Doctoral thesis

Yésica de los Ángeles Pallavicini Fernández

Effect of agricultural intensification on taxonomic and functional diversity of weed communities in cereal fields

Córdoba, November, 2015

TITULO: *Efecto de la complejidad del paisaje sobre la biodiversidad y servicios eco-sistémicos de la flora arvense en cultivos de cereales de secano.*

AUTOR: *Yésica de los Ángeles Pallavicini Fernández*

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Campus de Rabanales
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TESIS DOCTORAL

Effect of agricultural intensification on taxonomic and functional diversity of weed communities in cereal fields

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Yésica de los Ángeles Pallavicini Fernández

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Directores de Tesis

Fdo: José Luis González Andújar

Fdo: Fernando Bastida Milián

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TÍTULO DE LA TESIS:

Effect of Agricultural Intensification on taxonomic and functional diversity of weed communities in cereal fields

DOCTORANDO: Yésica de los Ángeles Pallavicini Fernández

INFORME RAZONADO DE LOS DIRECTORES DE LA TESIS

(se hará mención a la evolución y desarrollo de la tesis, así como a trabajos y publicaciones derivados de la misma).

El Dr. D. José Luis González Andújar, Investigador Científico del Departamento de Protección de Cultivos del Instituto de Agricultura Sostenible (CSIC), y el Prof. Dr. D. Fernando Bastida Milian, Profesor Titular del Departamento de Ciencias Agroforestales, Universidad de Huelva

Informan:

Que el trabajo que lleva por título "*Effect of Agricultural Intensification on taxonomic and functional diversity of weed communities in cereal fields*" ha sido realizado, bajo nuestra supervisión, por la Ingeniera Agronóma D^a. Yesica Pallavicini Fernández, y consideramos que reúne los méritos para optar al grado de Doctor.

La presente tesis aborda un tema de máxima actualidad científica y social como es el estudio de la biodiversidad en sistemas agrícolas. Especialmente relevante para la agricultura y, específicamente, para la protección de los cultivos. En este sentido, existen muy pocos estudios que aborden el efecto de la intensificación experimentada por la agricultura en las últimas décadas sobre las comunidades de malas hierbas. Dentro de este contexto, la presente tesis presenta una aproximación original al estudio de los factores que afectan a la diversidad funcional y taxonómica de las malezas. Su desarrollo ha sido complementado con un programa de formación de la doctoranda que ha incluido estancias en el Institut National de la Recherche

Agronomique (INRA, Dijon) (Francia) y en el prestigioso centro de investigación Rothamsted Research (Gran Bretaña), así como, diversos cursos de especialización nacionales e internacionales.

Que dicha Tesis Doctoral se va a presentar como un compendio de capítulos donde se recogen lo objetivos perseguidos y ha dado lugar diferentes contribuciones.

Publicaciones

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Por todo ello, se autoriza la presentación de la tesis doctoral.

Córdoba, 7 de Noviembre de 2015

Firma de los directores

Dr. José Luis González Andújar

Prof. Fernando Bastida Milian

TÍTULO DE LA TESIS:
Effect of agricultural Intensification on taxonomic and functional diversity of weed communities in cereal fields.

DOCTORANDA: Yésica de los Ángeles Pallavicini Fernández

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(Ratificando el informe favorable del director. Sólo cuando el director no pertenezca a la Universidad de Córdoba).

Dr. Enrique Vargas Osuna, Profesor Titular de la Universidad de Córdoba, perteneciente al Departamento de Ciencias y Recursos Agrícolas y Forestales y responsable de la línea de investigación "Relaciones Planta-Insecto", ratifica el informe presentado por los directores de la presente Tesis Doctoral: Dr. José Luis González Andújar, Investigador Científico del Departamento de Protección de Cultivos del Instituto de Agricultura Sostenible (CSIC) de Córdoba, quien está adscrito como investigador ajeno a la Universidad de Córdoba a la mencionada línea de investigación, y Dr. Fernando Bastida Milián, Profesor Titular del Departamento de Ciencias Agroforestales de la Universidad de Huelva.

Dicha Tesis Doctoral se va a presentar como compendio de capítulos donde se recogen los objetivos perseguidos, la metodología utilizada y los resultados obtenidos y cumple con los requisitos de indicios de calidad (Artículo 25 de la Norma Reguladora de los Estudios de Doctorado, propuesta por la Comisión de Másteres y Doctorado de 14 de Diciembre de 2011 y aprobada por el Consejo de Gobierno de 21 de Diciembre de 2011). En cumplimiento con este artículo se presenta la internacionalización de la tesis doctoral como indicios de calidad.

Por todo ello, se autoriza la presentación de la tesis doctoral.

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Fdo.: Dr. Enrique Vargas Osuna

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CSIC
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INSTITUTO DE AGRICULTURA SOSTENIBLE IAS

Universidad de Huelva

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Supervisors:

Dr. José Luis González Andújar

Dr. Fernando Bastida Milián

Tutor:

Dr. Enrique Vargas Osuna

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To my beloved family

Nancy, Ermes, Noelia and Chuchi

¡Qué pequeña eres, brizna de hierba!
Sí, pero tengo toda la tierra a mis pies.
Rabindranath Tagore

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ABSTRACT

Agricultural intensification at field and landscape scales has lead to a dramatic decline of weed diversity in cereal crops during the last few decades across Europe. Intensification at the field scale is related to the increasing of external inputs (e.g. fertilizers and pesticides). At the landscape scale, agricultural intensification is associated to a decrease in landscape complexity, because of the increasing proportion of arable land at the expense of natural or semi-natural habitats. Research on the response of weed diversity to agricultural intensification has been mostly focused on taxonomy (e.g. number of species). However, intensification may also impact the functional diversity of weed communities. Functional traits (e.g. life form, seed mass, pollination type) are key components of diversity that, to date, have received little attention. In this context, the general goal of the present thesis was to study the impact of agriculture intensification at field and at landscape scale on the taxonomic diversity, functional diversity and the distribution of functional traits of weed communities in cereal crops systems under conventional management. The overall structure of this thesis is composed of six chapters; the first, fifth and sixth correspond to the general introduction, general discussion and general conclusions respectively, while chapters II, III and IV correspond to three researching studies. Chapter II is focused on the plant communities inhabiting field margins and attemps to assess the effect of margin width and landscape complexity on plant diversity. Chapter III aims to compare the effects of intensification on weed diversity inside crop fields in climatically and floristically contrasting countries, UK and Spain. Finally, chapter IV is devoted

to study the effects of intensification on weed seed bank diversity in cereal fields in two Mediterranean regions of Spain, Andalusia and Catalonia. The most striking results emerging were that field margin width positively influenced species richness and functional diversity of species inhabiting field margins (Chapter II). Taxonomic diversity was similar at the edge and at the centre of fields, indicating that intensity of crop management is homogeneous throughout the entire field (Chapter III and IV). In addition, crop management also impacted beyond the cropped area affecting the diversity of plants inhabiting field margins (Chapter IV). The three studies showed that functional diversity was extremely low in the cereal systems studied probably as a consequence of the long-term filtering effect of conventional agriculture (Chapter II, III and IV). Mean functional trait values were remarkably similar among different components of weed communities that were analysed along the three studies, indicating that these communities are highly adapted to the recurrent, predictable disturbance regime imposed by the cereal crop system. Most common functional traits were related to a high reproductive capacity, self dispersal mechanisms and reproductive phenology allowing to escape crop management practices (Chapter II, III and IV). The landscape context affected neither taxonomic diversity nor functional diversity nor distribution of functional traits of cereal weed communities. The content developed in this doctoral thesis represents an original approach and aim to contribute to understanding the extent to which current intensified agriculture shapes weed diversity in dryland cereal crops.

Keywords: Functional traits, landscape complexity, species richness, conventional agriculture, Rao´s quadratic entropy index.

RESUMEN

La intensificación agrícola es un proceso que ocurre a escala de campo y de paisaje que constituye una de las causas principales de la drástica disminución de la diversidad de especies arvenses observada en los cultivos cerealistas europeos a lo largo de las últimas décadas. A nivel de campo, la intensificación está relacionada con el creciente uso de agroquímicos (por ejemplo, fertilizantes y pesticidas). A escala de paisaje, la intensificación agrícola ha determinado una disminución de la complejidad del paisaje, debido al aumento de la proporción de tierras de cultivo a expensas de los hábitats naturales o seminaturales. La mayoría de los estudios acerca del efecto de la intensificación agrícola sobre la diversidad de especies arvenses se ha centrado en un enfoque taxonómico (por ejemplo el número de especies). Sin embargo, la intensificación también puede afectar la diversidad funcional y/o los rasgos funcionales (por ejemplo, las formas de vida, el peso de semillas, el tipo de polinización) de las comunidades arvenses; los cuales son componentes clave de la diversidad y que, hasta la fecha, han sido poco estudiados. En este contexto, el objetivo de la presente tesis fue analizar el impacto de la intensificación agrícola a nivel de campo y de paisaje sobre la diversidad taxonómica, la diversidad funcional y la distribución de los rasgos funcionales de las especies de plantas asociadas a los cultivos cerealistas de secano bajo manejo convencional. La estructura general de esta tesis comprende seis capítulos; el primero, quinto y sexto corresponden a la introducción general, la discusión general y las conclusiones generales, respectivamente, mientras que los capítulos II, III y IV corresponden a tres trabajos de investigación. El trabajo

que se presenta en el capítulo II se centra en las comunidades de plantas que habitan los márgenes de cultivos y evaluó el efecto de la anchura del margen y la complejidad del paisaje sobre la diversidad vegetal. El capítulo III presenta un trabajo de comparación de los efectos de la intensificación sobre la diversidad de especies arvenses en dos países de clima contrastante: el Reino Unido y España. Por último, el trabajo expuesto en el capítulo IV compara los efectos de la intensificación sobre la diversidad del banco de semillas en cultivos cerealistas de dos regiones mediterráneas españolas; Andalucía y Cataluña. Entre los resultados más llamativos se encontró que tanto la riqueza como la diversidad funcional de las especies de los márgenes de cultivos aumentaron con la anchura del margen (capítulo II). La diversidad taxonómica fue similar en el borde y en el centro de los campo de cultivo, lo que sugiere que la intensidad del manejo es homogénea en todo el campo (capítulo III y IV). Además, el manejo del cultivo también afecta a la diversidad de plantas que habitan en los márgenes de campo (capítulo IV). Los tres estudios abordados mostraron siempre una diversidad funcional extremadamente baja, probablemente debido al efecto de filtrado a largo plazo producido por la agricultura convencional (capítulo II, III y IV). Los valores medios de los caracteres funcionales fueron notablemente similares entre los diferentes componentes de la diversidad estudiados a lo largo de la investigación, e indicaron que las comunidades de arvenses están adaptadas a las perturbaciones recurrentes características del sistema de cultivo. Los caracteres funcionales mas comunes se relacionaron con una elevada capacidad

reproductiva, un modo de dispersión autócora y una fenología reproductiva que permite eludir los daños causados por las prácticas agrícolas (Capítulo II, III y IV). El contexto paisajístico no afectó la diversidad taxonómica ni funcional, ni la distribución de los rasgos funcionales en ningún caso. El contenido desarrollado en esta tesis doctoral representa un enfoque original que intenta contribuir a la comprensión de la medida en que la intensificación agrícola modela los diferentes aspectos de la diversidad de las plantas arvenses.

Palabras claves: Rasgos funcionales, complejidad de paisaje, riqueza de species, agricultura convencional, Índice de entropía cuadrática de Rao.

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Chapter I

GENERAL INTRODUCTION AND OBJECTIVES

GENERAL INTRODUCTION

I.1 IMPORTANCE OF CEREAL CROPS

Agriculture is an essential activity aimed to produce food and raw material to maintain human well-being. Among all crops, cereals are crucial for human nutrition since they are an important source of carbohydrates, fats, proteins and vitamins (Sarwar *et al.*, 2013). For this reason, land under cereal production is one of the major land-use types in the world (Bruinsma, 2003). In Spain, the area devoted to cereal cropping is currently 6.3 million hectares which yield 22 thousand tons per year (Figure 1, MAGRAMA, 2012). In the last decades, there have been a decreasing tendency of cereal land area as a result of unprecedented declining in cereal world prices and an increase of production cost; especially fertilizers (MAGRAMA, 2012). Nevertheless, cereals are still the dominant crops in Spain.

I.2 WEEDS, AN OVERVIEW

A weed has been simply defined as"a*ny plant growing in a field other than the crop*" (Pujadas Salvà and Hernández Bermejo, 1988; Radosevich *et al.*, 2007). These plants have traditionally been considered an important economic pest because they can compete with the crop for water, nutrients and light thus constraining crop yield and reducing its quality (Radosevich *et al.*, 2007). A large number of taxonomically diverse plant species behave as a crop weeds with families such as *Poaceae*, *Asteraceae*, *Brassicaceae*, *Apiaceae* being predominant in the weed flora (Figure 2, Hidalgo *et al.*, 1990). In Mediterranean cereal systems, species such as *Lolium rigidum* Gaudin, *Avena sterilis* L. and *Phalaris spp.* are among the most problematic weeds because of competition with the crop and because they are difficult to control (González-Andújar and Saavedra, 2003). Weeds show biological characteristics that allow them to thrive in regularly disturbed environments such as short life cycle, frequent self pollination, high reproductive capacity, seed dormancy, growth and phenological plasticity; non-specific pollination vectors etc. (Grime, 1977, Inderjit, 2004).

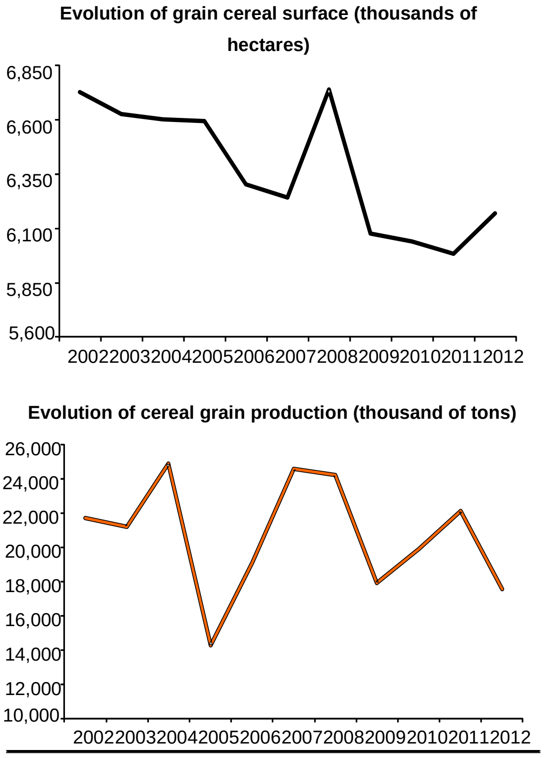

Figure 1. Evolution of total area and total yield of winter cereals in Spain from 2002 to 2012 (MAGRAMA, 2012).

Because of the negative impact on crop production or quality of most weeds, much effort has been devoted to weed control. In fact, chemical weed control is one of the most expensive and time consuming aspects of crop protection; for instance in Spain it represents currently 34% of pesticide market (AEPLA, 2013).

However, weeds play a crucial role in biodiversity conservation and agro-ecosystem functioning as they provide several agronomic and ecosystem services. Weeds help recycling of nutrients, prevent soil erosion and contribute to remotion of noxious chemicals (Altieri, 1999). Moreover, weeds provide a range of resources to support taxa of higher trophic levels, e.g. leaves, stems and fruits may be eaten by herbivores, whereas pollen and nectar provide resources for pollinating insects. Furthermore, plants provide cover and reproduction sites for a number of animals (Marshall *et al.*, 2003; Storkey and Westbury, 2007). Several species considered as noxious weeds such as *Avena fatua* L, C*henopodium album* L., *Cirsium arvense* (L.) Scop., *Fumaria officinalis* L., *Galium aparine* L., *Papaver rhoeas* L., *Poa annua* L., *Polygonum aviculare* L., *Sonchus oleraceus* L., among others, also host many phytophagous insects, being most of them beneficial or neutral species (Marshall *et al.*, 2003), being some of them important or present in birds diet (Marshall *et al.*, 2003).

Given that food production and security is a priority for sustaining humanity, a remarkable research effort has been traditionally focused on weed control (Sharma and Gauttam, 2014). However, the role of weeds in supporting biodiversity is being increasingly acknowledged, so the number of studies focusing on weed diversity has also been steadily increasing during the last decades (Marshall *et al.*, 2003; Storkey *et al.*, 2013). These studies showed that weed diversity has dramatically declined during the last few decades and agricultural intensification has been identified as a major cause.

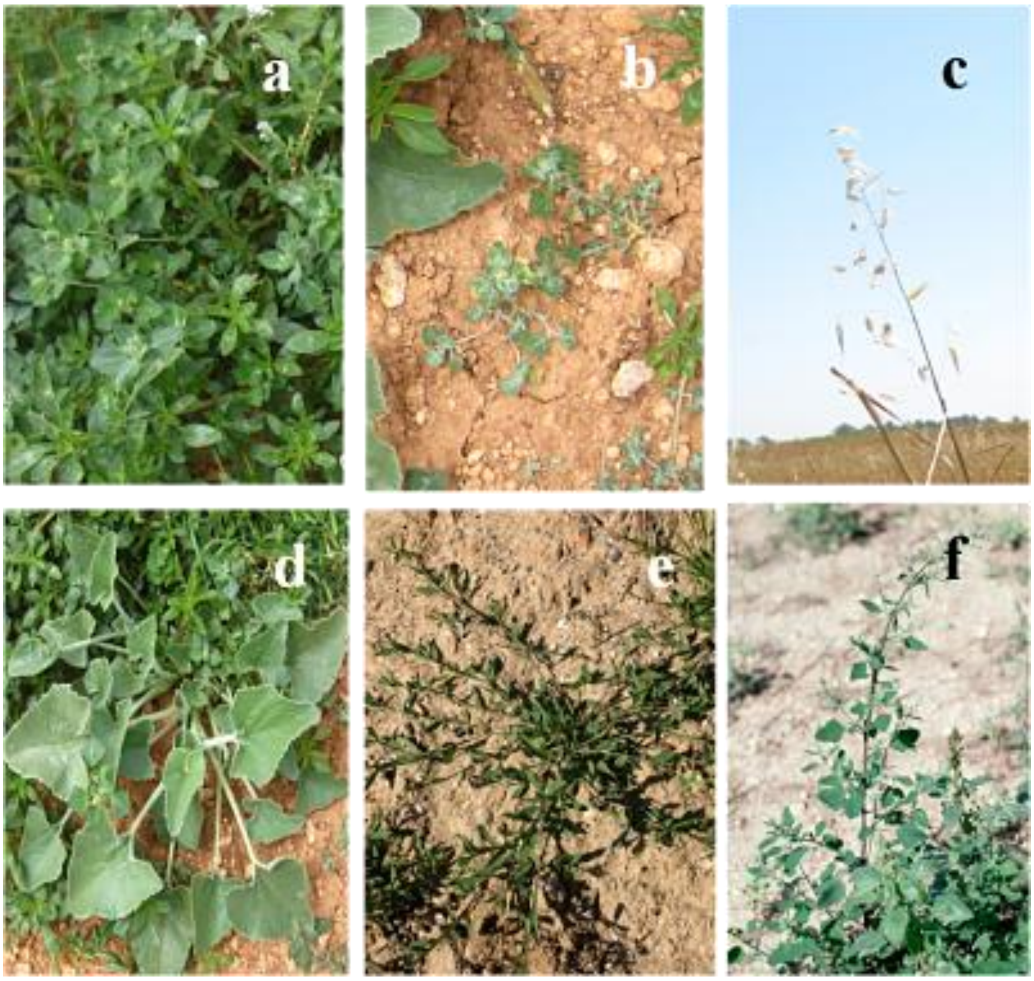

Figure 2. Some common weed species. a) *Amaranthus blitoides* S. Watson, b) *Chenopodium vulvaria* L., c) *Avena sterilis* L., d) *Ecballium elaterium* (L.) A. Rich., e) *Polygonum aviculare* L., f) *Chenopodium album* L.

I.3 AGRICULTURAL INTENSIFICATION AT THE FIELD SCALE

New farming technologies have been developed and widely applied since the "Green Revolution" in the 1960´s allowing significant yield increases on roughly the same amount of land. These technologies included new synthetic fertilizers, herbicides and pesticides, the development of high yielding cereal cultivars, improved methods of seed cleaning, among others. The development of synthetic fertilizers made possible to supply crops with extra nutrients and therefore, increase yield (Figure 3). Synthetic herbicides and pesticides controlled weeds, insects, and prevented diseases, which also resulted in higher crop productivity (Matson *et al.*, 1997).

