the species instead of their abundance. The perimeter-area ratio is determined by to components, the size of the patches and the complexity of their geometry, which leads to variation in the relative edge length. An increase in edge length has been hypothesized to foster larger diversity, as boundary areas offer specific resources such as hosts and micro-habitats conditions to many species (Smart et al., 2002). Therefore, complex shapes harbour a larger number of species because the increase in the perimeter in relation to the area provides more safe havens for rare arable plants at field edges. However, this also may lead to the dominance of specific species (lower Shannon diversity). The species pool of rare arable plants hosted at boundaries and edges of fields with complex shapes foster mass effect to inner-field positions, probably because dispersal can be enhanced from the outer field positions, thus enabling the entry of species at short distance to the inner-fields (Poggio et al., 2010). On the other hand, the effect of landscape heterogeneity in species assemblages irrespective of the field position was stronger for rare arable plants than for the rest of the species (Chapter 4). In this context, our study suggests that heterogeneous landscapes, which present high levels of connectivity, are beneficious for rare arable plants. In those landscapes subjected to simplification processes, rare arable plants may establish metapopulations, particularly in edges, in response to habitat modification, as it has been previously observed in other organisms with limited dispersion such as butterflies (Thomas and Hanski, 1997; Perović et al., 2015), bees (Holzschuh et al., 2006; Martins et al., 2015; Nayak et al., 2015) or carabids (Madeira et al., 2016).

Functional diversity at landscape scale

The species diversity approach conducted in Chapters 3 and 4 was also applied in terms of functional diversity (Chapters 3 and 5). One of the major goals of this comparison is to find whether environmental filters (the impact of agricultural intensification among habitats within a landscape in Chapter 3 and along field positions and gradients of landscape heterogeneity in Chapter 5) constrain coexisting species from the regional species pool to share similar traits. The results point out that ecological dynamics in plant communities show independent trajectories, thus indicating that different management practices associated to each habitat create particular conditions that provide specific ecological niches. Moreover, agricultural intensification at field scale not only impacts directly on the functional diversity of plants, but also generates specific functional assemblages (Chapter 3 and 5). This finding suggests that functional diversity patterns are the result of the interaction between patch and regional processes. Hence, local diversity is the sum of the species present in the regional pool that successfully disperse and persist in the patch. This dispersion and persistence ability in one patch will stem from its functional traits (Violle et al., 2007).

On the other hand, we defined a group of response traits to assess the arable communities' resistance to disturbance, and a suite of effect traits to assess their impact on the potential provision of resources for pollinators (Chapters 3 and 5) and the provision of suitable habitat for biodiversity (Chapter 5). The partition of the components of Rao's Quadratic Entropy index (Q) at different spatial scales reveals that β-diversity contribution to the total landscape diversity (γ-landscapes) both for response and effect traits were in stark contrast to its contribution to the total species richness (Chapter 3). Previous studies (De Bello et al., 2009; Mason et al., 2013; Carlucci et al., 2015) support our observations and suggest that among-communities, differentiation for particular traits can be smaller than processes acting within-community. For example, the functional differentiation among plant communities took place among habitats subjected to different levels of agricultural intensification over the whole landscape (β-functional diversity between 6% and 8%), although most of the differentiation in terms of species richness took place at that level (β-diversity around 85%). Therefore, at landscape scale, a high replacement in species composition (compositional turnover) entails stable functional assemblages (low functional turnover). The fact that trait-group composition converged, whereas species composition remained sharply divergent indicates that deterministic rules governed assembly at the trait-group level of community organization (Fukami et al., 2005).