Agricultural intensification is related to an increasing use of these farming technologies in space and time (known as "conventional agriculture", Krebs *et al.*, 1999; Stoate *et al.*, 2001; Benton *et al.*, 2003; Storkey *et al.*, 2011). One of the most striking negative effects of agricultural intensification is the global declining of biodiversity in the agricultural landscapes (Krebs *et al.*, 1999). Diversity of plants, among other organismshas sharply declined in many countries including Germany (Albrecht, 1995), Finland (Erviö and Salonen, 1987), Denmark (Andreasen *et al.*, 1996), France (Fried *et al.*, 2009), United Kingdom (Robinson and Sutherland, 2002), Argentina (de la Fuente *et al.*, 2006) or Spain (Romero *et al.*, 2008; Cirujeda *et al.*, 2011). Herbicides have a direct impact on weed diversity. Furthermore, the continued reliance on herbicides has selected for resistant populations of steadily increasing number of weed species including the Mediterranan cereal weeds *L. rigidum* and *A. sterilis* (Heap, 2014) creating additional weed control problems. Fertilizers have an indirect impact on plant diversity (Kleijn and van der Voort, 1997; Stoate *et al.*, 2001; Kleijn *et al.*, 2009). They not only increase crop vigour promoting an effective competition of the crop against weeds, but also promote competitive weeds, which in turn, exclude less competitive species (Kleijn and van der Voort, 1997; Stoate *et al.*, 2001; Begon *et al.*, 2006; Stoate *et al.*, 2009).

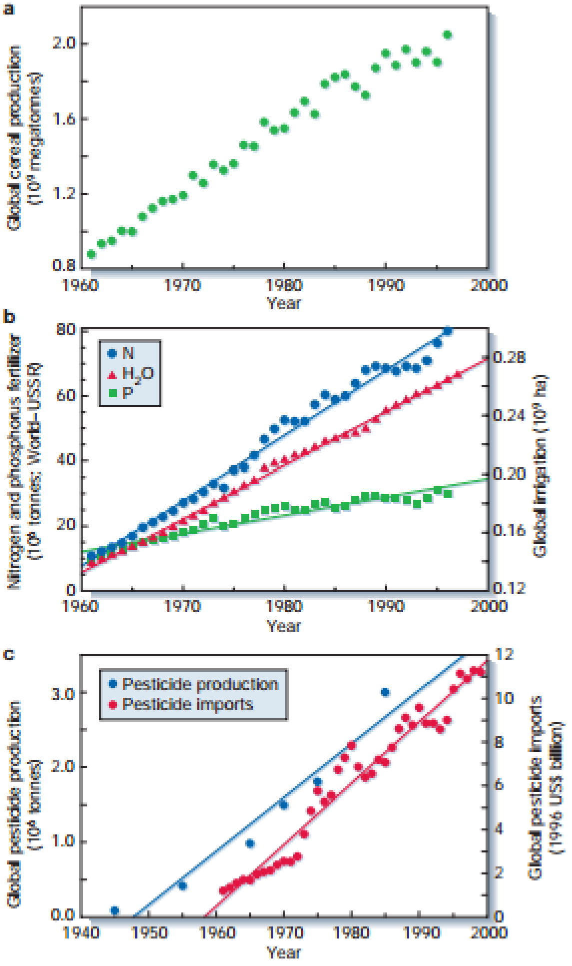

Figure 3. Agricultural trends over the past 40 years. **a**, Total global cereal production, **b**, total global use of nitrogen and phosphorus fertilizers (except former USSR not included) and area of global irrigated land; **c**, total global pesticide production and global pesticide imports (summed across all countries). Source: Tilman *et al.* (2002).

The impact of crop management practices is not homogeneous throughout the field, rather it tends to be lower at field edges (firsts drill rows) compared to the field centre (Figure 4) where soil cultivation, fertilizers and herbicides are more efficiently applied (Romero *et al.*, 2008; Fried *et al.*, 2009). Thus, the edge weed communities may reflect conditions across the whole field prior to intensification, harbouring higher number of species than the field centre, including species with conservation value (Marshall, 1989; Romero *et al.*, 2008; Fried *et al.*, 2009; Poggio *et al.*, 2010; José-María and Sans, 2011).

A field margin, i.e. the uncropped vegetation strip next to the cropped part of a field (Figure 4), is an intrinsic part of the crop field usually used to separate contiguous fields from different owners or different land-uses (Marshall and Moonen, 2002). Plant diversity in field margins may indirectly be affected by adjacent crop management practices. Conversely, field margins may act as a seed source for the cropped field, contributing to increase species richness, especially at the field edges (Marshall, 1989; Romero *et al.*, 2008).

Figure 4. Representation of the different positions in the field; margin (uncropped vegetation strip next to the field crop), edge (firsts meters within the field crop), and centre. The impact of the crop management practices increases from the margin towards the centre of the field

I.4 AGRICULTURAL INTENSIFICATION AT THE LANDSCAPE SCALE

Agricultural intensification at the landscape scale is associated with the increase in size and number of intensively managed crop fields at the expense of (semi)natural habitats and field margins (Figure 5, Benton *et al.*, 2003;

Baessler and Klotz, 2006; Aparicio, 2008). The predominance of crop field in the landscape might negatively impact field diversity because the loss of non-cropped habitats (Figure 5) may suppress seed sources for adjacent fields, which potentially could counteract the effect of intensive crop management (Gabriel *et al.*, 2005; Roschewitz *et al.*, 2005). However, reported effects of landscape complexity on diversity are inconsistent; while some authors found that weed diversity increased with landscape complexity (Gabriel *et al.*, 2005; Roschewitz *et al.*, 2005; José-María *et al.*, 2010; Poggio *et al.*, 2010), other studies have found no such effect (Marshall, 2009; Gaba *et al.*, 2010; Jonason *et al.*, 2011). Indeed, some studies found that the effect of landscape complexity depends on the position in the field, being highest at the field margins, medium at the field edge and negligible at the field centre (José-María *et al.*, 2010; Solé-Senan *et al.*, 2014). These differences have been attributed to crop management practices, which are more intense at the field centre, thus hindering the effect of landscape complexity (José-María *et al.*, 2010; Armengot *et al.*, 2011).

I.5 MEASURING DIVERSITY

I.5.1 Taxonomic diversity

Agriculture intensification has been shown to negatively impact different aspects of weed diversity; the number of species and their abundance. Diversity can be measured by different indices such as:

-Species richness (S) is understood as the number of species in a community and it is completely insensitive to species abundance (Magurran, 2004).

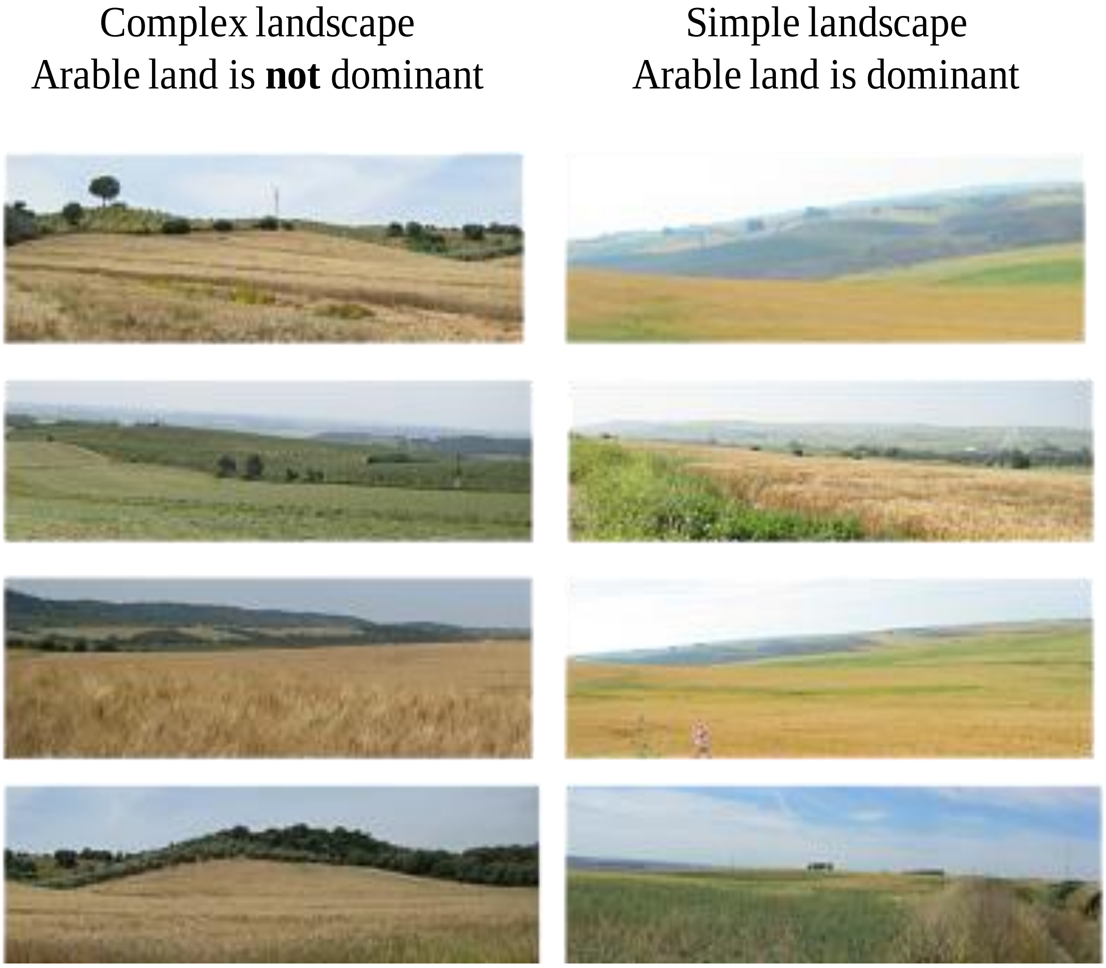

Figure 5. Panoramic views of the landscape surrounding eight of the sampled cereal fields. More complex landscapes (left column) and simpler landscapes (right column) are shown. Complex landscapes are composed of different land-use types, in these pictures, olive orchards and forest. Simple landscapes are dominated by arable land.

-Shannon-Weaver index (H´) is the most commonly used index in ecological studies. This index weights all species in a community by their abundance, without favouring either common or rare species (Magurran, 2004). Although this is used as a diversity index, formally it is a measure of entropy. It is denoted as

$$H' = -\sum_{i=1}^{S} p_i \cdot \ln(p_i)$$

where p_i is the proportion of individuals belonging to the i_{th} species and ln is the natural logarithm of p_i. However, other logarithm bases can also be used leading to different measurement units of H´; digits (bits), decimal digits (decits) and natural digits (nats), for the bases 2, 10 and natural, respectively. H´ values range between 0 and 5; communities with H´= 5 are highly diverse. As it is an entropy index, the interpretation and comparison among communities is difficult. Transforming entropy into *effective number of species*, (i.e. the number of equally-common species) eases the interpretation and comparison of diversity among communities. This transformation is the **exponential of Shannon-Weaver (eH';** Jost, 2006**)** and it is used in the following chapters.

-Evenness measures the regularity of species abundance in a community, the most common index is the Pielou's evenness index (J) and its calculation includes S and H´. Its values range between 0 and 1 with 1 being complete even community (Magurran, 2004). It is denoted as

$$J = \frac{H'}{\ln(S)}$$

Where *H´* is the Shannon-Weaver index and ln(*S*) is the natural logarithm of species richness.

I.5.2 Functional traits

Weed species loss and abundance reductions as a consequence of agriculture intensification are not random, but rather species with *functional traits* poorly adapted to the new set of agricultural practices are selectively filtered out.

-Functional traits are defined as any morphological, physiological or phenological feature measurable at the individual level (Garnier and Navas, 2012). Functional traits have shown to respond to environmental drivers including intensification. Plants possessing trait combinations allowing them to overcome the new conditions are likely to remain while species with maladapted traits are likely to reduce their abundance or even disappear (Garnier and Navas, 2012; Gaba *et al.*, 2014).

Several plant functional traits appear to be particularly responsive to agricultural intensification, namely plant height, seed mass, flowering timing, flowering duration, Raunkiaer's life forms, growth form, pollination type and dispersal type (Westoby, 1998; McIntyre *et al.*, 1999; Storkey *et al.*, 2010; Gaba *et al.*, 2014; Guerrero *et al.*, 2014; Pinke and Gunton, 2014).

-Plant height is related to the ability to compete for light; taller plants are better competitors because they have a greater light and water acquisition (Gaba *et al.*, 2014; Storkey *et al.*, 2015). It is also related to regeneration time after disturbance with short plants regenerating faster (Westoby, 1998).

-Seed mass is related to plant fecundity; there is a trade-off between production of numerous small seeds vs. fewer larger seeds per carbon unit. A higher amount of light seeds in soil increases the chances to recover after disturbance and they can be self-buried in soil cracks avoiding seed predation (Westoby, 1998). Heavy seeds have the advantage of higher seedling survival in competitive environments because they have more energy reserves (Westoby, 1998).

-Flowering timing and **Flowering duration** are functional traits related to the ability to reproduce under the disturbance regime imposed by management practices (Fried *et al.*, 2012; Pakeman and Eastwood, 2013).

-Raunkiaer´s life form carries information on the type of disturbance regime that a plant species is able to cope with (McIntyre *et al.*, 1999).

-Growth form (monocotyledons *vs*. dicotyledons) is related to plant architecture, resource acquisition and resistance to selective herbicides (Roschewitz *et al.*, 2005; Hawes *et al.*, 2010).

-Pollination type and **Dispersal type** are related to dispersal distances of pollen or seeds, and to reliance on animals for reproduction (Benvenuti, 2007).

I.5.3 Functional diversity

Loss of species with functional traits poorly adapted to agricultural intensification leads to a new community with a narrower range of trait values than the original community, i.e. showing lower *functional diversity* (Díaz and Cabido, 2001).

-Functional diversity can be defined as the value and range of the functional traits in a community (Díaz and Cabido, 2001). Functional diversity can be measured using several indices. Most of them have been developed during the past decade when the functional approach has gained research interest (Petchey and Gaston, 2002; Mason *et al.*, 2005; Pavoine *et al.*, 2005; Laliberté and Legendre, 2010). The indices may take into account only one trait at a time, or combine multiple functional traits. In addition, some indices take into account species abundance.

-Community weighted mean represents the mean values of a single trait in a community weighted by the relative abundance of the species carrying each trait value (Díaz *et al.*, 2007).

-Functional diversity based on dendrograms; is the total length of the branches of the dendrogram constructed from species traits where species in the community are on the top of the tree (Petchey and Gaston, 2002). This index does not take into account species abundance. A distance matrix of species x traits is constructed by hierarchical clustering the distance matrix. Functional diversity results may change depending on the method used to construct the distance matrix and the method used in the hierarchical cluster analysis (Mouchet *et al.*, 2008). These authors proposed the use of a combination of distance matrices and clustering techniques and then select the best set of methods using a cophenetic correlation coefficient.

Mason *et al*. (2005) and Villéger *et al*. (2008) stated that functional diversity have different aspects homologues to taxonomic diversity: Functional richness, Functional evenness and Functional divergence (Figure 6).

-Functional richness is calculated as a convex hull that determines a functional space in which all species in a community are contained. The perimeter of the Convex hull is delineated by the traits with extreme values. The higher the volume of the Convex hull, the greater the functional richness. This index does not take into account species abundance. Its disadvantage is that it is correlated to species richness (Figure 6; Villéger *et al.*, 2008).

-Functional evenness is the regularity with which the functional space is occupied by species weighted by their abundance (Mason *et al.*, 2005). It is calculated with a minimum spanning tree which links all the species in a functional space (Villéger *et al.*, 2008). It ranges between 0 and 1 and increases when abundance is evenly distributed among species and functional distances are regular (Figure 6; Villéger *et al.*, 2008). This index is independent from species richness.

-Functional divergence measures how abundance is distributed within the volume of the functional trait space. The first step is to determine the centroid of the convex hull and then calculate the mean distance of each species to the centroid. Functional divergence corresponds to the deviation of the distances of each species to the mean (Villéger *et al.*, 2008). It ranges between 0 and 1 and increases when abundant species have extreme functional trait values. This index is also independent from species richness (Figure 6, Villéger *et al.*, 2008).

-**Rao's quadratic entropy** is defined as the sum of the dissimilarities in the trait space among all possible pairs of species weighted by the product of relative species abundances (Botta‐Dukát, 2005). This index ranges between 0 and 1; with values near 1 indicating high functional diversity (i.e. high dissimilarities of functional trait values among species). It is denoted as

$$\mathrm{Rao} = \sum_{i=1}^{s}\sum_{j=1}^{s} dij\ pipj$$

where, s is the number of species, d_{ij} is the distance between species i and j, and p_i and p_j are the relative abundances of species i and j. Rao has some desirable properties: i) measures two important functional diversity properties in a single index: functional richness (the volume of niche space occupied by the species) and divergence (the distribution of abundance in the extremities of occupied trait space in community, Rao, 1982; Laliberté and Legendre, 2010; Mason *et al.*, 2013), ii) it can be calculated for both single traits and a combination of traits (Laliberté and Legendre, 2010), iii) it is independent from species richness (Laliberté and Legendre, 2010) and iv) it can be used to assess partitioning of functional diversity into alpha (within community diversity) and beta (among-communities) components (De Bello *et al.*, 2009).

I.6 WEED COMMUNITIES ASSOCIATED TO CROP FIELDS

It can be considered that a crop field has three different communities associated to different habitats that differ in structure, functions and are differentially sensitive to agriculture intensification: the communities inhabiting the field margins, the communities within the crop field and the seed bank communities of both habitats.

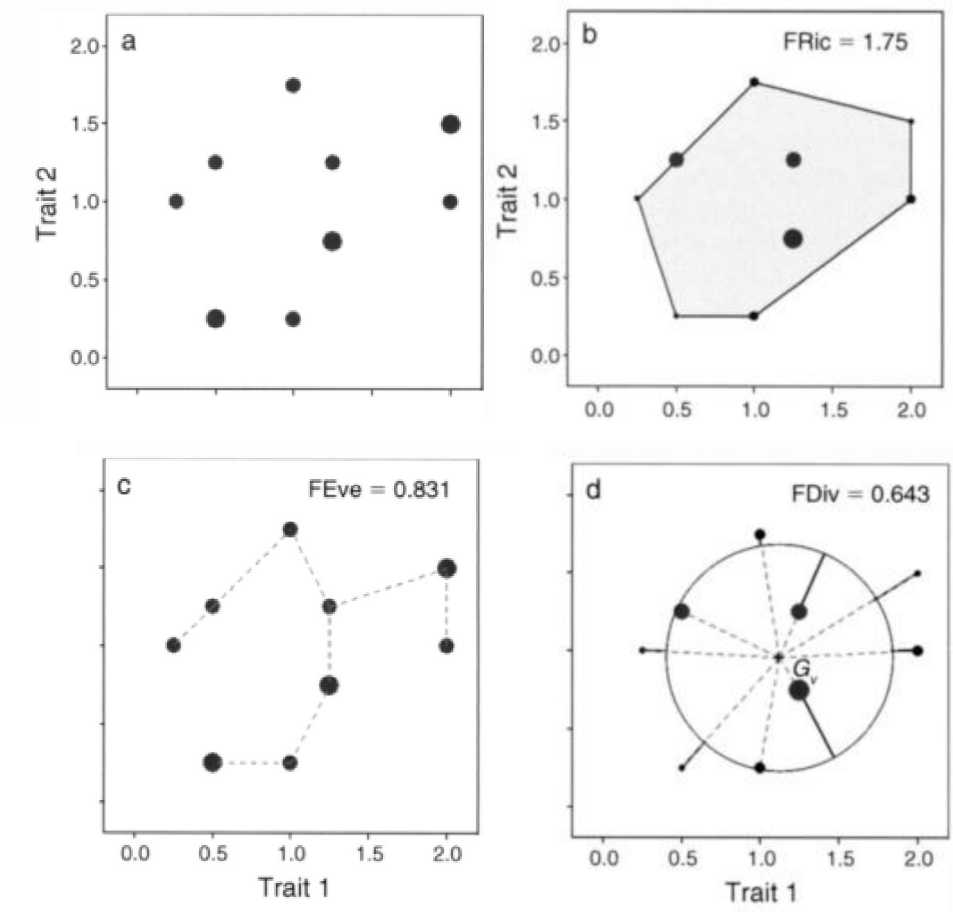

Figure 6. Representation of the three functional diversity indices: Functional richness (FRic), Functional evenness (FEve) and Functional divergence (FDiv). Two traits and nine species are considered. a) the points are plotted in the functional trait space according to their trait values; circle diameters are proportional to species abundances. b) The convex hull volume is drawn with a solid black line joining the points with extreme trait values and shaded in grey. The volume corresponds to FRic. c) The minimum spanning tree linking all the points in the functional trait space. FEve is the regularity of points along this tree and the regularity in their abundances. d) G*v* corresponds to the centroid of the functional trait space, the dashed lines represent the distance of each species to the centroid, the large circle represents the mean distance to the centroid and the black lines are the deviation of each species to the mean distance to the centroid. FDiv is the distance of species to the mean distance; the more abundant species are greater than the mean, the higher the functional divergence. Source: Villéger *et al.* (2008)

-Field margins are non-cropped areas adjacent to the crop field which have traditionally been used to delimit land ownership or separate fields with different land-uses (Marshall and Moonen, 2002). Field margins have often been perceived by farmers as useless areas because they are not productive and because may also host weeds potentially infesting the crop field (Cordeau *et al.*, 2011). However, vegetation of field margins have other useful agronomic functions such as stock fencing, windbreaking, weed and pest control barrier, crop pollination, human and machinery access etc. (Marshall and Moonen, 2002). In addition, field margins play important roles for environment and biodiversity conservation. For instance, field margins buffer pesticide drift preventing pollution of rivers (Cordeau *et al.*, 2011) and control soil erosion (Marshall and Moonen, 2002). Regarding biodiversity conservation, field margins often harbours a considerable higher number of species than the crop field (José-María *et al.*, 2010; Poggio *et al.*, 2010). These areas also offer food and shelter for many species from different taxa such as birds, mammals and insects (Marshall and Moonen, 2002; Vickery *et al.*, 2009).

Field margins largely differ in structure and composition depending on the local idiosyncrasy and conditions. Marshall and Moonen (2002) described field margins of England as a complex structure composed by a strip of herbaceous vegetation next to the crop field and a hedgerow composed of woody and shrubby species. Different temperate European countries including France, Netherland, UK or Belgium have recently implemented Agri-environmental schemes to manage field margins to enhance biodiversity and avoid water pollution from pesticides. These schemes propose a margin structure composed by a minimum of 4 m width herbaceous vegetation strip sowed with different plant mixtures or naturally regenerated (Kleijn *et al.*, 1998; De Cauwer *et al.*, 2008). In Spain, apart from ruderal vegetation and depending on management intensity and slope cereal field margins are also composed of

Mediterranean grassland and shrubby communities (Bassa *et al.*, 2011, 2012; Cirujeda *et al.*, 2015).

Plant diversity of field margins has been affected by agriculture intensification at field and at landscape scales. At field scale, intensification is reflected in the reduction of margin width, aimed to maximize the cropped area (Bassa *et al.*, 2012). Reducing the available area of the habitat has a direct negative effect on diversity (Kleijn *et al.*, 1998; Tarmi *et al.*, 2009; Bassa *et al.*, 2012). Furthermore, narrow margins are more negatively affected by herbicide drift or accidental tillage causing detriment to plant diversity (Schippers and Joenje, 2002; Bassa *et al.*, 2012). At the landscape scale, some studies reported a beneficial effect on diversity of a complex landscape structure surrounding the field margins (José-María *et al.*, 2010; Bassa *et al.*, 2012). However, other authors have found no such effects (Marshall, 2009).

Recent studies have attempted to relate the effect of agriculture intensification to the distribution of functional traits in weed communities. These studies showed a dominance of perennial and zoochorous species in wide margins within complex landscapes, while annual species were more associated to narrow margins within simple landscapes (Poggio *et al.*, 2010; Bassa *et al.*, 2011; José-María *et al.*, 2011).

Regarding functional diversity, to our knowledge there is only one study linking agricultural intensification and the functional diversity in field margins (Ma and Herzon, 2014). These authors found that functional diversity decreased in field margins adjacent to conventionally managed crop fields and also with landscape simplification.

-Established plant communities of crop fields have been the focus of most research effort on effects on agricultural practices on diversity. These established weed communities rapidly respond to environmental changes and management practices and thus they are good indicators of intensity of farming practices of the current year (Hawes *et al.*, 2010). In conventionally managed crops weed diversity is often higher at the field edges due to, as mentioned earlier, a lower efficiency of management practices (e.g. tillage) compared to the field centre (Marshall, 1989; Romero *et al.*, 2008; Fried *et al.*, 2009; Poggio *et al.*, 2010; José-María and Sans, 2011). In addition, field margins may serve as a seed source, contributing to enhancing plant diversity in field edges (Marshall, 1989).

Regarding functional traits, it has been reported that short stature, large seeds and late flowering conform a trait syndrome vulnerable to intensification (Storkey *et al.*, 2010). In contrast fast-growing, short-statured, early flowering plants producing small seeds are successful in more intensified sites (Fried *et al.*, 2012; Perronne *et al.*, 2015). Simple landscapes tend to favour anemogamous species because pollen can disperse further through wind in open spaces (José-María *et al.*, 2011), whereas in complex landscapes zoochorous species can be favoured because they promote animal activity (Poggio *et al.*, 2010).

It has also been shown that functional diversity decrease with intensification, indicating a strong environmental filtering imposed by intensive crop management practices (Pakeman, 2011; Guerrero *et al.*, 2014). However, landscape complexity appears to do not affect functional diversity (Guerrero *et al.*, 2014).

-The Seed bank is the soil reserve of viable seeds. It is annually replenished by seeds from established vegetation and from distant populations (Tamme *et al*., 2013). Seeds in the soil represent a compartment of the weed flora less sensitive to crop management practices than the established plants. Thus, the seed bank has the potential to restore diversity of the established vegetation. The seed bank flora is a good indicator of long-term intensification process (Hawes *et al.*, 2010; Pakeman and Eastwood, 2013). Taxonomic diversity of the seed bank has been shown to decline with intensification, although this effect seems to be attenuated at the field edges (Armengot *et al.*, 2011; José-María and Sans, 2011). Moreover, seed bank diversity increases with landscape complexity, especially at the field edges (Roschewitz *et al.*, 2005; José-María and Sans, 2011).

There are few studies on functional diversity and functional traits of seed banks. Pakeman and Eastwood (2013) found that functional diversity in the seed bank decreased with disturbance intensity and intensification, and that in more disturbed habitats favoured species with shorter life span, shorter-lived leaves and higher plant stature.

The seed bank flora is also sensitive to soil properties since physical characteristics influence seed dormancy and seed germination, and chemical properties affects plant growth and fecundity (Hawes *et al.*, 2010).

I.7 GENERAL OBJECTIVES

The aim of the present thesis was to assess whether taxonomic and functional diversity of the plant communities of rainfed cereal fields are responsive to agricultural intensification at both field and landscape scales.

I.7.1 Specific objectives

To assess whether taxonomic and functional diversity of plants inhabiting field margins respond to agricultural intensification measured at the field and landscape scales (Chapter II).

To assess whether (1) taxonomic and functional diversity of established weed communities of cereal fields are responsive to intensification at field and landscape scales, (2) the patterns and extent of responses are similar in two climatically-contrasting countries, United Kingdom and Spain and (3) the role of field edges as refugia for a functionally maladapted, declining weed flora (Chapter III).

To assess the extent in which taxonomic and functional diversity of plants represented in the soil seed bank of cereal fields is shaped by soil properties and agricultural intensification at the field and landscape scales in two contrasting Mediterranean regions of Spain (Chapter IV).

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Chapter II

LOCAL FACTORS RATHER THAN LANDSCAPE COMPLEXITY AFFECT SPECIES RICHNESS, FUNCTIONAL DIVERSITY AND FUNCTIONAL TRAITS OF PLANTS AT MARGINS OF CEREAL FIELDS IN THE MEDITERRANEAN

II. Local factors rather than landscape complexity affect species richness, functional diversity and functional traits of plants at margins of cereal fields in the Mediterranean

ABSTRACT

Arable field margins are habitats worthy of conservation efforts as they provide a wide range of ecological and agronomic services in rural landscapes. Agricultural intensification is often cited as a major cause for the decline of taxonomic plant diversity in these habitats but the functional consequences are poorly documented in Mediterranean field margins. We analysed the effect of margin width and landscape complexity on species richness, functional diversity and functional traits of plants inhabiting 94 margins of dryland cereal fields in southern Spain. A set of landscape variables and five plant functional traits were quantified: life form, growth form, seed mass, dispersal type and pollination type. RLQ and Fourth-corner analyses were employed to link plant functional traits and landscape variables obtained from a previous Principal Component analysis. A total of 306 plant species were recorded, the most frequent species being weeds typical of cereal crops. Species richness and functional diversity were positively related to margin width, but not to landscape complexity. The distribution of individual functional traits was neither affected by margin width nor by landscape variables. Our results suggest that increasing the width of cereal field margins would enhance the plant taxonomic and functional diversity in these habitats.

Keywords: plant diversity, plant functional traits, margin width, agricultural intensification, seed mass.

II.1 INTRODUCTION

Agricultural intensification is a worldwide phenomenon (Stoate *et al.*, 2001; Storkey *et al.*, 2012), adversely impacting biodiversity and ecosystem services within agricultural systems (Benton *et al.*, 2003; Tscharntke *et al.*, 2005). The landmark features of agricultural intensification are (i) increased crop management intensity, e.g., high use of agrochemicals and short rotation schemes (Stoate *et al*, 2001; Benton *et al.*, 2003; Storkey *et al.*, 2012) and (ii) decreased landscape complexity with a higher proportion of land designated for annual crops at the expense of land use diversity, semi-natural habitats and field margins (Le Coeur *et al.*, 1997; Benton *et al.*, 2003; Petit *et al.*, 2003; Tscharntke *et al.*, 2005; Baessler and Klotz, 2006).

Field margins are habitats worthy of conservation efforts as they provide a wide range of ecological and agronomic services (Marshall and Moonen, 2002; Vickery *et al.*, 2009). For instance, field margins contribute to protect soil from erosion and water courses from pesticide drifts (Marshall and Moonen, 2002; Cordeau *et al.*, 2012). These habitats harbour considerably higher plant diversity than adjacent field crops and support a large diversity of vertebrate and invertebrate species (Vickery *et al.*, 2009; Poggio *et al.*, 2010). The significant role of field margins in agro-ecosystems has prompted efforts to investigate the impacts of agricultural intensification on margin plant communities (Bassa *et al.*, 2012). Locally, the width and management of margins as well as the farming system in place in the adjacent crop can alter both the richness and the composition of plant communities in these habitats (Schippers and Joenje, 2002;

Tarmi *et al.*, 2009; Bassa *et al.*, 2012). At broader spatial scales, the compositional diversity and structural complexity of the surrounding landscape may affect the plant composition of field margins but results reported in the literature are inconsistent (Marshall, 2009; José-María *et al.*, 2010; Poggio *et al.*, 2010; Jonason *et al.*, 2011; Bassa *et al.*, 2012). In addition, local and landscape factors affecting margin plant communities have mostly been described in Northern and Central Europe (Marshall and Moonen, 2002; Cordeau *et al.*, 2012) whereas margins in Southern Spain have been poorly documented (Bassa *et al.*, 2012), although their characteristics starkly differ from those found in other European areas, e.g. the occurrence of remarkably narrow field margins (Aparicio, 2008; Rodriguez *et al.*, 2009).

Agricultural intensification at a local and/or landscape scale may also impact the functional diversity of plant communities regardless of the change in taxonomic diversity (Flynn *et al.*, 2009). This process can occur via the filtering out of plant species with functional traits maladapted to the new environmental conditions (Keddy, 1992; Diaz *et al.*, 1998). As a consequence, the initial proportions of functional trait values are shifted towards the most successful combination of traits and a subsequent narrowing of functional trait values and of functional diversity takes place that have potentially detrimental effects on the provision of ecosystem services (Díaz and Cabido, 2001). Such processes have been described in the flora of arable fields (José-Maria *et al.*, 2011; Fried *et al.*, 2012) suggesting that in some cases species richness and functional responses can be decoupled (Ma and Herzon, 2014), but to date, it has not been documented in arable field margins.

The objective of this paper was to assess whether intensification at the local scale, measured here as margin width, and at the landscape scale, measured here as proportion cover of the different land uses, field size and landscape diversity, affect plant species richness, functional diversity and the proportion of functional traits of plants inhabiting field margins in dryland cereal fields. The objective is framed in the following hypotheses: (1) Species richness and functional diversity will increase with margin width and landscape complexity; (2) The frequency of trait values related to life form, growth form, pollination type, dispersal type and seed mass will be affected by margin width and landscape complexity

II.2 MATERIAL AND METHODS

II.2.1 Study area

The study area was located along the Guadalquivir River Basin (Southern Spain; Figure 1). Land use was dominated by cereal crops, followed by olive orchards and other annual crops such as sunflower or cotton (Junta de Andalucía, 2013). Natural habitats, such as forest, are a minor land use composed of unconnected small patches of different species of pines and oaks (Aparicio, 2008; Junta de Andalucía, 2013). Climate in the study area is Mediterranean, with an average annual temperature of 18.6 ºC, and an average annual precipitation of 590 mm. Altitude in the area ranges from 12 to 106 m a.s.l.

II.2.2 Margin characterization

Ninety-four field margins adjacent to conventionally managed dryland cereal fields were selected along a gradient of arable land cover. Selected margins were located at least 2 km away from each other in order to avoid overlapping landscape properties. Soils in margins were alkaline with a texture varying from clayish to sandy loam.

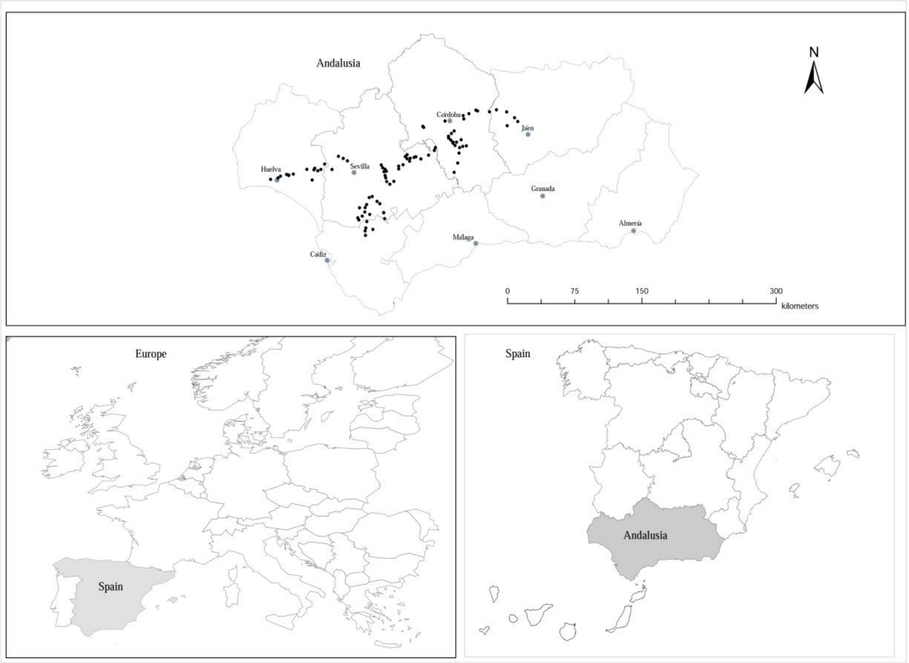

Figure 1. Map showing the location of 94 sampled field margins.

II.2.3 Agricultural intensification variables

Margin width was considered as an indicator of local agricultural intensification and was measured *in-situ* during the plant survey. Margin width ranged from a few centimetres to more than three meters wide and were categorized as narrow, medium or wide (Table 1, Figure 2).

Figure 2. Examples of different cereal field margin width. From left to right: wide, medium and narrow margins.

Six landscape intensification variables were assessed within a 1 km radius centred on each margin (Roschewitz *et al*., 2005), using the Geographic Information System, SIGPAC (Sistema de Información Geográfica de Parcelas Agrícolas; http://sigpac.mapa.es/fega/visor/). Five variables were compositional, including percentage cover of arable land, grassland, forest, and human settlements (Table1). The proportion cover of perennial crops (olive orchards and fruit trees) was strongly negatively correlated with arable land cover (r= -0.87, p<0.0001), and thus it was not kept as individual variable. The fifth compositional variable was the Shannon-Wiener's diversity index. The sixth variable was the size of the cereal crop field associated with each margin.

II.2.4 Plant survey

Plant surveys were conducted before harvest, between May and June (peak flowering months) in 2009, 2010 and 2011. The margins were located between a cereal field and a road to ensure that the margins were associated to only one cereal field. In each margin, plant species were recorded walking 20 m along the field margin. The total number of species recorded was used as a measure of species richness. Plant nomenclature followed Blanca *et al*. (2011).

Table 1: Mean ± standard deviation (SD), minima and maxima of agricultural intensification variables obtained in the 94 studied field margins.

Landscape variables	Abbreviation	Category	Mean±DS	Min.	Max.
Arable land cover (%)	AL	-	73.80±29.90	2.00	100
Field size (ha)	FS	-	9.00±49.10	0.16	281.00
Shannon habitat diversity index	SHDI	-	0.50±0.30	0.00	1.10
Forest (%)	FO	-	0.90±3.70	0.00	30.00
Grassland (%)	GR	-	0.90±5.10	0.00	47.00
Human Settlements (%)	HS	-	4.00±6.10	0.00	40.00
Margin width (m)	MW	Narrow		0.00	0.99
		Medium		1.00	1.99
		Wide		>2	-

SD=standard deviation

II.2.5 Plant functional traits

A set of five functional traits related to plant persistence, growth form and reproduction was used to characterize plant species´ strategies. Only species recorded in at least 10% of the margins were considered in order to avoid the influence of rare species in subsequent analyses (Mueller-Dombois and Ellenberg, 1974; Kenkel *et al.*, 2002). Trait values were obtained from existing plant trait databases (Table 2 and Appendix A) and included:

(i) Raunkiær's life forms: therophytes, geophytes and hemicryptophytes. These traits are related to strategies of plant persistence (McIntyre *et al*., 1995; Lososová *et al*., 2006); (ii) Growth form: dicotyledons and monocotyledons. This trait is related to plant architecture, resource acquisition and resistance to selective herbicides (Roschewitz *et al*., 2005; Hawes *et al*., 2010); (iii) Pollination type: entomogamy, anemogamy and autogamy; (iv) Dispersal type: zoochory, anemochory and barochory. Both pollination and dispersal type categories represent contrasting strategies for pollen and seed dispersal in space and time, and are related to colonization ability (Benvenuti, 2007; Holzschuh *et al.*, 2007; Petit *et al.*, 2012); and (v) Seed mass: trait related to reproductive investment, seedling establishment ability and persistence in the soil seed bank (Leishman, 2001; Pakeman *et al.*, 2008).

II.2.6 Functional diversity index

Rao's quadratic entropy index (FD; Rao, 1982) was used to measure plant functional diversity in each margin (Mouchet *et al.*, 2010). This index incorporates both the relative abundance of species and a measure of the pair-wise functional differences between species, by measuring species distance in a functional trait space:

$$\mathrm{Rao} = \sum_{\mathrm{i=1}}^{\mathrm{s}} \sum_{\mathrm{j=1}}^{\mathrm{s}} dij\ pipj$$

where s is the number of species considered (≥10% frequency), d_{ij} is the distance between species i and j, p_i and p_j are the relative abundances of species i and j. We used species presence/absence with present species assigned an abundance of 1 and absent species an abundance of 0. Rao's index based on presence/absence data is largely a measure of functional richness, i.e. the volume of niche space occupied by the species (Mason *et al.*, 2013). Here, it was calculated for each single trait (FDS- Raunkiær's life forms, FDS-growth form, FDS-pollination type, FDS- dispersal type, FDS-seed mass) and for the combination of all functional traits (FDT).

Two complementary types of three-table analysis methods were further conducted to associate plant traits with agricultural intensification variables (Dray *et al.*, 2014), RLQ and Fourth-corner analysis. RLQ analysis is a multivariate technique which provides combinations of traits that have the highest covariances with combinations of environmental variables (Dolédec *et al.*, 1996). Fourth-corner analysis tests relationships between individual functional traits and individual environmental variables (Legendre *et al.*, 1997). Both analyses are complementary and require three tables, i.e. R is the environment x site table (here, the agricultural intensification variables of the 94 sampled margins), L is the species composition table x site (here, the species with ≥ 10% frequency found in the 94 sampled margins) and Q is the trait x species table (here, the five functional trait values of each considered species, Appendix A). The RLQ analysis performs a simultaneous ordination of the three tables in different steps. First, correspondence analysis (CA) and Hill and Smith analyses are used to analyse respectively the L, R (with row weights equal to the row weights of CA), and Q (with row weights equal to the column weights of CA) tables. RLQ then calculates two separate co-inertia on the R-L and L-Q tables and identify axes in which the species scores are rearranged to maximize the covariance between the sampling units, constrained by the intensification variables (the R table), and the species scores constrained

Table 2. List of qualitative and quantitative traits used for the species analyzed. Sources: A) Baseflor (Julve, 1998). B) Kew garden seed trait (SID; Royal Botanic Gardens Kew, 2008). C) Flora Vascular de Andalucía Oriental (Blanca *et al.*, 2011) and D) LEDA traitbase (Kleyer *et al.*, 2008).

Traits	Abbreviation	Category	Species	Mean±SD	Min.	Max.	Source
Raunkiær's life forms	LF	Geophytes	1	-	-	-	C
		Hemicryptophytes	10	-	-	-	C
		Therophytes	47	-	-	-	C
Growth form	GF	Dicotyledons	14	-	-	-	C
		Monocotyledons	44	-	-	-	C
Pollynation type	PT	Anemogamy	18	-	-	-	A
		Autogamy	3	-	-	-	A
		Entomogamy	37	-	-	-	A
Dispersal type	DT	Anemochory	18	-	-	-	A,D
		Barochory	28	-	-	-	A,D
		Zoochory	12	-	-	-	A,D
Seed mass (mg)	SM			3.70±5.20	0.05	22.50	B

SD=standard deviation

by the species traits (the Q table). This results in linear combinations of functional traits and agricultural intensification variables. A permutation model (model 6 with 999 permutations as proposed by Dray and Legendre, 2008) with Bonferroni correction for multiple comparisons was used to test the link between species traits and the environment. This permutation model encompasses two sub-models, model 2 and 4, which test the hypotheses that species presence is independent from their environment (row permutation of the R table) and their traits (row permutation of the Q table), respectively. Both sub-models must be rejected to confirm the relationship between R and Q tables. The Fourth-corner analysis assesses the values of the quantitative variables with the Pearson correlation coefficient, the qualitative variables with the Pearson Chi square and G statistic, and quantitative-qualitative variables with the Pseudo-F and Pearson correlation coefficient. The significance of these relationships was tested by 999 permutations based on model 6 with Bonferroni correction for multiple testing.