The trade-off of functional assemblages corresponds to different ecological plant strategies, suggesting that shifts in agricultural intensification among habitats (Chapter

3) and differences in the impact of agricultural intensification along three field positions and landscape heterogeneity (Chapter 5) lead to specialized functional strategies (trait divergence). Thus, in low managed habitats (Chapter 3) or where efficacy of farming practices is low, such as at boundaries (Chapter 5), plant species tend to be perennial and legumes, with tall stature, late flowering, low specific leaf-area (SLA) and high seed mass, whereas the increase of disturbance lead to plant communities composed by short annual species with early flowering, high SLA and low seed mass. These two contrasted functional groups would correspond to competitive and ruderal strategies respectively (Grime, 1974; Storkey et al., 2013). The higher proportion of perennial species in low managed habitats indicates that plant community is in its secondary succession stage (Kahmen and Poschlod, 2004), as well as a neighbouring effect of the adjacent semi-natural habitats (Devlaeminck et al., 2005), thus corroborating the importance of the local species pool for recruitment. Concurrently, we found that an increasing intensification lead to a trait convergence of Q and a trait dominance (in terms of community-weighted means CWM), which implies not only a reduction of trait diversity, but also a direct effect on ecosystem services since dominant traits in a community exert the greatest effect on ecosystem functions (Grime, 1998).

Field positions shaped a functional resemblance in terms of Q and CWM of response traits among plant species thriving in inner-fields and edges (Chapter 5). Regarding effect traits, boundaries and edges showed a functional resemblance in terms of Q, whereas for CWM, functional resemblance of plant species was observed in inner-fields and edges, differing from those at boundaries. This finding highlights for the first time that although the increasing disturbance regime from boundaries to inner-field leads to the dominance of the same effect traits in inner-fields and edges, plants thriving at boundaries and edges can potentially provide similar ecosystem services since plant communities in those positions converge to a similar structure. The high level of functional redundancy in terms of Q of effect traits between the outer-field positions indicates that shifts in species assemblages, as well as species turnover, tells us little about functional shifts when trait redundancy is high.

Although landscape heterogeneity has been found to affect plant traits in Mediterranean agricultural fields (José-Maria et al., 2011), our results highlight that concurrent shifts in trait values along gradients of landscape heterogeneity will depend on a single trait (Chapter 5). This is in strong contrast to Guerrero et al. (2014), who found no influence of landscape heterogeneity on single trait values. However, they exclusively focused on inner-field positions, where decreasing plant diversity was a function of the impact of crop management and the lower probability of seed arrival from boundaries, leading to the community homogenization through trait filtering (Armengot et al., 2016). Our results demonstrate that landscape heterogeneity may buffer in-field management intensification, favours spill-over and filters the species pool by individual functional traits, thus supporting the landscape-moderated traits selection hypothesis (Tscharntke et al., 2012).

Response-effect trait framework: Implications for management and conservation

Intensification at field and landscape scale filters response traits that can correlate and overlap with effect traits (Chapter 5). Resulting trait syndromes are characterized by floral attributes that provide resources for pollinators (Ricou et al., 2014) and for a suite of traits that strongly provides a suitable habitat for biodiversity (Woodcock et al., 2005; Cardador et al., 2015). Although several studies have developed a response-effect trait framework throughout different trophic levels (Lavorel et al., 2013; Moretti et al., 2013; Storkey et al., 2013), the inclusion of landscape heterogeneity as a trait filter has been scarcely studied.

We highlight for the first time that while increasing configurational landscape heterogeneity is related to a suite of traits linked to the potential provision of resources for pollinators, increasing compositional landscape heterogeneity is related to the selection of a suite of traits linked to the provision of suitable habitats for biodiversity (Chapter 5). Besides, shifts in traits assemblages along field positions directly impact in these two ecosystem services. Starting from these results, we have proposed in this thesis a framework summarizing these functional linkages along different trophic levels within the agroecosystem. Using species traits to construct a response-effect trait framework is a promising method to understand ecosystem stability and ecosystem services provision.

Hitherto, most of the conservation measures in agricultural landscapes have been addressed to the application of agri-environment schemes aimed at increasing taxonomical diversity (Whittingham et al., 2007). However, the current shift of nature conservation trends from a management based on target species to that based on dynamic properties of ecosystems (Bengtsson et al., 2003), needs an appropriate knowledge of the functional characteristics of plant communities since the enhancement of species diversity does not imply an increase in associated services. Our framework is addressed to fill this gap after disentangling how agricultural intensification modulates the functional structure of arable plant communities at field and landscape scale.

Boundaries and the increasing configurational landscape heterogeneity are linked to the selection of a trait syndrome related to the potentiality of providing resources for pollinators (Chapter 5). These elements favour a greater floral diversity that enhances the abundance and richness of prominent ecosystem service-providers such as bees (Kohler et al., 2007), bumblebees and hoverflies (Holland et al., 2015), suggesting a positive plant-plant interaction in community assembly (Rae et al., 2006). Thus, the maintenance of fields with complex shapes instead of land consolidation processes, as well as the implementation of agro-environmental schemes based on the limitation of the management intensity in field edges are expected to positively affect, not only the species diversity of plants and particularly rare arable plants (Chapter 4), but also the selection of plant traits to which pollinators may underpin. On the other hand, regarding the provision of suitable habitat for biodiversity, we populate the use of this framework aimed at enhancing predator insects and birds' populations (Chapter 5). However, it will be required to focus on the target organisms and its ecological requirements to maximize the effectiveness of the conservation measures.

Metodological remarks

Results of our work show that additive partitioning of diversity method is a useful tool for analysing diversity at different spatial scales (Chapters 3 and 4) (Allan, 1975; Lande, 1996). In fact it has been recently showed that this method is able to reveal spatial patterns of plant diversity (see Wagner et al., 2000; Gering et al., 2003; Chandy et al., 2006; Gabriel et al., 2006; Clough et al., 2007; Klimek et al., 2008; Armengot et al., 2012). Despite Baselga (2010) suggested to use Whittaker's multiplicative β-diversity since the components in which can be decompounded are independent, additive partitioning further allows the partitioning of diversity on an unlimited number of scales, the components are expressed in the same units (Wagner et al., 2000) and it can be used with the functional diversity measure of Rao's quadratic entropy index (Q) (De Bello et al., 2009) (Chapter 3).

The trait-based approach applied in this work has allowed us to identify functional groups of plants and the attributes that promote their success at different levels of agricultural intensification at different spatial scales. Furthermore, it provides additional support to the usefulness of the functional perspective in the identification of the assembly rule of plant communities (Storkey, 2006; Fried et al., 2009) and the intrinsic factors linked to the provision of ecosystem services (Lavorel et al., 2013; Wood et al., 2015).

Hitherto, many studies have identified traits related to the success of plant species due to agricultural intensification at different spatial scales (José-María et al., 2011; Fried et al., 2012; Juárez-Escario et al., 2013; Guerrero et al., 2014; Hernández Plaza et al., 2015; Armengot et al., 2016; Juárez-Escario et al., 2016). Although the latter studies have attempted to explain the success of plant species by using functional traits, it is widely accepted that there is not a universal profile of traits that define the success of plants, but rather it depends on the ecological constraints and characteristic of the study sites (Lloret et al., 2005, Storkey et al., 2013; Juárez-Escario et al., 2016). Accordingly, the selection of the correct traits candidates when we are aimed at disentangling how shifts in functional traits are expected to affect the delivery of ecosystem services of plant species to other trophic levels is crucial to avoid biased conclusions (Lavorel et al., 2013), as we have also proved (Chapters 3 and 5). In this work, we have selected those traits related to disturbance – response traits- and those related to specific ecosystem services' delivery –effect traits-. The robustness of the selected traits to achieve the objectives of our study relies on the fact that similar results have been obtained after carrying out similar analyses at different levels of agricultural intensification along different spatial scales throughout the chapters of this thesis.

On the other hand, this study shows the importance of taking into account different indexes when biodiversity is assessed (Chapters 3, 4 and 5). This consideration is needed not only in terms of species diversity (Chapter 4), but also in terms of functional diversity (Chapters 3 and 5), otherwise misinterpretation of the results may raise. For example, the turnover of plant species at different spatial scales and the concurrent low shift in terms of functional diversity, reflect the replacement of species by other with similar traits, thus suggesting a high level of redundancy. The misinterpretation of the results may lead to erroneous management with negative consequences on ecosystems when these management measures are addressed at conservation, both in terms of species and ecosystem functionality.