All statistical analyses were performed with R software version 2.15.1 (R Development Core Team, 2013), using the libraries Ade4 (Dray and Dufour, 2007), Hmisc (Harrell and Dupont, 2014) and pgirmess (Giraudoux, 2013).

II.3 RESULTS

A total of 306 plant species (see Appendix B) were recorded, with an average richness of 21±9 species per margin. The most frequent species were arable weeds typical of Mediterranean cereal cropping systems: *Lolium rigidum* Gaudin (77.6%), *Avena sterilis* L. (59.6%), *Hordeum murinum* L. (54.3%) and

Anagallis arvensis L. (53.2%) (Appendix B). We detected only one species, *Malvella sherardiana* (L.) Jaub. and Spach catalogued as endangered (Moreno, 2008). Fifty eight out of 306 species occurred in more than 10% of the sampled margins and were used for computing functional diversity indices. Most species were therophytes, dicotyledons, entomogamous and barochorous (Table 2, Appendix A). There were also many wind-dispersed species including *Sonchus oleraceus* L., *Silybum marianum* (L.) Gaertn., *Lactuca serriola* L, *Papaver rhoeas* L. which are considered colonizers in cropping systems (Benvenuti, 2007). Functional diversity was generally low for individual traits and for the combination of functional traits (Table 3).

Table 3. Mean±SD, minima and maxima for functional diversity.

	Mean±SD	Min.	Max.
FDT	0.11 ± 0.02	0.03	0.15
FDS-life form	0.08 ± 0.05	0.00	0.19
FDS-growth form	0.22 ± 0.05	0.00	0.25
FDS-pollination type	0.16 ± 0.02	0.00	0.20
FDS-dispersal type	0.18 ± 0.03	0.00	0.22
FDS-seed mass	0.24 ± 0.10	0.00	0.43

II.3.1 Landscape complexity gradient

The first two axes of the PCA accounted for 40% of total variability (24% for the first axis and 16% for the second axis). All intensification variables showed a stronger correlation with the first axis than with the second axis and thus only the first axis was further considered. This axis represented a gradient of landscape complexity (Table 4, Figure 3). It split margins located in complex landscapes (small field sizes, high SHDI and high proportion cover of grassland, forest and human settlements) from margins within simple landscapes (large field sizes, high proportion cover of arable land).

Table 4. Correlations of the different intensification variables with the first PCA axis showing that it represents a gradient of landscape complexity. For quantitative variables, Spearman´s rank correlations coefficient (ρ) was used and for the qualitative variable MW the Kruskal-Wallis (χ^2) test was employed. See Table 1 for abbreviations.

	PCA 1		
	ρ	χ^2	p-value
AL	0.84	-	<0.001
FS	0.28	-	<0.001
SHDI	-0.58	-	<0.001
FO	-0.33	-	<0.001
GR	-0.27	-	<0.001
HS	-0.58	-	<0.001
MW	-	χ^2=2.03	<0.001

Margin width differed along the first PCA axis (Table 4) and partially accompanied the gradient of landscape complexity; wide margins were more frequent in complex landscapes, medium margins were more frequent in simple landscapes, and narrow margins appeared unrelated to landscape complexity (Figure 3).

II.3.2 Agricultural intensification effects on species richness, functional diversity and functional traits

Species richness, FDT and FDS-dispersal type were affected by margin width (Figure 4, Table 5). Wide and medium margins had significantly higher species richness than narrow margins (28±10, 23±9, 15±6 species, respectively). FDT was significantly higher in wide margins than in narrow margins (Figure 4, Table 5). FDS-dispersal type was significantly higher in wide margins

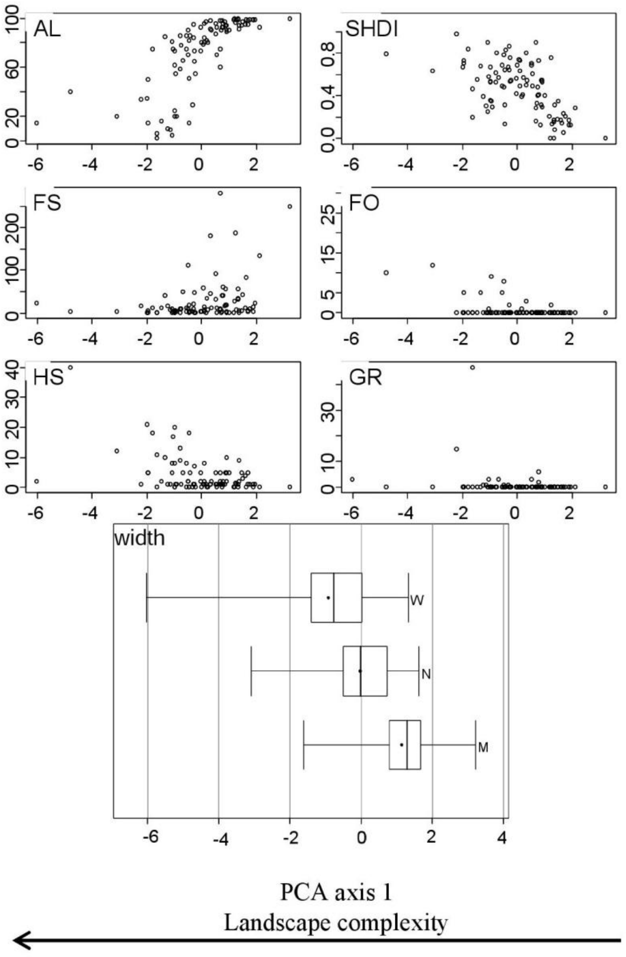

Figure 3. Landscape variables significantly associated with the first PCA axis. AL =arable land cover, SHDI= Shannon habitat diversity index, FS=field size, FO= forest cover, GR= grassland cover, HS= human settlements cover, and width=margin width, W= wide margins (>2m), N=narrow margins (<1m), M= medium margins (1-2 m). Boxplots show median values (bold line) and mean (dot); box limits represent lower an upper quartiles and whiskers represent minimum and maximum values.

than in medium and narrow margins (Figure 4, Table 5). Neither species richness nor FDT or the FDS of individual traits were correlated with the landscape complexity gradient (PCA first axis) or with any individual landscape variable (Table5).

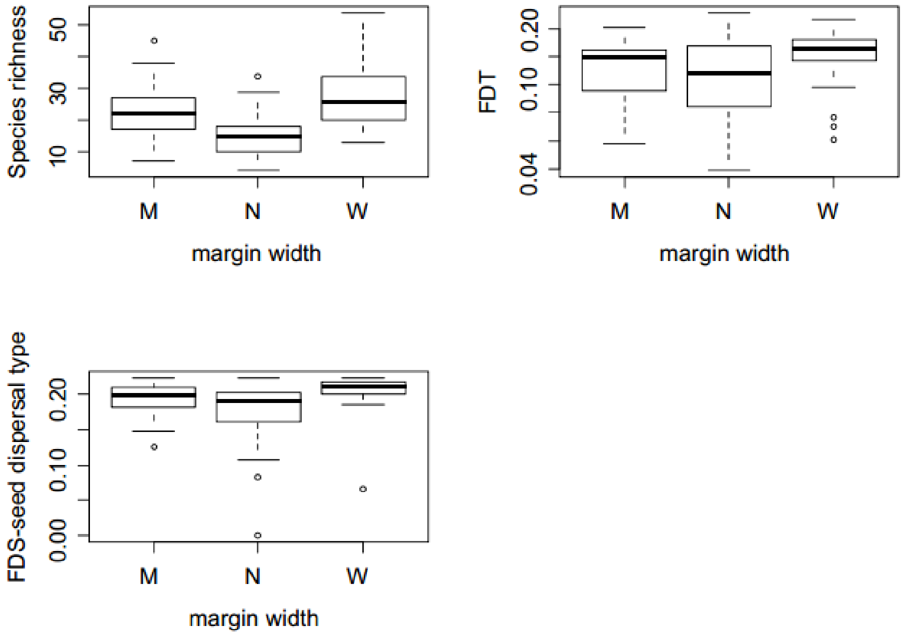

Figure 4. Relationship of species richness, FDT and FDS- dispersal type to margin width. M= medium margins , N=narrow margins, W= wide margins. Boxplots show median values (bold line), box limits represent lower and upper quartiles and whiskers represent minimum and maximum values.

Regarding functional traits, the RLQ analysis revealed that functional traits were not related to intensification variables. Random permutations of the rows of the R and Q tables indicated no significant association of the co-structure between intensification variables (model 2; p=0.27, species presence is independent from their environment) and functional trait values (model 4; p=0.30, species are independent from their traits). In concordance with the RLQ analysis, the fourth-corner analysis detected no significant association between individual traits and margin width or any individual landscape variables (Table 6).

Table 5. Relationship of species richness, functional diversity for the combination of traits (FDT) and for individual traits (FDS) to the first PCA axis and to intensification variables. For two quantitative variables, Spearman´s rank correlation coefficient (ρ) was used. For one quantitative and one qualitative variables Kruskal-Wallis (χ^2) test was employed. In bold p-values< 0.05. See table 1 for abbreviations

	PCA1	AL	FS	SHDI	FO	GR	BA	MW
Species richness	ρ=0.06	ρ=0.09	ρ=0.17	ρ=-0.11	ρ=-0.04	ρ=0.09	ρ=0.05	χ^2=**31.70**
FDT	ρ=-0.03	ρ=0.08	ρ=-0.07	ρ=-0.10	ρ=0.0 0	ρ=-0.03	ρ=0.09	χ^2=**6.45**
FDS-Raunkiær's life forms	ρ=-0.07	ρ=0.01	ρ=-0.02	ρ=0.02	ρ=0.00	ρ=-0.01	ρ=0.19	χ^2=2.74
FDS-growth form	ρ=0.04	ρ=0.06	ρ=-0.04	ρ=0.02	ρ=0.05	ρ=0.03	ρ=-0.01	χ^2=0.36
FDS-pollination type	ρ=-0.14	ρ=-0.15	ρ=-0.17	ρ=0.02	ρ=0.13	ρ=-0.03	ρ=-0.07	χ^2=2.43
FDS-dispersal type	ρ=-0.07	ρ=0.05	ρ=0.05	ρ=0.03	ρ=0.03	ρ=-0.11	ρ=-0.06	χ^2=**16.50**
FDS-seed mass	ρ=0.02	ρ=0.03	ρ=0.00	ρ=-0.04	ρ=-0.07	ρ=-0.02	ρ=0.07	χ^2=2.29

II.4 DISCUSSION

In this study, we investigated the role of margin width and landscape complexity on plant richness, functional diversity and functional traits of species inhabiting the field margins of dryland cereal fields in Southern Spain. Our results suggest that margin width had a significant effect on plant taxonomic richness and functional diversity of margin plant communities, whereas the landscape context appeared to be of little importance. In addition, we showed that the functional traits life form, growth form, seed mass, dispersal type and pollination type in margin plant communities responded neither to margin width nor to landscape complexity. In agreement with our hypotheses, a positive effect of margin width was detected both on plant species richness and functional diversity. Wider margins were found more effective in promoting taxonomic diversity than narrow margins. This could be because the margin width considerably varied in the sampled transect and affected the total available area for plant establishment. As consequence,

Table 6. Relationships between functional traits and intensification variables provided by the Fourth-corner analysis. See Table 1 and 2 for abbreviations. None of the relationships was significant ($p>0.05$ in all cases).

	AL	FS	SHDI	FO	GR	HS	MW
LF	F=0.40	F=2.37	F=0.00	F=0.90	F=0.32	F=0.23	χ^2=4.61
GF	F=0.50	F=0.13	F=2.86	F=0.46	F=0.87	F=0.25	χ^2=1.61
PT	F=1.26	F=0.43	F=1.99	F=0.25	F=0.19	F=0.25	χ^2=3.24
DT	F=1.26	F=0.11	F=0.42	F=1.91	F=0.92	F=0.55	χ^2=6.52
SM	r=-0.01	r=-0.1	r-0.00	r=0.01	r=-0.01	r=0.00	F=0.55

For two quantitative variables, Pearson correlation coefficient (r) was used. For one quantitative and one qualitative variable Pseudo-F was employed (F). For two qualitative variables Chi square test was used (χ^2). Significance was tested using 999 permutations under model 6 using Bonferroni correction for multiple comparisons.

wider margins (medium and wide) harboured approximately 40% more species than narrower margins. Therefore, a direct effect of the species-area-relationship cannot be ruled out but the effects of margin width on plant taxonomic richness have often been reported in the literature (Schippers and Joenje, 2002; Tarmi *et al.*, 2009; Bassa *et al.*, 2012). These effects result primarily from an increase of habitat heterogeneity in wider margins (Ma *et al.*, 2002). Furthermore, a number of studies have provided evidence that narrow margins are more strongly impacted by disturbances associated to the agronomic management of adjacent crops (e.g. herbicide drift and nutrient leaching) than wider margins that have a buffering capacity against disturbances (Ma *et al.*, 2002; Schippers and Joenje, 2002; Schmitz *et al.*, 2014). Our study also showed that wide margins (>2m) harboured a higher plant functional diversity than narrow ones (<1m) and a higher diversity of attributes for specific traits, in our case, dispersal type. This result suggests that taxonomic and functional diversity were not decoupled here, i.e. that the loss of species translated into losses in functions, thus indicating low functional redundancy. This finding reinforces the view that Mediterranean crop margins often shelter a low functional diversity, most likely due to their narrow character, disturbance and restricted species pool of the neighboring crops (Ma and Herzon, 2014). Indeed, dominant therophytes recorded here are pernicious weeds of cereal fields (Gonzalez-Andujar and Saavedra, 2004), which would suggest that narrower margins offer environmental conditions similar to those of crop fields rather than those of semi-natural habitats.

Here, the taxonomic and functional plant responses were mostly driven by agricultural intensification at the field scale (margin width), rather than by landscape scale intensification. Although landscape scale effects on margin plant diversity have been described in some studies (Poggio *et al.*, 2010; Jose-Maria *et al.*, 2011; Bassa *et al.*, 2012), our results are in agreement with other studies suggesting an overriding role of local management on arable plant taxonomic and functional diversity (Weibull *et al.*, 2003; Marshall, 2009; Jonason *et al.*, 2011; Ma and Herzon, 2014). This lack of landscape effect may have several plausible causes that could act in isolation or in combination: (i) as suggested earlier, a very intensive management of cereal field margin that would override or mask the effect of the landscape context of arable fields, (ii) a confounding effect of margin width and landscape complexity (i.e. wider margins were located in the more complex landscapes) that would hinder the detection of landscape scale effects (Figure 3) and/or (iii) the very low proportion cover of habitats that are favourable to wild plant species such as grassland (Table 1) so that plant species pool may not have differed enough along our landscape gradient to detect deferences.

Finally, our expectation was that the width and landscape context of margins would act as “environmental filters” of functional traits within plant communities. Previous studies have provided evidence that agricultural intensification could select for arable plants within arable fields (Poggio *et al.*, 2010; Jose-Maria *et al.*, 2011) and in field margins (Bassa *et al.*, 2011; Ma and Herzon, 2014). However, in our study the representation of individual plant functional traits were unaffected by margin width, landscape complexity or individual landscape variables. There are two plausible explanations for this lack of response. First, as mentioned earlier, most margins under focus here were strongly affected by disturbances, as suggested by the dominance of therophytes and short lived perennial species (Table 2). This disturbance regime could have impeded the establishment of long-lived perennial plants, such as woody species (Lososová *et al.*, 2006). It is, therefore, not surprising that the response most commonly reported in the literature, i.e. an increase in herbaceous perennial and woody species in wide margins and in complex landscape (Poggio *et al.*, 2010; Bassa *et al.*, 2011; José-María *et al.*, 2011) could not be detected in the present study. Second, most of the margins studied were located within simple landscapes and the gradient of landscape complexity under study may have been too short to filter out functional trait values.

II.5 CONCLUSIONS

Even though a total of 306 species were recorded in this study, it appears that the structure and management of the studied margins is currently the main factor limiting their plant taxonomic and functional diversity. Despite the selection of margins located along gradients of margin width and landscape complexity, the flora of the selected margins were functionally not diversified, with a clear dominance of therophytes (of which many were pernicious weeds) and limited occurrence of perennial species. Such low functional diversity is most likely a result of intensive crop and margin management practices, whose effects are multiplied by the narrowness of the margins. Promoting species richness and functional diversity in dryland cereal margins could therefore be achieved by widening existing margins so that some woody species can establish and the proliferation of weed species can be limited. Further investigations are needed to establish the importance of margin width as a management tool aimed to conserve plant diversity in rain-fed cereal field margins.

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Chapter III

THE EFFECT OF AGRICULTURAL INTENSIFICATION ON WEED COMMUNITIES: A FUNCTIONAL COMPARISON ACROSS TWO COUNTRIES

III. The effect of agricultural intensification on weed communities: a functional comparison across two countries.

ABSTRACT

Agricultural intensification is a process occurring at field and at landscape levels and is one of the main causes of loss of taxonomic and functional diversity in agricultural landscapes. Within intensively managed fields, inputs of fertilizers and herbicides tend to be lower at field edges, which potentially can serve as refugia habitats for species that have been driven out of field centres. Additionally, the landscape context may also influence the diversity within field. In the present study, we assessed whether species richness, functional diversity and the distribution of functional traits of cereal weed communities in United Kingdom (UK) and Spain responded to intensification at the field and landscape scales and if such responses were similar in patterns and extent in the two climatically and floristically contrasting countries. At the field scale, position in the field (related to distance from the field margin) was analysed in the context of other variables associated with intensity of management: margin width, margin management and crop cover, while at landscape scale field size and proportion arable land cover in the surrounding landscape was analysed. The studied traits were plant height, month of first flowering, seed mass and life form. Functional diversity was calculated using Rao´s quadratic entropy for the combination of the four traits. Whereas in Spain species richness was insensitive to habitat type and to the different intensification variables, in UK species richness was higher at the edge compared to the field centre, and decreased with crop cover and with intensive managed field margins. In both countries, neither functional diversity nor the distribution of functional traits was associated with position in the field or any other intensification variable. We suggest that the conventional agriculture system that has been carried out for several decades in both countries has been the main environmental filter modulating community assembly in our study and field edges do not represent a functionally discrete habitat. Mean and range of trait values were similar in both countries, resulting in an extremely low functional diversity, suggesting a convergence in trait values of weed communities in response to conventional agriculture pressure.

Keywords: Functional traits, Functional diversity, Rao´s quadratic entropy, landscape complexity, seed mass, disturbance, field margin, diversity.

III.1 INTRODUCTION

Loss of arable weed diversity has been cited as one of the major consequences of agricultural intensification (Robinson and Sutherland, 2002; Storkey *et al.,* 2012; Meyer *et al.*, 2013), which in turn may potentially impair the provision of agro-ecosystem services (Storkey and Westbury, 2007; Moonen and Barberi, 2008).

Intensification is a process occurring at field and at landscape scales. At the field scale, it is associated with the adoption of conventional agriculture which is based on the use of herbicides, synthetic fertilizers, increasing sowing density and other intensive farming practices aimed to increases crop yield (Storkey *et al.,* 2012). Crop management practices (e.g. soil cultivation, application of fertilizers and herbicides) tend to be less efficient at crop edges than in crop centre (Romero *et al.*, 2008; Fried *et al.*, 2009). Thus, the edge weed communities may reflect conditions across the whole field prior to intensification and can act as refugia for species that have no longer been able to persist in field centres (Kleijn and van der Voort, 1997). In addition, field edges are often richer in species than the field centres due to the contribution of seeds from the adjacent field margins (Marshall, 1989; Romero *et al.*, 2008). At larger scales, agricultural intensification is associated with landscape simplification resulting from the increase in size and number of intensively managed crop fields at the expense of (semi)natural habitats and habitat diversity (Baessler and Klotz, 2006; Aparicio, 2008).

The impact of agricultural intensification on taxonomic diversity is widely recognized (Gabriel *et al.*, 2005; Gaba *et al.*, 2010; José-María *et al.*, 2010; Storkey *et al.*, 2012). However, intensification may also impact the functional diversity of plant communities regardless of the change in taxonomic diversity (Flynn *et al.*, 2009; Pinke and Gunton, 2014). This process can occur by the filtering out of species with trait syndromes poorly adapted to the new environmental conditions (Keddy, 1992; Díaz and Cabido, 2001; Garnier and Navas, 2012). For instance, it has been reported that short stature (i.e. shorter than crop), large seeds and late flowering constitute a trait syndrome vulnerable to intensification (Storkey *et al.*, 2010). In contrast fast-growing, small-sized plants with early flowering onset are successful in intensified sites (Fried *et al.*, 2012; Perronne *et al.*, 2015). As a consequence, the initial proportions of functional trait values are shifted towards the most successful combination of traits, as it has been documented for seed mass in the weed flora of the UK (Figure 1; Storkey *et al.*, 2010), thus affecting functional diversity which can be strongly related to the provisioning of ecosystem services (Díaz *et al.*, 2007). Intensification may have opposite effects on functional diversity on the one hand, it restricts the possible survival strategies displayed by plants (Pakeman and Eastwood, 2013; Guerrero *et al.*, 2014) and on the other hand, it promotes niche opportunity to allow different strategies to coexist (Moles *et al.*, 2008; Maire *et al.*, 2012; Hernández Plaza *et al.*, 2015).

Therefore, there is a need for studies combining taxonomic and functional approaches to contribute to a more complete understanding of the effect of intensification processes on plant diversity in agricultural landscapes. Moreover, it would be highly useful to explore general patterns of taxonomic and functional responses under the same intensification filters, but across different climate conditions and floras. In addition, the extent to which field edges can act as refugia plant functional diversity needs to be explored.

In this study we investigated the effect of agricultural intensification at field scale, measured as position in the field, crop cover, margin width and margin management, and at landscape scale, it was measured as field size and percentage cover of arable land in the surrounding landscape, on plant diversity in conventionally managed cereal systems of Spain and UK. We assume that field edges and centres represent contrasting habitats which differ in the intensity of agricultural practices, lower in field edges (Marshall, 1989). Both countries differ in terms of climate, soil types and weed flora but have been devoted to cereal cropping under conventional system for several decades and have followed Common Agricultural Policy prescriptions. Also, both countries have experienced simplification of agricultural landscapes (Marshall, 2009; Aparicio, 2008).

The aim of this study was to assess whether (1) species richness, functional diversity and the distribution of functional traits of cereal weed communities in UK and Spain respond to intensification at field and landscape scales, (2) the patterns and extent of response are similar in both countries, and (3) field edges are distinctive habitats acting as refugia for a functionally more diverse weed flora.

III.2 MATERIALS AND METHODS

III.2.1 Study areas

In UK, the study was conducted on 39 rainfed conventionally managed arable fields located in 13 farms across the South East of the UK (Figure 2) as part of a wider study on farmland biodiversity (Henderson *et al*., 2012). The UK climate is maritime with an average annual temperature of 9.8 ºC and an average annual precipitation of 733 mm. The sites represented a range of soil types from light chalk soils to heavy clay loams. In Spain, the study was conducted in 22 rainfed, conventionally managed cereal fields located along the Guadalquivir River Basin (Andalusia; south Spain). The climate is Mediterranean with an average annual temperature of 18.6 ºC and mean annual precipitation of 590 mm. Soils of the sampled field crops were alkaline with textures varying from clayish to sandy loam.

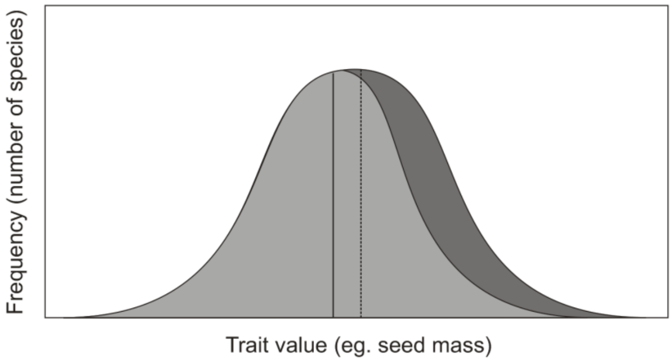

Figure 1. Conceptual representation of the impact of intensification on the arable weed flora. Dark shading represents the distribution of trait values prior to intensification with the median indicated by the dotted line. The light shading represent the trait distribution post intensification, in this case, large seeded species have been lost from the flora with a shift in the median, indicated by the solid line**.**

The main land-uses in the UK experimental area were cereal crops in association with other annual crops, human settlements, grassland and small and unconnected forest patches. In Spain the main land uses in the studied area were cereal crops followed by olive orchards and other annual and perennial crops. Natural habitats such as forest and grassland are a minor land-use, generally located in mountainous and riparian areas (Aparicio, 2008; Junta de Andalucía, 2013).

Figure 2. Location of the sampling fields in Spain and UK. The black quadrats of the top image represent the areas of study. The bottom images show location of the sampled fields in Spain (left) and UK (right). For Spain, dots indicate the location of the sampled fields while for UK they represent the location of the 13 farms within which fields were sampled.

III.2.2 Weed sampling

In UK, the fields were surveyed in spring from 2006 to 2009 and some of the 39 cereal fields were revisited three or four times, resulting in 85 comparisons of field centre and edge floras. In each field, four transects of 32 m were placed perpendicular to a south facing field margin and in each transect, four 0.5 m^2 quadrats were positioned at 0, 4, 8 and 32 m from the margin (Figure 3). Plant species present in the quadrats were recorded and their abundance was estimated using the following scale: 1, one individual; 2, two-three individuals; 3, more than three individuals. Nomeclature followed Rose *et al*., (2006). Then, the species compositions of the quadrats were merged into two groups (averaging weed abundance) according to their position within field: edge (the quadrats placed at 0 and 4m from the field margin) and centre (the quadrats placed at 8 and 32 m from the margin). In Spain, the fields were surveyed once in spring of 2010 or 2011. In each field, one margin between the crop field and a road was selected and two positions were defined: the field edge (0 to 5 m from the field margin) and centre, 25 m away from the field margin. In each position, five 1m^2 quadrats were placed every five meters; at the edge, they were taken in zigzag along the field margin and in the centre they were taken diagonal towards the inner part of the field in the centre (Figure 3). In each quadrat, plant species were identified and abundance was measured by counting the number of individuals per species. Nomenclature followed Flora de Andalucía Oriental (Blanca *et al.*, 2011).

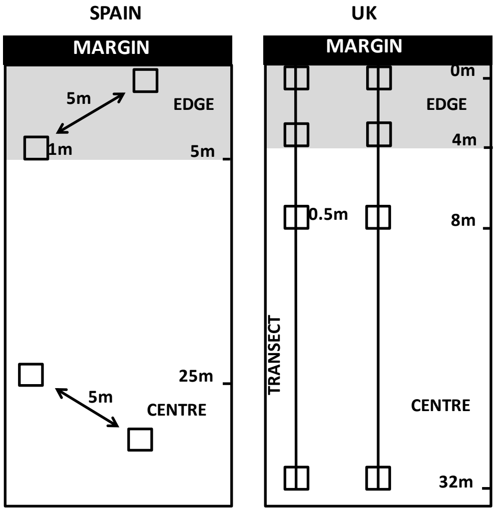

Figure 3. Scheme of the sampling design in UK and Spain.

III.2.3 Agricultural intensification variables

The following data sets were collected (Table 1a) aimed to reflect intensification at local and at landscape scales. At field scale: i) position in the field: edge and centre as defined previously (Figure 3); ii) crop cover: In UK, it was visually estimated in each quadrat and their values were averaged for each position in the field. In Spain, crop cover was not estimated and, therefore, this variable was not taken into account; iii) margin width, measured in situ for each sampled field; iv) margin management: In UK farmers were interviewed about their margin management. In Spain margins were not purposely managed, thus this variable was not taken into account. At landscape scale: v) arable land cover: in UK, it was assessed within a circular area of 3 km radius centred on each farm, using Google Earth©, and thus the different sampled fields from the same farm had the same value for this landscape variable; in Spain, this variable was assessed within a circular area of 1 km radius centred at each field using SIGPAC, (Sistema de Información Geográfica de Parcelas Agrícolas, http://sigpac.mapa.es/fega/visor/); vi) field size: in Spain, it was measured using SIGPAC whereas in UK, it was measured in situ.

III.2.4 Plant functional traits

A set of functional traits known to vary in response to agricultural intensification were considered (Table 1b): plant height, seed mass, month of first flowering and Raunkiaer´s life form (Westoby, 1998; McIntyre *et al.*, 1999; Storkey *et al.*, 2010; Guerrero *et al.*, 2014; Pinke and Gunton, 2014). Plant height is related to the ability to compete for light and resistance to disturbance (Westoby, 1998; Fried *et al.*, 2012). Seed mass is related to plant fecundity, seedling establishment ability and persistence in the soil seed bank (Westoby, 1998; Pakeman *et al.*, 2008). Month of first flowering is related to the ability to reproduce avoiding disturbance caused by management practices (Fried *et al.*, 2012; Pakeman and Eastwood, 2013). Raunkiaer´s life form is related to the ability to resist disturbance (McIntyre *et al.*, 1999). To avoid influence of rare species in subsequent analyses, only species recorded in at least 5% of the fields were considered (Kenkel *et al.*, 2002). Trait values were obtained from the TRY trait data base (Kattge *et al.*, 2011) with the exception of the phenological trait month of first flowering, which was obtained from national floras (Fitter and Peat, 1994; Blanca *et al.*, 2011).

III.2.5 Species richness and functional diversity

The total number of species recorded was considered as a measure of species richness. Functional diversity was quantified using the Rao's quadratic entropy index (Rao, 1982) calculated for the combination of the four functional traits for species with a frequency of occurrence ≥ 5% in each country. This index incorporates both the relative abundance of species and a measure of the pair-wise functional differences between species, by measuring species distance in a functional trait space. It is denoted as

$$\text{Rao} = \sum_{\mathrm{i}=1}^{\mathrm{s}} \sum_{\mathrm{j}=1}^{\mathrm{s}} dij\ pipj$$

where s is the number of species considered, d_{ij} is the distance between species i and j; p_i and p_j are the relative abundances of species i and j. Rao's quadratic entropy index measures two important functional diversity properties: functional richness (the volume of niche space occupied by the species) and divergence (the distribution of abundance in the extremities of occupied trait space in community Rao, 1982; Mason *et al.*, 2013). The value of this index ranges between 0 and 1 with values near one indicating a high functional diversity, i.e. high dissimilarities of functional trait values among species.

Functional diversity indices were calculated using standardized traits (mean=0, SD=1). Gower distance was selected because of the presence of categorical and continuous traits, and Cailliez correction was used to correct for the non-euclidean distribution of traits (Laliberté *et al.*, 2014). All the indices were calculated using R software version 2.15.1 (R Development Core Team, 2012), using the library Vegan (Oksanen *et al.*, 2007) for taxonomic diversity and FD (Laliberté *et al.*, 2014) for functional diversity indices.

III.2.6 Statistical analyses

The response of species richness and functional diversity of each data set to agricultural intensification was analysed using linear mixed-effect models, a suitable approach to account for fixed and random effects and nested sampling designs (Pinheiro and Bates, 2000). A full model containing all environmental variables and relevant interactions was built for each dataset. For the UK data, arable land cover, field size, position in the field, margin width, margin management, crop cover and their interactions with position in the field were tested as fixed factors. For the Spain data, arable land cover, field size, position in the field, margin width and their interactions with position in the field were tested as fixed factors. Field identity was introduced as a random factor in all analyses. Statistical analysis was performed using the multimodel inference approach (Burnham and Anderson, 2002). From the full model, a set of submodels were created comprising all possible combination of

Table 1. Mean ±standard deviation (SD), minima and maxima of agricultural intensification variables obtained in the 39 fields in UK and the 22 fields in Spain. b) Mean ± standard deviation (SD) and minima and maxima of the four functional traits of the 25 and 66 most frequent species in UK and Spain respectively.

		UK			Spain		
	Abbreviation	Mean±SD	Min.	Max.	Mean±SD	Min.	Max.
a) Agricultural intensification variables							
Arable land cover (%)	AL	77.50±10.80	56.2	94.50	61.90±35.50	6	100
Field size (has)	FS	17.50±12.80	1.90	49.00	24.49±34.30	0.65	135.00
Margin width (m)	MW	3.90±2.80	0.90	14.00	1.58±1.40	0.38	5.80
Crop cover (%)	CCedge	57.00±22.12	5.00	90.00			
	CCentre	63.80±18.75	7.50	88.75			
Margin management	MM	mown grass margin =6 unmown grass margin =23 cultivated=8 cultivated and sprayed with herbicides=2					
Position in the field	PF	edge centre			Edge Centre		
b) Plant functional traits							
Plant height (m)	PH	0.69±0.40	0.20	1.51	0.50±0.30	0.07	1.50
Month of first flowering (month)	MFF	4.60±2.15	1	7	3.60±1.80	1	12
Seed mass (mg)	SM	3.66±7.06	0.04	34.90	1.90±4.10	0.01	19.40
Raunkiær's life form	LF	Therophytes=19 Hemicryptophytes=4 Geophytes=2			Therophytes=59 Hemicryptophytes=5 Geophytes=2		

the variables, including the null model (i.e. intercept only). These submodels were ranked according to the corrected Akaike's Information Criterion (AICc, Burnham and Anderson, 2002); the model with the lowest AICc ($AICc_{min}$) is considered the most parsimonious. Additionally, we calculated Delta Akaike ($\Delta i = AICc_i - AICc_{min}$) which measures the loss of information respecting the $AICc_{min}$ and Akaike weights (w_i) interpreted as approximate probabilities of each model being the actual best model if the data were collected again (Burnham and Anderson, 2002). Models with $\Delta i < 2$ were not considered different from $AICc_{min}$ (Burnham and Anderson, 2002) and then, these models were deemed as the best set of submodels. The presence of the null model among the best set of submodels, indicates that none of the tested variables affected the response variable. Model averaged parameters and their unconditional standard errors were calculated for the best set of submodels ($\Delta i < 2$) which did not included the null model. The 95% confidence intervals (CI) were calculated to assess the magnitude of effect of each environmental variable. Variables which included zero in their CI indicates that have no influence on the response variables. Species richness was square root transformed to achieve normality of the residuals. In all models, assumptions of equal variances, normal distribution and uncorrelated residuals were evaluated graphically. All analyses were conducted in the R environment (R Development Core Team, 2012). Linear mixed effects models were adjusted using the lme4 function from the nlme library (Pinheiro *et al.*, 2012).

The relationships between species traits and environmental variables were analyzed using two complementary analyses: RLQ and Fourth-corner analysis (Dray *et al.*, 2014) separately for UK and Spain. RLQ analysis is a multivariate analysis which provides combination of traits that have the highest covariances with combination of environmental variables (Dolédec *et al.*, 1996) the Fourth-corner method tests associations between individual intensification variable and individual functional traits. Both analyses require three tables, R, L and Q. R is the environment x field table (here, six intensification variables in for UK and four variables for Spain). The L table is the species x field table and the Q table is the trait-species table (here, the four traits values of each considered species, Appendix C and D). The RLQ analysis performs a simultaneous ordination of the three tables in different steps. First, correspondence analysis (CA) and Hill and Smith analyses are used to analyse respectively L, R (with row weights equal to the row weights of CA) and the Q (with row weights equal to the column weights of CA) tables. RLQ then calculates two separate co-inertias on the R-L and L-Q tables and identifies axes in which the species scores are rearranged to maximize the covariance between the sampling units constrained by the intensification variables (the R table) and the species scores constrained by the species traits (the Q table). This results in linear combination of functional traits and agricultural intensification variables. A permutation model 6 (n= 999 permutations) with Bonferroni corrections for multiple comparisons was used to test the link between species traits and the environment. This permutation model encompasses two sub-models, model 2 and 4, which test the hypotheses that species are independent from their environment (row permutation of the R table) and their traits (row permutation of the Q table) respectively. Both sub-models must be rejected to confirm the significant relationship between R and Q tables. The Fourth-corner analysis assess the association between two quantitative variables with

Pearson correlation coefficient, between two qualitative variables with the Pearson Chi square and G statistic between one quantitative and one qualitative variables with Pseudo F and Pearson correlation coefficient. The significance of these relationships was tested again using the model 6 (n= 999 permutations) with Bonferroni corrections for multiple testing. All statistical analyses were performed with R software version 2.15.1 (R Development Core Team, 2012), using the libraries Ade 4 (Dray and Dufour, 2007).

III.3 RESULTS

III.3.1 Overview

A total of 88 and 116 species were recorded in UK and in Spain, respectively (Appendix E and F) with an average richness ± standard deviation of 7±3.7 and 4±3.3 species at the field edge and centre, respectively in UK, and of 13±5.5 and 11±6.0, respectively in Spain. In UK the most frequent species were *Galium aparine* L., *Alopecurus myosuroides* Huds. and *Anisantha sterilis* (L.) Nevski at field edges, and *G. aparine*, *A. myosuroides* and *Senecio vulgare* L. at field centres. In Spain, the most frequent species were *Polygonum aviculare* L., *Lolium rigidum* Gaudin and *Convolvulus arvensis* L. in field edges, and *P. aviculare*, *C. arvensis*, and *Anagallis arvensis* L. in field centres.

Functional diversity was very low in both datasets. In UK it was 0.03±0.02 and 0.02±0.02 at the edge and centre, respectively while in Spain it was 0.02±0.01 and 0.02±0.02, respectively. For the functional traits study, 25 species in UK and 58 species in Spain fulfilled the criteria of being present at a frequency of at least 5% (Appendix C and D) and only five were shared between both countries.

III.3.2 Effect of agricultural intensification on species richness, functional diversity and the distribution of functional traits in UK and Spain.

In the UK, species richness was influenced by position in the field and crop cover. There was a greater number of species at the edge compared to the centre and decreased with crop cover. These variables were within the best set of submodels (i.e. models with lowest Delta Akaike (Δ_i<2 units) and highest Akaike weight (w_i), see Table 2) and were supported by their confidence intervals which did not include zero (Table 3). In Spain species richness and functional diversity were not affected by any environmental variable; the null model was present within the best submodels in both cases (Table 2).

Regarding functional traits, the RLQ Monte-Carlo permutation tests indicated non significant associations between intensification variables and species traits in both countries ($p>0.05$ for models 2 and 4). In concordance with the RLQ analysis, the permutation tests of the Fourth-corner analysis did not reveal any significant relationship between individual functional traits and individual intensification variables in Spain and UK (Table 4).

Table 2. Ranking of the best set of submodels (Δ_i <2 units) generated from the full model analyzed with the linear mixed model models for richness and functional diversity in UK and Spain. Each row represents a submodel composed by the variables marked with x. The symbol ":" indicates interaction between variables. Corrected Akaike Information Criterion (AICc), Delta Akaike (Δ_i), and Akaike weights (w_i) are shown for each model. See Table 1 for abbreviations.

	null	AL	FS	MW	CC	MM	PF	FS:PF	PF:MW	AICc	Δ_i	w_i
Species richness												
UK												
			x	x	x		x		x	353.06	0.00	0.13
				x	x		x		x	353.28	0.22	0.11
			x		x		x			353.39	0.33	0.11
					x		x			353.72	0.66	0.09
			x	x	x		x			353.78	0.72	0.09
				x	x		x			354.10	1.04	0.08
		x	x	x	x		x		x	354.19	1.13	0.07
		x	x		x		x			354.22	1.15	0.07
			x	x	x		x	x	x	354.78	1.71	0.05
				x	x	x	x		x	354.81	1.74	0.05
		x	x	x	x		x			354.82	1.75	0.05
			x		x		x	x		355.01	1.94	0.05
		x		x	x		x		x	355.06	1.99	0.05
Spain							x			115.35	0.00	0.35
	x									115.91	0.56	0.27
Functional diversity												
UK												
					x		x			-816.85	0.00	0.20
		x			x		x			-816.48	0.38	0.17
					x					-816.33	0.53	0.15
		x			x					-816.10	0.76	0.14
				x	x		x		x	-815.39	1.46	0.10
				x	x		x			-815.16	1.69	0.09
		x		x	x		x		x	-815.03	1.83	0.08
		x		x	x		x			-814.89	1.96	0.08
Spain				x						-239.91	0.00	0.35
	x									-239.32	0.59	0.43

Table 3. Model averaged parameters, unconditional standard error (UnSE) and their 95% confidence intervals (CI) for each intensification variable and interactions present within the best set of submodels (Δ_i <2units) when it did not contain the null model. It was only performed for the UK data, since in Spain the null model was always present within the best set of submodels (See table 2). In bold the variables which their CI did not contained zero.

	Estimate	UnSE	lower CI	upper CI
Species richness				
Intercept	2.294	0.485	1.337	3.251
CC	-0.009	0.002	**-0.014**	**-0.003**
FS	0.012	0.007	-0.002	0.028
PF (edge)	0.552	0.17	**0.216**	**0.888**
MW	-0.012	0.029	-0.071	0.046
MW:PF (edge)	-0.054	0.031	-0.117	0.008
AL	0.007	0.007	-0.008	0.023
FS:PF (edge)	-0.005	0.006	-0.018	0.008
MM (cultivated and sprayed)	-0.761	0.415	-1.584	0.06
MM (grass margin)	-0.111	0.202	-0.511	0.288
MM (unmown grass margin)	-0.313	0.174	-0.658	0.031
Functional diversity				
Intercept	0.003	0.017	0.000	0.068
CC	0.000	0.000	0.000	0.000
PF(edge)	0.000	0.000	0.000	0.014
AL	0.000	0.000	0.000	0.000
MW	0.000	0.000	0.000	0.002
MW:PF(edge)	0.000	0.000	0.003	0.000

III.4 DISCUSSION

In the present study, we compared the response to agricultural intensification of cereal weed communities of UK and Spain in terms of species richness, functional diversity and distribution of functional traits.