MAIN CONCLUSIONS OF THE THESIS

The characterization of plant assemblages, species richness and diversity as well as functional diversity of the plant communities in landscapes dominated by agriculture in the Mediterranean area highlights the high levels of diversity hosted in such communities compared to those of northern and central Europe. Agricultural intensification from the field up to the surrounding landscape scale helps to explain the different trajectories of such plant communities at different spatial scales. Most of the species richness and diversity as well as functional diversity values are hosted at low agricultural intensification. Changes on species assemblages along the gradient of intensification lead to different functional groups that are expected to affect the provision of ecosystem services. The results obtained in this thesis provide new and original reasons for supporting elements at low agricultural intensification in Mediterranean agricultural landscapes and illustrate the usefulness of functional trait approaches in unravelling plant assemblages rules and to develop measures for preventing and controlling the loss of ecological functions.

The main conclusions of the study are:

1. The structural indicators used to characterize arable field boundaries –width, slope, percentage of cover of perennial species, presence of stone-walls- constrain the hosted plant communities. Up to five different types of boundaries are described regarding these indicators.

2. Plant assemblages of the arable communities thriving in the structurally most simplified boundaries (flat, narrow, scarcely perennial species, absence of stone-wall) are similar to the species assemblages in their respective inner-fields. Particularly, this similarity is corroborated in terms of the abundance of the most harmful weeds.

3. In an agricultural landscape mosaic, up to three levels of agricultural intensification are identified in several habitats, namely: low (abandoned fields, boundaries, road-verges), medium (alfalfa edges and inner-fields) and high (cereal edges and inner-fields). This intensification gradient highlights significant dissimilarities in terms of species assemblages among such levels.

4. Habitats within each level of agricultural intensification host plant communities with similar species assemblages. Such similarity is higher within habitats located in the far ends of the gradient of such intensification (Low against High).

5. Among the three positions considered within an arable field, boundaries most contribute to the species richness and diversity of the total species, whereas edges most contribute to the species richness and diversity of rare arable plants.

6. Compositional landscape heterogeneity (percentage of natural vegetation) affects positively to the species richness and diversity of both total species and rare arable plants. The highest effect for the total species is accounted in boundaries and it decreases towards the inner-fields, whereas for rare arable plants the highest effect is accounted in field edges.

7. Configurational landscape heterogeneity (perimeter-area ratio of arable fields) exclusively affects rare arable plants, being the effect positive on their species richness but negative on their diversity. The contrast between species richness and diversity highlights the dominance of few species in their pool.

8. The study of plant communities both among landscapes at regional scale (La Noguera, La Segarra, el Pallars Jussà) and among habitats within a local landscape (Ager Valley) highlights a similar contribution of the beta-diversity components. Such contribution reaches around three quarter parts of the total species richness and diversity.

9. The species turnover between spatial scales does not imply a functional turnover. Thus, species divergence is concurrent to functional convergence.

10. The gradient of intensification defined in two scenarios such as the different habitats within a local landscape (Ager) or among the field positions in the arable fields of the agricultural landscape of three regions (La Noguera, La Segarra and El Pallars Jussà) selects the same type of functional groups. The most heterogeneous functional groups are enhanced at low agricultural intensification. This pattern is observed both for response and for effect traits.

11. The gradient of intensification along three field positions in an arable field (low at boundaries, medium in edges and high in inner-fields) entails changes in the functional traits of the species in such positions. Shift in these traits lead to changes on the potential provisioning of resources for pollinators and the provision of suitable habitat for biodiversity. On the other hand, regarding landscape heterogeneity, compositional heterogeneity (percentage of natural vegetation) constrains shifts in traits linked to the provisioning of suitable habitats for biodiversity, whereas configurational heterogeneity (perimeter-area ratio of arable patches) constrains shifts in traits linked to the provisioning of resources for pollinators.

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