Species richness in UK was affected by crop cover, which is related to intensive management practices such as higher sowing density, narrower rows

Table 4. Relationship between functional traits and intensification variables provided by the Fourth-corner analyses. None of the relationships were significant (p>0.05 in all cases). See Table 1 for abbreviations.

	PH	MFF	SM	LF
UK				
AL	r= 0.03	r= 0.02	r= 0.06	F=4.14
FS	r=-0.02	r=-0.02	r=-0.13	F=2.52
MW	r= 0.01	r=-0.04	r=-0.04	F=2.05
CC	r=-0.07	r=-0.01	r=-0.01	F=1.67
MM	F= 0.69	F=0.20	F=2.40	χ^2 =7.81
PF	F= 1.07	F=0.03	F=0.07	χ^2 =0.79
Spain				
AL	r=0.06	r=-0.07	r=-0.28	F =240.21
FS	r=-0.08	r= 0.27	r=-0.12	F=636.87
MW	r=-0.03	r= 0.04	r=-0.03	F=37.26
PF	F =85.8	F =85.24	F =103.6	χ^2 =435.87

Relationship between functional traits and intensification variables were obtained using a Pearson correlation coefficient (r) for two quantitative variables, Chi-square(χ^2) for two qualitative variables and pseudo-F for one quantitative and one qualitative variable (abbreviations for environmental variables and traits are in table 1).

and also reflects efficiency of crop management. The negative effect of crop cover on species richness is probably due to dense crop canopy suppresses weed development by competition for light.

In UK, species richness was higher at the edge than at the centre of the field and this result has been reported before (Marshall, 1989; Romero *et al.*, 2008; Fried *et al.*, 2009; José-María *et al.*, 2010). This positional effect has been attributed to the lower pressure of crop management practices at the field edge compared to the field centre, leading to the argument that this field area can be considered as a valuable habitat for diversity conservation. Increased taxonomic diversity at the edges has largely been due to a greater proportion of perennial species being recorded at the edge samples as they include both perennial species adapted to the field margin and annual species adapted to the disturbed centre (Fried *et al*. 2009, José-María *et al*. 2010). We contend that, as opposed to the field edges representing a separate habitat characterised by reduced fertility and crop competition, this observation is an example of the *mass effect phenomenon* that predicts species diversity will be greatest at habitat boundaries (Shmida and Wilson., 1985). Fried *et al*. (2009) found no significant difference in Ellenberg nitrogen numbers between edge and centre plant communities in France, which concurs with our results that indicate both habitats support exclusively nitrophilous plant communities. Indeed, in Spain species richness was similar between edges and centre suggesting that the intensity of crop management practices was similar throughout the entire field. Probably the machinery can access until the perimeter of the parcel because of the large size of the crops fields and their flat topography, thus differences in management efficiency between edge and centre are negligible (Rodríguez and Wiegand, 2009).

Functional traits were not affected by any intensification variable in both countries; likely due to the strong long term filtering effect imposed by conventional farming (Storkey *et al*., 2012). This intensive management system that has been carried out for many decades in both countries may have progressively filtered species leading to the contemporary weed communities (Lososová and Simonová, 2008; Gunton *et al*., 2011). This is supported by the starkly low functional diversity found in both countries reflecting a strong environmental filtering effect forcing a convergence in successful trait values and excluding poorly adapted species (Maire *et al*., 2012). Indeed, it is noteworthy that mean and range trait values in UK and Spain were very similar despite low taxonomic overlap (Table 1b). Weed communities were characterized by being mostly therophytes with short stature (shorter than the crop), that flowered between March and April and had a low seed mass (less than 2.5 mg, Storkey *et al*., 2010). These trait syndromes have been reported as the most successful for weeds thriving under high agricultural intensification pressure (Storkey *et al*., 2010; Gunton *et al*., 2011; Fried *et al*., 2012; Perronne *et al*., 2015). This combination of traits confers the species advantages to cope with agricultural management. For instance therophytes are highly adapted to recurrent disturbance (McIntyre *et al*., 1995; Trichard *et al*., 2013), while species with short stature have a rapid growth rate with less investment in stem structure and can be shade-tolerant (Westoby, 1998; Perronne *et al*., 2015). Flowering in early spring allows plants to shed their seeds after post-emergence herbicide application and before crop harvest (Gunton *et al*., 2011). The advantages of light seeded species reside in a high productivity per plant and longer seed bank longevity (Westoby, 1998). The average of the values of seed mass in UK was higher than 2.5mg due to the presence of few heavy seeded species such as *Vicia sativa* L. and *Fumaria officinalis* L. although most species were relatively lighter than 2.5 mg (Appendix C). However, slightly different trait syndromes have been reported by Guerrero *et al*., (2014) in central Spain who found that species tended to be taller and with higher seed mass in intensive managed fields and by Pinke and Gunton (2014) in Hungary who found both taller and shorter species in intensive systems. This discrepancy might be due to differences in their studies. Successful trait syndromes were related to a high competitive ability at seedling and adult stages (Westoby, 1998). While in other cases, including our study, the best strategy was related to a high colonization capacity and avoidance of damage caused by agronomic practices (Storkey *et al*., 2010; Fried *et al*., 2012; Perronne *et al*., 2015).

The flora of the field margin can contribute to enhance plant diversity within the crop field (Marshall, 1989; Romero *et al*., 2008). However, this effect was not detected in our study. A plausible explanation for Spain may be that field margins were generally narrow. Narrow margins are likely to be exposed to the same disturbances than the field crop and, consequently, support the same weed species (Shippers and Joenje, 2002; De Cauwer *et al.*, 2008; Bassa *et al*., 2011). Therefore, the contribution of new species from field margins would be unlikely. The same explanation can be given to intensively managed field margins in UK (e.g. herbicide, mown, etc.; De Cauwer *et al*., 2008), whereas less intensively managed margins harbour a different flora of mostly perennial species that cannot thrive within field (Marshall, 1989, De Cauwer *et al*., 2008).

In the case of field size, it has been stated that machinery efficiency increases with field size. In our study, however, fields were generally large and this fact can explain the abscence of field size effect (Rodríguez and Wiegand, 2009).

The lack of effect of landscape complexity perhaps is due to the effect of crop management exceeded the influence of the landscape context, as has been reported in other English and Spanish studies (Marshall, 2009; José-María *et al*., 2010, José-María *et al.*, 2011). Other likely explanation may be the low landscape complexity based mainly in arable land cover (mean >60% in both countries) therefore, the gradient of landscape complexity considered was not ample enough to detect changes.

III.5 CONCLUSIONS

Results of this study established that variability in management intensity in conventional cereal cropping systems, either at local and landscape scales, are very low, and thus it cannot contribute to preserve the functional and taxonomic diversity that has been lost due to agricultural intensification. With the only exception of crop cover, that showed to negatively affect species richness. The low functional diversity and the notorious similarity in functional trait values between cereal weed communities of both study countries suggest a strong long-term filtering effect imposed by conventional agriculture which is a management system that has been carrying out for decades in both countries. This strong filtering effect has led to weed communities composed of species with trait syndromes highly adapted to intensification pressure despite low taxonomic overlap. We contend that field edges cannot be considered to be a functionally discrete habitat that can be relied on to preserve populations of arable plant species adapted to less fertile environments and that have declined in Europe in the post war period.

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Chapter IV

THE RESPONSE OF TAXONOMIC AND FUNCTIONAL DIVERSITY OF THE SEED BANK TO AGRICULTURE INTENSIFICATION AND SOIL PROPERTIES IN TWO MEDITERRANEAN CEREAL AREAS IN SPAIN

IV. The response of taxonomic and functional diversity of the seed bank to agriculture intensification and soil properties in two Mediterranean cereal areas of Spain

ABSTRACT

Weed seed bank diversity has been severely impacted by agriculture intensification. However, the functional consequences have been poorly studied in highly intensified agro-ecosystems. This study evaluated the importance of soil properties and agriculture intensification at field and at landscape scale on taxonomic, functional diversity and the distribution of functional traits of plants represented in the soil seed bank in 47 conventionally managed cereal fields in two Mediterranean regions of Spain, Andalusia and Catalonia. Field intensification was measured according to position in the field (margin, edge and centre) which reflects different intensities of management practices. Intensification at the landscape scale was measured as percentage arable land cover within circular sectors of 1 km radius around the focus field. Functional diversity and the distribution of functional traits were evaluated based on eight traits related to the whole plant life-cycle. In total, 175 and 116 species were recorded in the seed bank in Andalusia and Catalonia, respectively. We found that taxonomic and functional diversity, and the distribution of functional traits in the weed seed bank were unaffected by soil properties, position in the field or landscape structure in any of the two studied regions. The results suggest that intensity of management practices was similar throughout the entire field, and that field margin flora is highly affected by adjacent crop management. The lack of impact of landscape structure may be due to a high mean percentage arable land cover in both territories, therefore indicating a limited availability of alternative habitats acting as a source of propagules. Long-term agricultural intensification at local and landscape scale in cereal systems has led to weed communities characterized by an extremely low functional diversity with functional traits adapted to recurrent disturbance and with a high reproduction capacity.

Kewwords: Functional traits, Rao´s quadratic entropy, field margins, arable weeds, plant height.

IV.1 INTRODUCTION

Agriculture intensification is one of the major causes of loss of biodiversity in the agro-ecosystem, and plants, which are the base of the food chain, are among the organisms most seriously threaten (Storkey *et al.*, 2011). The soil seed bank is a key component for plant diversity resilience, and it is a good indicator of the long-term intensification process (Hawes *et al.*, 2010).

The soil seed bank is annually replenished by seeds from the standing vegetation of local populations and from populations located in the surroundings (Tamme *et al.*, 2013). It also contains seeds from previous years that remain dormant until environmental conditions are suitable for germination. Thus, it may contain a larger and even different species pool than the observed in the standing vegetation (Pakeman and Eastwood, 2013).

Diversity and size of the seed bank largely depend on local intrinsic characteristics and to agriculture intensification (Hawes *et al.*, 2010). Soil properties, like texture and nutrient content, modulate soil water storage capacity and fertility which, in turn, regulate individual plant growth and competitive interactions at the community level, largely influencing plant fecundity and thus seed availability for seed bank replenishing (Hawes *et al.*, 2010). In addition, soil properties directly influence seed persistence in the soil reservoir. For instance, nitrate concentration in the soil solution modulates seed dormancy and germination responses (Booth *et al.*, 2003; Baskin and Baskin, 1998), and clay content may influence the risk of seed death due to waterlogging (Hawes *et al.*, 2010).

In conventional agriculture, decades of intensive weed control practices such as the use of herbicides or soil cultivation have progressively reduced seed bank diversity and size (Armengot *et al.*, 2011; José-María and Sans, 2011). The efficiency of management varies across the cropped field being higher at the field centre than at the edges. This fact contributes to explain the greater number of species found at field edges compared to field centres (Romero *et al.*, 2008; Fried *et al.*, 2009; José-María and Sans, 2011). Futhermore, field margins are another important element of the agricultural landscape enhancing biodiversity (Marshall and Moonen, 2002). Field margins are much less affected by crop management intensification as they are uncropped (Marshall *et al.*, 2006). Although field margins represent a considerable smaller area than crop fields, they are often richer in plant species (José-María *et al.*, 2010; Poggio *et al.*, 2010).

Landscape complexity is an indicator of agricultural intensification at the landscape scale and has been related to the percentage cover of arable land in a given area (Roschewitz *et al.*, 2005). Increased landscape complexity benefits field seed bank diversity because seed dispersal may occur from the surrounding alternative habitats (Roschewitz *et al.*, 2005; José-María and Sans, 2011).

It is known that these field and landscape factors affect taxonomic diversity; however, functional diversity and the distribution of functional traits have been rarely studied at the seed bank level (Pakeman and Eastwood, 2013). A plant functional trait (FT) is defined as any morphological, physiological or phenological feature measurable at the individual level (Garnier and Navas, 2012). FT responds to environmental drivers; plants with trait syndromes successful to overcome changes in the habitat are likely to persist while species with maladapted traits are likely to reduce their abundance or even disappear (Garnier and Navas, 2012). Environmental drivers might select for a same set of trait values reducing the original range of traits, thus reducing the functional diversity, which in turn is strongly related to ecosystem processes (Díaz and Cabido, 2001).

In the present study we investigated the taxonomic and functional diversity and the distribution of plant functional traits in the seed bank of 47 conventionally managed, rainfed cereal fields in two Mediterranean regions of Spain: Andalusia and Catalonia (Figure 1). Large areas in both regions are traditionally devoted to cereal crops and other characteristic Mediterranean crops such as olive orchards, vineyards and fruit trees. These areas reflect long-term use of herbicides and pesticides in conventionally managed field crops and their landscape have been simplified by the replacement of (semi)natural areas for arable land through decades (Aparicio, 2008; José-María *et al.*, 2010; Armengot *et al.*, 2011). Much investigation efforts have been focused on comparing contrasting intensification intensities (e.g. conventional *vs*. organic farming), but studies on field and landscape effects within intensively managed agricultural areas are scarce. Therefore, the aims of the present study were: i) to assess the extent to which soil properties, agricultural intensification at the field scale (i.e. position in the field) and landscape scale (landscape complexity) affect the taxonomic and functional diversity, and the distribution of functional traits of plant species represented in the seed bank in conventionally managed rainfed cereal fields, ii) to rank the relative importance of each variable, and iii) to determine whether these variables influence the weed communities similarly in two Mediterranean regions. We hypothesized that all the environmental variables will have some effect on weed communities and position in the field will have the strongest effect and these effects will be similar between both regions.

IV.2 MATERIALS AND METHODS

IV. 2. 1 Study areas

The study was conducted in two regions of Spain, Andalusia (along the Guadalquivir River Basin) and central Catalonia. In total, 47 conventionally managed rainfed cereal fields were selected; 23 fields in Andalusia and 24 in Catalonia (Figure 1) along a gradient of arable land cover. Both areas share a Mediterranean climate, with an average annual temperature of 18.6 ºC and 15.5 ºC, and mean annual precipitation of 590 mm and 640 mm in Andalusia and Catalonia, respectively. The soils of the sampled fields were alkaline with textures varying from clayish to sandy loam. The main land-uses in both areas are cereals crops followed by olive orchards, vineyards, other arable crops and human settlements.

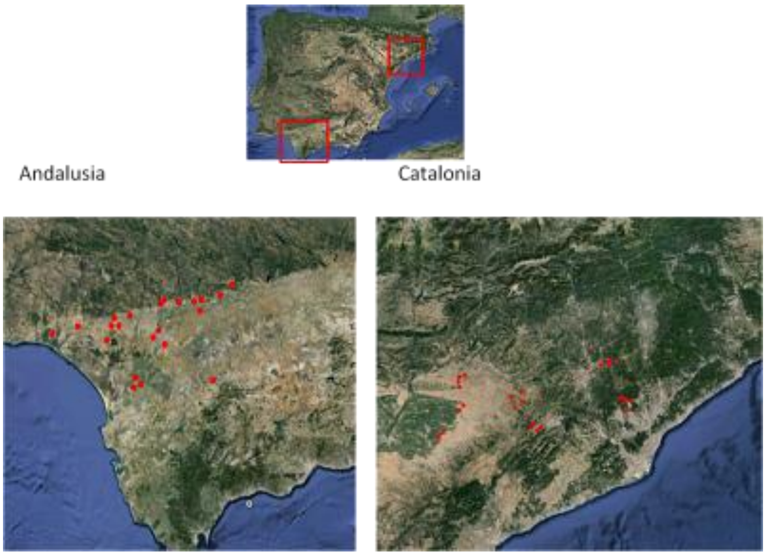

Figure1. Location of the sampled cereal fields in Andalusia (23 fields) and Catalonia (24 fields).

IV. 2. 2 Seed bank sampling

Soil samples were collected during September-October of 2010 and 2011 before cereal sowing. First, in each field, a side next to a road or path was selected to avoid influence of management of neighbouring fields (Le Coeur *et al.*, 2002). Then, three positions were delimited: the field margin (uncropped vegetation strip next to the crop, Bassa *et al.*, 2011), the field edge (the first five cultivated meters adjacent to the field margin) and the field centre (at least 25m away from the field margin). In each position, 27 soil cores of 4 cm diameter and 15 cm depth, or 20 soil cores of 3 cm diameter and 15 cm depth, were taken after removing surface plant litter in Andalusia and Catalonia, respectively. At the margin and edge, the soil cores were taken in zigzag every 1 meter and at the centre, they were taken every 5 meters in diagonal towards the field centre (Figure 2).

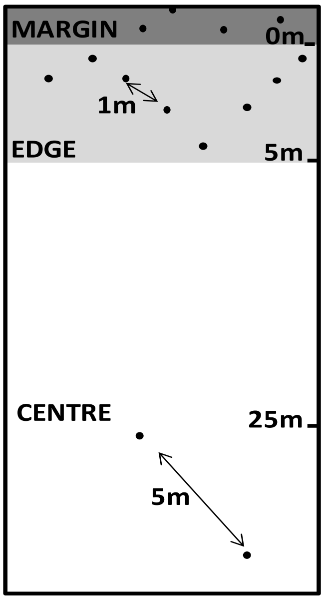

Figure2. Scheme of the sampling method. The three field positions are represented in different grey tones. Dots represent soil sampling points.

The soil samples were pooled for each position in the field keeping each field separated (3 positions x 47 fields = 141 samples). The resulting composite samples were placed in plastic trays (45 cm x 29 cm x 10 cm) forming thin soil layers of 1 cm height. A vermiculite layer of 1 cm height covered with an organza sheet, aimed to buffer against soil water content fluctuations, was previously added to the trays. The trays were randomly placed on benches in a non-heated greenhouse under natural light conditions and they were kept moist by regular watering. Positions of the trays were randomized every 2 weeks and soil was mixed bi-monthly in order to favour germination of seeds and prevent growth of mosses. Emerged seedlings were identified, counted and removed as they emerged, or marked/transplanted for later identification. The census lasted eight months each year up to when there was no further emergence for a period of two weeks (Hawes *et al.*, 2010).

IV. 2. 3 Soil properties and agricultural intensification variables

The following data sets were collected (Table 1) aimed to reflected soil characteristics and agricultural intensification at field and landscape scale: At field scale: i) Soil properties: simultaneously to seed bank sampling, four soil cores 15 cm depth were taken randomly at each position in each field and then pooled per position and field (2kg approx.). The percentage of sand, silt and clay, organic nitrogen, organic matter, extractable phosphorus, and available potassium were measured. Finally, two variables reflecting physical (percentage clay, C) and chemical soil properties (organic nitrogen content, N) were selected as putative explanatory variables. C was correlated to percentage of sand ($r= -0.73$, $p<0.01$ and $r= -0.5$, $p<0.01$, in Andalusia and Catalonia, respectively) and N was strongly correlated to the remaining soil chemical properties (Andalusia: phosphorus, $r=0.47$, $p<0.05$; organic matter $r=0.9$, $p<0.05$; potasium $r=0.39$, $p< 0.05$. Catalonia: phosporus, $r=0.3$, $p<0.05$; organic matter, $r=0.93$, $p<0.05$; potassium $r=-0.56$, $p<0.05$). ii) Intensification at field scale was measured according to position in the field: margin, edge and centre as defined previously (Figure 2). iii) Intensification at landscape scale was measured as the proportion cover of arable land within a circular area of 1 km radius centred at each field margin, using SIGPAC, (Sistema de Información Geográfica de Parcelas Agrícolas, http://sigpac.mapa.es/fega/visor/). Arable land cover has been largely used as an estimate of landscape complexity, the lower the proportion of arable land, the highest the landscape complexity (Gabriel *et al.*, 2005).

IV. 2.4 Plant functional traits

A set of eight functional traits associated to the vegetative and reproductive phases of the plant life-cycle was considered (Table 2, Appendix G and H): plant height, seed mass, month of first flowering, flowering duration, Raunkiaer's life form, growth form, pollination type and dispersal type (Westoby, 1998; McIntyre *et al.*, 1999; Storkey *et al.*, 2010; Guerrero *et al.*, 2014; Pinke and Gunton, 2014). Plant height (PH) is related to the ability to compete for light, resistance to disturbance and seed dispersal distances (Westoby, 1998; Fried *et al.*, 2012). Seed mass (SM) is related to plant fecundity, seedling establishment ability and persistence in the soil seed bank (Westoby, 1998; Pakeman *et al.*, 2008). Month of first flowering (MFF) and flowering duration (FD) are related to the ability to reproduce under the disturbance regime imposed by agricultural practices (Fried *et al.*, 2012; Pakeman and Eastwood, 2013). Raunkiaer´s life form (LF) is related to disturbance resistance and the

Table 1. Mean ±standard deviation (SD), minima and maxima of agriculture intensification variables and soil properties obtained in the 23 sampled fields in Andalusia and the 24 fields in Catalonia.

			Andalusia			Catalonia		
Variable	Abb.	Position	Mean± SD	Min.	Max.	Mean± SD	Min.	Max.
Position in field	PF		Margin, Edge, Centre			Margin, Edge, Centre		
Organic nitrogen (%)	N	Margin	0.12 ± 0.01	0.04	0.24	0.19 ± 0.02	0.06	0.40
		Edge	0.10 ± 0.01	0.04	0.17	0.17 ± 0.03	0.09	0.50
		Centre	0.09 ± 0.01	0.04	0.15	0.18 ± 0.02	0.07	0.70
Clay (%)	C	Margin	23.90 ± 1.94	10.4	44.2	15.70 ± 0.82	9.00	23.00
		Edge	25.99 ± 2.61	8.20	61.3	17.30 ± 0.73	10.30	22.80
		Centre	29.60 ± 2.75	12.00	61.6	18.44 ± 0.88	11.70	27.90
Arable land cover (%)	AL		61.30 ± 34.89	6.00	100	75.60 ± 22.66	25.00	100

capacity of vegetative propagation (McIntyre *et al.*, 1999). Pollination type (PT) and Dispersal type (DT) are related to the extent of pollen and seed flow, and reliance on animals for reproduction. To avoid influence of rare species in subsequent analyses, only species recorded in at least 5% of the fields were further considered (Kenkel *et al.*, 2002). DT was assessed according to propagule size and morphology. Seeds 0.5 to 10 mm in length lacking appendages were considered to experience mainly unassisted dispersal (barochory) whereas smaller seeds and seeds showing wings or pappus were classified as wind dispersed. Fleshy fruited species and species with spiny or awned propagules were deemed as zoochorous. Pollination type was obtained from Bocci (2015), seed mass from Royal Botanic Gardens Kew (2015) and life form, growth form, MFF and FD from Blanca *et al.* (2011) and de Bolòs *et al.* (1984).

IV. 2.5 Taxonomic and Functional diversity indices

Taxonomic diversity was measured by *Species richness* (*S*), the *Exponential of the Shannon-Wienner index* (eH), an estimation of the number of equally abundant species (Jost, 2006),*Evenness* (*J*), expressing the regularity of species abundance in a community, and seedling *abundance* (*Ab*, m^{-2}).

Functional diversity was assessed using the *Rao`s quadratic entropy index* (FD) calculated for the combination of the eight functional traits for species with a frequency of occurrence ≥ 5% (Rao, 1982). This index incorporates both the relative abundance of a species and a measure of the pair-wise functional differences between species, by measuring species distance in a functional trait space. It is denoted as

$$\mathrm{Rao} = \sum_{i=1}^{s}\sum_{j=1}^{s} dij\ pipj$$

where, s is the number of species, d_{ij} is the distance between species i and j; p_i and p_j are the relative abundances of species i and j. FD measures two important functional diversity properties: functional richness (the volume of niche space occupied by the species) and divergence (the distribution of abundance in the extremities of occupied trait space in community Rao, 1982; Mason *et al.*, 2013). The values of FD range between 0 and 1 with values near one indicating a high functional diversity, i.e. high dissimilarities of functional trait values among species.

Functional diversity indices were calculated using standardized traits (mean=0, SD=1). Gower distance was selected because of the presence of categorical and continuous traits, and Cailliez correction was used to correct for the non-euclidean distribution of traits (Laliberté *et al.*, 2014). All the indices were calculated using R software version 2.15.1 (R Development Core Team, 2012), using the library Vegan (Oksanen *et al.*, 2007) for taxonomic diversity and FD (Laliberté *et al.*, 2014) for functional diversity indices.

IV.2.6 Statistical analyses

Mixed effect models were used to assess the influence of soil properties, position in the field and landscape complexity on the taxonomic and functional diversity of plants inhabiting cereal fields, separately for Andalusia and Catalonia. This is a suitable approach to account for fixed and random

Table 2. Mean ± standard deviation (SD) and minima and maxima of the eight functional traits of the most frequent species in Andalusia and Catalonia.

		Andalusia			Catalonia		
Functional traits	Abbreviation	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Plant height (m)	PH	0.60 ± 0.40	0.07	2.00	0.54 ± 0.30	0.12	2.00
Seed mass (mg)	SM	1.99 ± 3.70	0.01	19.90	1.90 ± 4.10	0.02	19.90
Month first flowering (months)	MFF	3.50 ± 1.80	1	12	4.21 ± 1.60	1	7
Flowering duration (months)	FD	5.40 ± 2.90	1	12	4.90 ± 2.70	1	12
Raunkiær's life forms	LF	Geophytes = 3 Hemicryptophytes = 11 Therophytes = 63			Chamaephytes = 2 Geophytes = 1 Hemicryptophytes = 5 Therophytes = 54		
Growth form	GF	Dicotyledons = 61 Monocotyledons = 16			Dicotyledons = 50 Monocotyledons = 12		
Pollination type	PT	Anemo/entomogamous = 5 Anemogamous = 21 Autogamous = 14 Entomogamous = 37			Anemo/entomogamous = 2 Anemogamous = 13 Autogamous = 15 Entomo/autogamous = 8 Entomogamous = 24		
Dispersal type	DT	Anemochorus = 24 Barochorous = 48 Zoochorous = 5			Anemochorus = 15 Barochorous = 38 Zoochorous = 9		

effects in nested sampling designs (Pinheiro and Bates, 2000). AL, C, N and their interaction with position were considered as fixed effects. Field identity was tested as a random effect. Initially, a full model containing all environmental variables and relevant interactions was built for each response variable and, thereafter, submodels were created including all possible combination of variables, including the null model (i.e. without variables). They were ranked by Akaike´s information criterion corrected for small sample size (AICc), being the model with the lowest AICc ($AICc_{min}$) the most parsimonious. Additionally, Delta Akaike ($\Delta_i = AICc_i - AICc_{min}$) and Akaike weights ($w_i$) were calculated. The former measures the loss of information respecting the $AICc_{min}$ while the latter is interpreted as approximate probabilities of each model being the actual best model if the data were collected again (Burnham and Anderson, 2002). Models with $\Delta_i < 2$ were not considered different from the model with $AICc_{min}$ (Burnham and Anderson, 2002) and then, these models were deemed as the best set of submodels. The presence of the null model within the best set of submodels indicates the tested variables do not affect the response variable. Model averaged parameters and their unconditional standard errors were calculated for the best set of submodels only if they do not include the null model. The 95% confidence intervals (CI) were calculated for each parameter to assess the magnitude of effect of each environmental variable. CI including zero are indicative of a lack of influence of an environmental variable on the response variable. Species richness and eH were square-root transformed, and J and Ab were arcsin square-root transformed to achieve normality of the residuals. In all models, assumptions of equal variances, normal distribution and uncorrelated residuals were graphically evaluated.

The response of individual functional traits to environmental variables was analyzed with Fourth-corner analysis (Dray *et al.*, 2014) separately for Andalusia and Catalonia, following Fried *et al.* (2012). This analysis tests associations between individual environmental variables and individual functional traits. It requires three tables, R, L and Q. R is the environment x field table. L is the species x field table and Q is the trait x species table (Appendix G and H). The Fourth-corner analysis combines these tables to calculate Pearson correlation coefficient between two quantitative trait and environmental variable, Pseudo F and Pearson correlation coefficient for one qualitative and quantitative trait or environmental variable, and Pearson Chi square and G statistic when trait and environmental variable are both qualitative. The significance of these relationships was tested using the model 6 (n= 999 permutations) with Bonferroni corrections for multiple testing. All statistical analyses were performed with R software version 2.15.1 (R Development Core Team, 2012), using the library Ade 4 (Dray and Dufour, 2007).

IV.3 RESULTS

We recorded a total of 32,833 seedlings belonging to 175 species in Andalusia and 8,751 seedlings belonging to 116 species in Catalonia (Figure 3, appendix I and J). Average, standard deviation, minima and maxima of species richness, exponential Shannon-Wiener, Evenness, seedling abundance and Rao´s quadratic entropy index are summarized in Table 3 based on field position, cereal field and region levels. In Andalusia, the most frequent plant species in the seed bank of cereal fields were *Conyza bonariensis* (L.) Cronq. (75%), *Heliotropium europaeum* L. (68%) and *Amaranthus blitoides* S. Watson (68%), and the most abundant species were *Polypogon monspeliensis* (L.) Desf. (8426 seedlings/m^2), *Lolium rigidum* Gaudin. (3005 seedlings/m^2) and *Juncus bufonius* L. (2570 seedlings/m^2). The most frequent species in Catalonia were also the most abundant; *Papaver rhoeas* L. (86% and 731 seedlings/m^2) and *L. rigidum* (76% and 819 seedlings/m^2). A total of 77 species in Andalusia and 62 species in Catalonia showed frequency of occurrence ≥ 5% and these species were included in the analyses (Appendix G and H). The Rao´s quadratic entropy was extremely low in both areas (Table3) indicating a high similarity

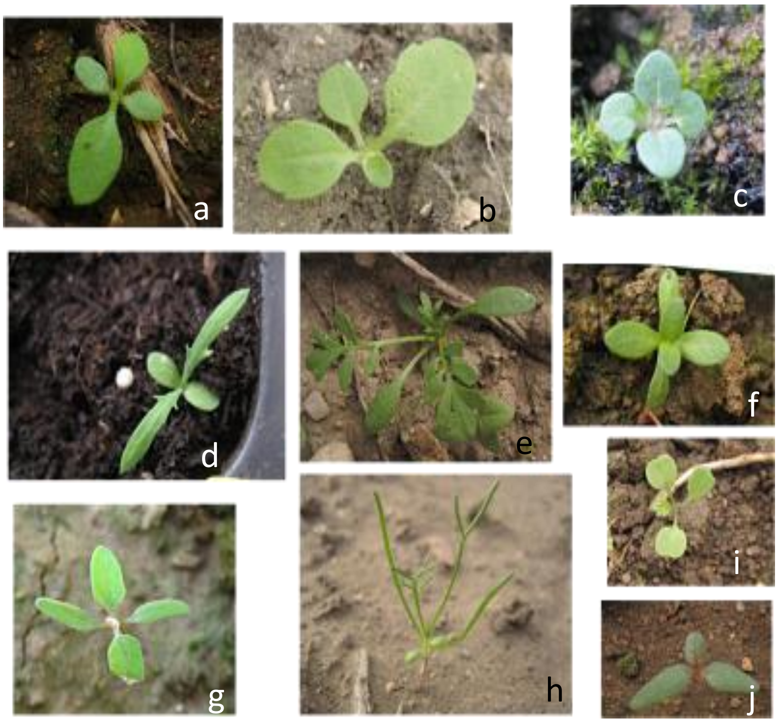

Figure 3. Seedlings of 11 species present in the soil seed bank of conventionally managed cereal fields. a*) Conyza bonariensis* (L.) Cronq., b) *Conyza sumatrensis* (Retz.) E. Walker, c) *Kickxia spuria* (L.) Dumort., d) *Glebionis segetum* (L.) Fourr., e) *Coronopus didymus* (L.) Sm., f) *Lythrum hyssopifolia* L., g) *Chenopodium album* L. , h) *Cladanthus mixtus* (L.) Chevall., i) *Rapistrum rugosum* (L.) All., j) *Amaranthus blitoides* S. Watson.

in trait values among species. The fitted mixed models indicated that none environmental variable affected any taxonomic or functional diversity index in any of the two study regions. For Andalusia, the null model was within the best set of models for eH, J, Ab and FD (Table 4). In the case of species richness; pos, C, AL and the interaction between C and pos were the variables present within the best set of submodels. However, the model weights were generally low (i.e. low probability of being the best model) and, indeed, CI of the associated parameters included zero for all the variables (Tables 4 and 5). In Catalonia, the null model was present within the best set of models for J, Ab and FD. For S and eH, the variables PF, N, C, Al, and the interactions C x PF and Al x PF were present within the best set of submodels however they were not supported by their CI (Table 4 and 5). Accordingly, the Fourth-corner analysis did not find any significant relationship between functional traits and environmental variables in any of the two regions (Table 6).

IV.4 DISCUSSION

In the present study, we found that taxonomic, functional diversity, and the distribution of functional traits of plants represented in the soil seed bank of cereal fields were unaffected by soil properties, field position or landscape complexity in any of the two studied regions of Spain.

The lack of influence of these variables may be due to an overall high intensification at field and landscape scale in both regions. The seed bank

Table 3. Mean ± standard deviation (SD) and minima and maxima for Richness, Exponential Shannon, Evenness and Abundance of the 175 and 116 species recorded in the soil seed bank of cereal fields in Andalusia and Catalonia, respectively; and Rao´s quadratic entropy index for the 77 and 62 species recorded at a frequency ≥5% in Andalusia and Catalonia, respectively

		Andalusia			Catalonia		
Indices	Position	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Richness	Total	18.50 ± 8.51	3	41	13.90 ± 5.50	5	31
	Margin	22.40 ± 8.29	8	41	15.50± 4.50	7	31
	Edge	18.60 ± 6.80	6	35	13.70 ± 4.90	5	25
	Centre	14.90 ± 8.91	3	39	12.5 ± 4.50	7	24
Exponential Shannon	Total	7.66 ± 3.94	1.40	16.80	6.60 ±2.60	1.95	12.20
	Margin	8.89 ± 3.80	2.80	16.80	7.30 ± 2.45	3.00	11.30
	Edge	7.53 ± 3.43	1.40	18.70	6.60 ± 2.60	2.25	12.20
	Centre	6.55 ± 4.35	2.20	19.50	5.80 ± 2.40	1.95	10.20
Evenness	Total	0.69 ± 0.17	0.11	0.96	0.70 ± 0.10	0.48	0.92
	Margin	0.69 ± 0.15	0.30	0.88	0.70 ± 0.10	0.48	0.92
	Edge	0.68 ± 0.17	0.11	0.86	0.70 ±0.14	0.35	0.92
	Centre	0.69 ± 0.18	0.29	0.96	0.60 ± 0.16	0.30	0.91
Abundance (m^2)	Total	249 ± 393.90	2.13	2864.00	86.20 ± 78.6	9.90	329
	Margin	278 ± 297.90	11.70	1026.00	85.1 ± 84.95	19.10	268
	Edge	294.4 ± 584.1	7.40	2864.00	79.1 ± 76.30	9.90	329
	Centre	174.5 ± 209.0	2.13	745.20	94.4 ± 76.70	19.50	268
Rao´s quadratic entropy	Total	0.05±0.02	0.00	0.08	0.04±0.020	0.01	0.08
	Margin	0.05±0.02	0.00	0.08	0.05±0.02	0.02	0.08
	Edge	0.05±0.02	0.01	0.08	0.04±0.02	0.01	0.07
	Centre	0.04±0.02	0.02	0.08	0.04±0.02	0.01	0.07

reflects the long term changes in the environmental conditions, thus it has been considered as a good indicator of gradual agricultural intensification through time (Hawes *et al.*, 2010). Both studied areas have been devoted to cereal crops under conventional management for decades and their landscape have been simplified by land consolidation and replacement of (semi)natural areas by cropland for long time (Aparicio, 2008; Rodríguez and Wiegand, 2009). Hence, it is possible that the lack of response of the soil seed bank in terms of

Table 4. Ranking of the best set of submodels (Δ_i <2 units) generated from the full model analyzed with the linear mixed model for Andalusia and Catalonia. Each row represents a submodel including the variables marked with x. Symbol ":" indicates interaction between variables. Corrected Akaike Information Criterion (AICc), Delta Akaike (Δ_i), and Akaike weights (w_i) are shown for each submodel. See table 1 and 3 for abbreviations.

	null	PF	N	C	AL	N:PF	C:PF	AL:PF	AICc	Δ_i	w_i
Andalusia											
S		x							188.60	0.00	0.33
		x		x					189.65	1.04	0.20
		x		x			x		189.97	1.37	0.17
		x			x				190.15	1.55	0.15
		x		x	x				190.25	1.65	0.15
eH		x			x				151.04	0.00	0.17
	x								151.73	0.69	0.12
J	x			x					-89.98	0.00	0.37
Ab									493.28	0.00	0.47
	x								493.90	0.69	0.34
FD	x								-363.80	0.00	0.37
Catalonia											
			x	x	x		x		123.75	0.00	0.32
S			x	x	x				124.71	0.96	0.20
		x	x		x				124.79	1.04	0.19
			x	x	x				125.22	1.47	0.15
eH		x			x				125.42	1.67	0.14
		x			x				98.95	0.00	0.25
		x			x				99.34	0.39	0.21
		x							99.39	0.44	0.20
		x	x		x				100.37	1.42	0.12
		x	x	x					100.44	1.49	0.12
		x		x					100.85	1.90	0.10
J	x								-120.10	0.00	0.54
Ab	x				x			x	332.17	0.00	0.31
FD	x								-444.50	0.00	0.65

S and eH were squareroot transformed and J and Ab were arcsin-squareroot transformed to meet the model assumptions.

taxonomic diversity and abundance is due to the present weed communities are adapted to these long-term agriculture intensification pressure. The functional

Table 5. Model averaged parameters, unconditional standard error (UnSE) and their 95%confidence intervals (CI) for each of the variables and interactions present within the best set of submodels (that did not contain the null model) for species richness in Andalusia and Catalonia and exponential Shannon in Catalonia. See table 1 for abbreviations.

Andalusia				
	Estimate	UnSe	lower CI	upper CI
Richness				
Intercept	4.25	0.39	3.48	5.04
PF(centre)	-0.33	0.49	-1.32	0.06
PF(margin)	0.48	0.38	-0.27	1.25
C	0.00	0.01	-0.04	0.02
C:PF (centre)	-0.30	0.01	-0.07	0.00
C:PF (margin)	-0.02	0.00	-0.06	0.02
AL	0.00	0.00	-0.00	0.01
Catalonia				
Richness				
Intercept	4.38	0.62	3.13	5.63
AL	-0.01	0.00	-0.02	0.00
C	0.00	0.03	-0.06	0.07
N	1.61	0.84	-0.08	3.31
PF(centre)	0.02	0.47	-0.93	0.09
PF(margin)	0.90	0.70	-0.50	2.30
C:PF(centre)	-0.01	0.03	-0.08	0.04
C:PF(margin)	-0.07	0.03	-0.13	0.01
Exponential Shannon				
Intercept	2.66	0.33	2.00	3.30
N	1.07	0.69	-0.31	2.46
PF(centre)	-0.21	0.10	-0.42	0.00
PF(margin)	0.08	0.10	-0.13	0.29
AL	0.00	0.00	-0.01	0.00
C	-0.01	0.01	-0.04	0.01

approach of this study supports this suggestion. On the one hand, Rao´s quadratic entropy index, measuring pair-wise functional differences between species, was extremely low (see table 3) indicating a filtering effect that restrict the range of plant phenotypes in the communities (Maire *et al.*, 2012; Pakeman and Eastwood, 2013). On the other hand, mean functional trait values of dominant species were similar in both regions resulting in trait syndromes highly adapted to intensification. The dominant species were mostly

Table 6. Relationship between functional traits and intensification variables and soil properties provided by the Fourth-corner analyses. See Table 1 and 2 for abbreviations. None of the relationships were significant ($p>0.05$ in all cases).

	PH	SM	MFF	FD	LF	GF	PT	DT
Andalusia								
PF	F=2061.90	F=309.43	F=9.97	F=383.70	χ^2=1403.70	χ^2=1728.50	χ^2=892.90	χ^2=1802.10
N	r=0.03	r=0.01	r=-0.06	r=0.08	F=60.50	F=335.12	F=360.46	F=647.17
C	r=0.21	r=-0.01	r=-0.06	r=0.00	F=27.90	F=785.60	F=186.88	F=226.60
AL	r=0.02	r=0.10	r=-0.05	r=0.08	F=390.03	F=330.89	F=49.40	F=436.63
Catalonia								
PF	F=5.59	F=2.70	F=33.88	F=3.39	χ^2=113.30	χ^2=36.01	χ^2=109.10	χ^2=89.22
N	r=0.04	r=0.09	r=-0.02	r=-0.09	F=0.27	F=130.16	F=86.26	F=56.28
C	r=-0.10	r=-0.11	r=0.00	r=0.06	F=2.80	F=526.63	F=58.01	F=138.34
AL	r=0.08	r=-0.05	r=0.17	r=0.12	F=47.70	F=172.06	F=103.40	F=140.37

Tests of significance were obtained using a Pearson correlation coefficient (r) for two quantitative variables, Chi-square(χ^2) for two qualitative variables and pseudo-F for one quantitative and one qualitative variable.

therophytes, shorter than the crop plants, with low seed mass (Storkey *et al.*, 2010) flowering before crop harvest (some species with high flowering phenology plasticity) and showing self and wind dispersal type (Table 2). These traits indicate a high reproductive capacity and adaptation to recurrent disturbance (Fried *et al.*, 2012; Pakeman and Eastwood, 2013; Trichard *et al.*, 2013; Pinke and Gunton, 2014). Pakeman and Eastwood (2013), investigating the response to disturbance of functional traits of the standing vegetation and the seed bank, found that after disturbance, there was a shift towards more fast-growing, shorter-lived species with selfing and insect pollination; similar to our results.

Several studies agree that disturbance intensity in crop fields (e.g. soil tillage and herbicide applications) is dependent on the position in the field, being highest at the centre, medium at the edge and minimum at the field margin, and weed species richness largely respond to this gradient either on the standing vegetation (Marshall, 1989; Romero *et al.*, 2008; Fried *et al.*, 2009; Poggio *et al.*, 2010) or the seed bank (José-María and Sans, 2011). Other studies using a functional approach and focusing only on the standing vegetation (no information available for seedbank), also found that the distribution of certain functional traits depended on position in the field; perennials were mostly found at the field margins while annuals were more common at the field centre, in accordance with differences in disturbance intensity (Poggio *et al.*, 2010; José-María *et al.*, 2011). In our study, the lack of response of taxonomic diversity and abundance of the seed bank to position in the field and the fact that most species were therophytes regardless position, suggest that intensity of crop management is uniform through the entire field (Pakeman and Eastwood,2013). The large size of crops fields and the flat topography of some areas may be factors facilitating effective access of the machinery to field edges, blurring differences in management efficiency between edge and centre (Rodríguez and Wiegand, 2009). Field margins can also be experiencing increasing disturbance intensity in these intensively managed systems. Field margins in both areas were mainly composed of a narrow strip of herbaceous vegetation that in few cases had more than two meters width (personal observation) consequently, they were prone to accidental or conscious cultivation. Many farmers assume that field margins are a source of weeds potentially entering into the crop and try cultivated as much land as possible. In our study we found weed species such as *P. rhoeas*, *L. rigidum* and *C. bonariensis* in Catalonia, and *Avena sterilis* L. and *Bromus* sp. in Andalusia (González-Andújar and Saavedra, 2003) which were present in more than 60% of the field margins. In order to prevent weed proliferation in margins, and at the same time enhance biodiversity, some authors suggest leaving the margins undisturbed and with a minimum width of 2 m to buffer against herbicide and fertilizer drift, these would promote growing of other plants than weeds (Marshall, 1989; Marshall and Arnold, 1995; Schippers and Joenje, 2002; Ma and Herzon, 2014). This practice should be encouraged as a first step to re-create field margins.

Diversity of the standing vegetation has been showed to be higher in crop fields located within complex landscapes compared to fields within simple agricultural landscapes because the former support more alternative habitat types that may act as a source of propagules potentially colonizing the fields (Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005). However, it seemed that the impact of landscape complexity largely depended on the position in the field; the positive effect was maximum in field margins and edges and negligible in field centres (José-María *et al.*, 2010; Armengot *et al.*, 2011). The lack of influence of landscape complexity inside the crop is probably due to an overwhelming effect of management practices prevent the establishment and reproduction of the immigrant propagules (Marshall, 2009; José-María *et al.*, 2010). Landscape complexity also influenced the functional traits of the standing vegetation; wind dispersed species and therophytes were more frequent in simple landscapes because seeds reach further distances in open landscapes and because of low availability of perennial propagules (Poggio *et al.*, 2010; José-María *et al.*, 2011). In our study, landscape structure influenced neither taxonomic diversity, nor functional diversity nor functional traits and there are three plausible explanations. First, as mentioned before, the high intensive management of cereal field regardless position in the field would have hindered the establishment of immigrant species. Second, our fields were mostly located within simple landscapes (i.e mean cover of arable land higher than 60%) and thus the gradient of landscape complexity may have been too short to detect changes in the weed communities. Finally, most of species were barochorus, suggesting a short dispersal distance.

Soil properties are major determinants of composition and diversity of weed communities modulating water and nutrient availability (Hawes *et al.*, 2010, Booth *et al.*, 2003; Baskin and Baskin, 1998). However, in the present study differences among fields in organic nitrogen and clay content did not influence either taxonomic or functional diversity of the weed seed bank. Mean content of organic nitrogen was medium to low in Andalusia, in accordance with levels in conventionally managed fields, but in Catalonia some fields showed high content (Table 1). Clay content of cereal field soils fluctuated considerably from low to high in Andalusia, but it was consistently medium to low in Catalonia. Low nitrogen content; which was also related to other nutrients, might by compensated by fertilization. Therefore, we suggest that soil properties were not extreme enough to induce changes in taxonomic or functional diversity, and that other environmental and agronomic factors have stronger effects in driving seed bank diversity in conventionally managed cereal fields.

IV.5 CONCLUSIONS

The present study showed that taxonomic and functional diversity, and the distribution of functional traits in the seed bank of conventionally managed cereal fields responded neither to position in the field nor to landscape complexity nor to soil properties. Results suggest that soil properties are not determinant factors of plant diversity in these areas. Regarding intensification, management intensity seems to be homogeneous through the entire field and field margins are highly influenced by adjacent crop management. The high proportion of arable land cover in the agricultural landscape, which is also associated to intensive land-use at the field scale, do not offer alternative habitats potentially acting as source of species. Long-tem agriculture intensification has resulted in communities with extremely low functional diversity with dominant traits adapted to recurrent disturbances. The seed bank could restore taxonomic diversity of the standing vegetation, but not the functional diversity in these highly intensified areas.

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Chapter V

GENERAL DISCUSSION

V. GENERAL DISCUSSION

Since the end of the Second World War, the development of agriculture in the European Union has been driven by the pursuit of ever-higher levels of productivity and efficiency. This has led to an agricultural intensification with the adoption of new farming methods, which have changed the face of the countryside to an unprecedented degree. Agricultural intensification has resulted in the loss of biodiversity and ecosystem services on farmland. The weed communities have been specially affected by this intensification process. Several studies have focused on the impact of intensification on taxonomic weed diversity. However, there are scarce or inexistent studies on plant functional diversity of the standing vegetation and the seed bank. In this thesis, we have tried to fill gaps in existing information on the influence of agricultural intensification in conventionally managed rainfed cereal fields on the taxonomic and functional diversity of weed communities.

V.1 AGRICULTURAL INTENSIFICATION AT FIELD LEVEL AND SOIL PROPERTIES

Field margins perform a range of important agricultural, environmental and ecological functions in agricultural landscapes. These habitats harbour considerably higher plant diversity than adjacent field crops and support a large diversity of vertebrate and invertebrates species. Margin width can alter both the richness and the composition of plant communities in these habitats (Schippers and Joenje, 2002; Tarmi *et al.*, 2009; Bassa *et al.*, 2012). Our results showed that species richness and functional diversity for the combination of traits and for seed dispersal type increased with margin width. This finding can be partly explained as a result of the direct effect of the species-area-relationship and also because wide margins offer better habitat quality buffering disturbances caused by the management of the adjacent crop field (Schippers and Joenje, 2002; Tarmi *et al.*, 2009; Bassa *et al.*, 2012; Ma and Herzon, 2014). Therefore, these favourable conditions allow the coexistence of a greater number of species and different functional strategies. However most of these species were annual weeds typical of the crop field, reflecting that the margins are somehow affected by the adjacent crop management (Bassa *et al.,* 2011).

It has been suggested that the flora of the field margin may enhance plant diversity of the adjacent crop field (Marshall, 1989; Romero *et al.*, 2008), but this effect was not detected in our study. As field margins, harboured the same weeds found within field, the contribution of field margins as source of new species from for the cropped field would be unlikely. The same explanation can be given to the field margins in UK cereal systems that were cultivated and/or sprayed with herbicides (De Cauwer *et al.*, 2008) while margins which are not disturbed (i.e. unmown margins) favour the presence of species that cannot thrive within field; for example perennial species (Marshall, 1989).

Crop cover was other field intensification variable affecting species richness in UK, probably because a dense crop canopy suppressed weeds through competition for light.

Farming intensity has been shown to vary through the entire field, increasing from the field margins towards the crop centre where soil cultivation, inputs of fertilizer and herbicides are more efficiently applied (Romero *et al.*, 2008; Fried *et al.*, 2009; Poggio *et al.*, 2010). Previous studies have shown that species richness decrease along this intensification gradient (Marshall, 1989; Romero *et al.*, 2008; Jose-María *et al.*, 2010). However, in Spain this effect was not found suggesting that crop management intensity is homogeneous throughout the entire field; probably because the predominantly large-sized and flat fields allow the movement of machinery until the perimeters of the field. Although UK presented a greater species richness at the field edges; it was attributed to the "*mass effect phenomenon*" (Shmida and Wilson,, 1985).

Functional traits were similar amongst positions in the field and showed syndromes adapted to management practices. Plant communities in the three studies, were composed of mostly therophytes, shorter than crop plants, with relatively low seed mass (Storkey *et al.*, 2010), flowering before crop harvest (some species with long flowering periods), insect and wind pollinated, and barochorous species. This syndrome is representative of species adapted to high intensity, temporarily predictable disturbance regimes (Grime, 1977; McIntyre *et al.*, 1995; Westoby, 1998). It was striking that functional trait values were similar between the two studied regions of Spain and, indeed, between Spain and UK, suggesting that the same environmental filters selected for the same suit of traits despite contrasting climatic condition and low species overlap.

However, different trait syndromes in response to intensification were also found by other studies (Guerrero *et al.* 2014; Pinke and Gunton, 2014).

The functional trait values were very low in the three studies suggesting a strong environmental filtering effect (Maire *et al.,* 2012) probably caused by the conventional farming system. Field margins are uncropped areas and the seed bank is a buffer memory of past conditions (Marshall and Moonen, 2002; Hawes *et al.*, 2010; Pakeman and Eastwood, 2013). The communities in these areas should show higher functional diversity than the inn-field vegetation. These results may indicate a long term filtering effect of conventional agriculture and reinforce the mentioned idea that field margins are also affected by crop management practices.

Soil properties are considered to be an important factor determining weed communities by modulating water and nutrient availability in the seed bank (Hawes *et al.*, 2010, Booth *et al.*, 2003; Baskin and Baskin, 1998). However in the present study they influence neither taxonomic nor functional diversity. In our study, levels of nitrogen were low to medium. The lack of response to N may be because farmers use fertilizers nutrients to overcome low levels of soil nutrient.

V.2 AGRICULTURAL INTENSIFICATION AT LANDSCAPE LEVEL

Intensification at the landscape scale is related to the increase in size and number of arable fields at the expense of (semi)natural habitats and habitat diversity. Some authors have found a beneficial effect of landscape complexity on diversity (Gabriel *et al.,* 2005, Roschewitz *et al.,* 2005), other studies found that the effect of landscape complexity is dependent on position in the field, being highest at the field margins and edges (José-María *et al.*,2010, José-María and Sanz, 2011, Solé-Senan *et al.*, 2014). Still other researchers did not find any effect of the landscape structure, like our study. Some authors stated that the high pressure of crop management may blur the effect of the landscape context (Marshall, 2009; Tarmi *et al.*, 2009; Armengot *et al.*, 2011). In our case, a likely explanation could be that fields were located in simple landscapes (i.e. mean arable land higher than 60%), therefore the range of landscape complexity may be too short to detect changes in the weed communities, although it is important to highlight that this characteristic is representative of the areas of study (Aparicio, 2008).

V.3 FINAL RECOMMENDATIONS

Two simple actions with extremely low cost are recommended in order to enhance plant diversity and prevent growing of weeds in field margins. First, farmers should delimit an area destined exclusively for field margins and these areas should have a minimum width of 2 m. Second, farmers should avoid causing any kind of direct or indirect disturbance on field margins. These simple actions would help creating different environmental conditions between field margins and crop fields and therefore, the field margins would develop other species than weeds. This is because in undisturbed areas, natural succession takes place and perennial species would establish in the field margins over time, recovering its ecological functions. Further investigations should aim to assess the effectiveness and the ecological and economic cost-benefit of these recommendations.

Regarding landscape configuration, the establishment and conservation of cereal field margins would create "green belts", which in turn, would increase the perimeter/area ratio of cropland at the landscape scale. A high ratio reflects a complex landscape because field margins are interconnected thorough the landscape and this fact has also showed to have an ecological and agronomic beneficial effect (Poggio *et al*., 2010).

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Chapter VI

GENERAL CONCLUSIONS

VI. GENERAL CONCLUSIONS

As a general conclusion we can state that:

1) Field margins of Mediterranean conventionally managed cereal fields were generally narrow.
2) Increased margin width favoured species richness and functional diversity for the combination of traits and for dispersal type of plant communities inhabiting cereal field margins. However, neither margin width nor margin management affected weed diversity within the crop field.
3) Position in the field (margin, edge and centre) did not affect taxonomic and functional diversity or the distribution of functional traits.
4) Soil properties did not affect taxonomic and functional diversity or the distribution of functional traits in the seed bank.
5) Functional diversity was very low at both the level of the established vegetation and the seed bank.
6) Mean values of the functional traits were very similar among all the studies and showed trait syndromes related to species adapted to intensification.
7) Landscape structure did not influence taxonomic and functional diversity or the distribution of functional traits in any study.

Appendix

APPENDIX

Appendix A. Functional trait values corresponding to the Q table of the 58 considered species in the sampled cereal field margins (chapter II).

Species	LF	GF	PT	DT	SM
Anacyclus clavatus (Desf.) Pers.	therophyte	dicot	entomogamy	anemochory	0.50
Anacyclus radiatus Loisel.	therophyte	dicot	entomogamy	anemochory	1.07
Anagallis arvensis L.	therophyte	dicot	entomogamy	barochory	0.50
Andryala integrifolia L.	hemicryptophyte	dicot	entomogamy	anemochory	0.15
Avena sterilis L.	therophyte	monoc	anemogamy	zoochory	19.94
Beta vulgaris L.	therophyte	dicot	anemogamy	barochory	12.70
Bromus diandrus Roth	therophyte	monoc	anemogamy	zoochory	11.24
Bromus lanceolatus Roth	therophyte	monoc	anemogamy	zoochory	3.90
Bromus hordeaceus L.	therophyte	monoc	anemogamy	zoochory	1.48
Bromus madritensis L.	therophyte	monoc	anemogamy	zoochory	3.33
Calendula arvensis L.	therophyte	dicot	entomogamy	zoochory	5.20
Campanula erinus L.	therophyte	dicot	entomogamy	anemochory	0.09
Centaurea melitensis L.	therophyte	dicot	entomogamy	anemochory	1.40
Chenopodium vulvaria L.	therophyte	dicot	anemogamy	barochory	0.40
Chrozophora tinctoria (L.) Raf.	therophyte	dicot	entomogamy	barochory	16.00
Cinchorium intybus L.	hemicryptophyte	dicot	entomogamy	anemochory	5.50
Convolvulus arvensis L.	geophyte	dicot	entomogamy	barochory	15.10
Crepis vesicaria L.	hemicryptophyte	dicot	entomogamy	anemochory	0.36
Cynodon dactylon (L.) Pers.	hemicryptophyte	monoc	anemogamy	barochory	0.20
Daucus carota L.	hemicryptophyte	dicot	entomogamy	zoochory	1.00
Diplotaxis virgata (Cav.) DC.	therophyte	dicot	entomogamy	anemochory	0.23
Ecballium elaterium (L.) A. Rich.	hemicryptophyte	dicot	entomogamy	barochory	12.10

Appendix A. *Continue*

Species	LF	GF	PT	DT	SM
Echium plantagineum L.	therophyte	dicot	entomogamy	barochory	4.30
Erodium malacoides (L.) L´Hér	therophyte	dicot	entomogamy	barochory	1.40
Erodium moschatum (L.) L′Hér.	therophyte	dicot	entomogamy	barochory	2.62
Euphorbia exigua L.	therophyte	dicot	anemogamy	barochory	0.35
Galium aparine L.	therophyte	dicot	entomogamy	zoochory	8.70
Galium parisiense L.	therophyte	dicot	entomogamy	zoochory	0.20
Glebionis coronaria (L.) Spach	therophyte	dicot	entomogamy	anemochory	1.50
Glebionis segetum (L.) Fourr.	therophyte	dicot	entomogamy	anemochory	1.52
Heliotropium europaeum L.	therophyte	dicot	entomogamy	barochory	1.10
Helminthotheca echioides (L.) Holub	hemicryptophyte	dicot	entomogamy	anemochory	1.31
Hirschfeldia incana (L.) Lagr. Foss.	therophyte	dicot	entomogamy	barochory	0.23
Hordeum murinum L.	therophyte	monoc	anemogamy	zoochory	10.50
Lactuca serriola L.	therophyte	dicot	autogamy	anemochory	0.58
Lavatera cretica L.	therophyte	dicot	entomogamy	barochory	7.01
Lolium rigidum Gaudin	therophyte	monoc	anemogamy	barochory	3.34
Malva nicaensis All.	therophyte	dicot	entomogamy	barochory	8.60
Malva parviflora L.	therophyte	dicot	entomogamy	barochory	2.80
Malva sylvestris L.	therophyte	dicot	entomogamy	barochory	5.40
Medicago polymorpha L.	therophyte	dicot	autogamy	zoochory	2.95
Papaver rhoeas L.	therophyte	dicot	entomogamy	anemochory	0.20
Phalaris brachystachys Link	therophyte	monoc	anemogamy	barochory	1.90
Phalaris minor Retz.	therophyte	monoc	anemogamy	barochory	1.60
Phalaris paradoxa L.	therophyte	monoc	anemogamy	barochory	1.30
Piptatherum miliaceum (L.) Coss.	hemicryptophyte	monoc	anemogamy	barochory	0.61
Plantago lagopus L.	hemicryptophyte	dicot	anemogamy	barochory	0.30
Polygonum aviculare L.	therophyte	dicot	autogamy	barochory	1.30

Appendix A. Continue

Species	LF	GF	PT	DT	SM
Polypogon monspeliensis (L.) Desf.	therophyte	monoc	anemogamy	barochory	0.10
Pulicaria paludosa Link	therophyte	dicot	entomogamy	anemochory	0.17
Rapistrum rugosum (L.) All.	therophyte	dicot	entomogamy	barochory	2.9
Ridolfia segetum L.(Moris)	therophyte	dicot	entomogamy	barochory	0.6
Scolymus maculatus L.	therophyte	dicot	entomogamy	anemochory	1.54
Sonchus oleraceous L	therophyte	dicot	entomogamy	anemochory	0.30
Silybum marianum (L.) Gaertn.	hemicryptophyte	dicot	entomogamy	anemochory	22.50
Torilis arvensis (Huds.) Link	therophyte	dicot	entomogamy	zoochory	2.10
Trisetaria panicea (Lam.) Paunero	therophyte	monoc	anemogamy	barochory	0.05
Urospermum picrioides (L.) F. W. Schmidt	therophyte	dicot	entomogamy	anemochory	1.6

Appendix B. List of the 306 species recorded in the 94 sampled cereal field margins and their frequency. The species are sorted alphabetically. In bold, are the 58 species considered in the functional analyses (chapter II).

Species	Frequency
Aegilops geniculata Roth	2.13%
Aegilops triuncialis L.	1.06%
Ajuga iva (L.) Schreb.	1.06%
Allium ampeloprasum L.	1.06%
Alyssum alyssoides (L.) L.	1.06%
Amaranthus albus L.	1.06%
Amaranthus blitoides S. Watson	9.57%
Amaranthus retroflexus L.	3.19%
Ammi majus L.	3.19%
***Anacyclus clavatus* (Desf.) Pers.**	11.70%
***Anacyclus radiatus* Loisel.**	18.09%
***Anagallis arvensis* L.**	53.19%
Anagallis foemina Mill.	2.13%
Anchusa azurea Mill.	3.19%
***Andryala integrifolia* L.**	21.28%
Anthemis arvensis L.	4.26%
Anthemis cotula L.	2.13%
Apera spica venti (L.) P. Beauv.	1.06%
Apium nodiflorum (L.) Lag.	1.06%
Apiaceae	1.06%
Aristolochia baetica L.	1.06%
Arundo donax L.	1.06%
Asparagus acutifolius L.	1.06%
Astragalus hamosus L.	4.26%
Atractylis cancellata L.	1.06%
Atriplex patula L.	2.13%
Atriplex prostrata L.	3.19%
Avena barbata Link	5.32%
***Avena sterilis* L.**	59.57%
Bartsia trixago L.	2.13%
***Beta vulgaris* L.**	15.96%
Biscutella auriculata L.	1.06%
Borago officinalis L.	8.51%
Brachypodium phoenicoides (L.) Roem. & Schult.	1.06%
***Bromus diandrus* Roth**	27.66%
***Bromus hordeaceus* L.**	24.47%
***Bromus lanceolatus* Roth**	11.70%
***Bromus madritensis* L.**	56.38%
Bromus rubens L.	4.26%
Bromus sp.	1.06%

Appendix B. *Continue*

Species	Frequency
Bromus tectorum L.	1.06%
Buglossoides arvensis (L.) I. M. Johnston	2.13%
***Calendula arvensis* L.**	10.64%
***Campanula erinus* L.**	12.77%
Campanula lusitanica L.	1.06%
Capnophyllum peregrinum (L.) Lag.	2.13%
Capsella bursa-pastoris (L.) Medik.	6.38%
Cardaria draba (L.) Desv.	1.06%
Carduncellus caeruleus (L.) C. Presl	1.06%
Carduus bourgeanus Boiss. & Reut.	7.45%
Carduus pycnocephalus L.	6.38%
Carduus tenuiflorus Curtis	2.13%
Carthamus lanatus L.	3.19%
Catapodium rigidum (L.) C. E. Hubb.	8.51%
Centaurea calcitrapa L.	1.06%
Centaurea diluta Aiton	9.57%
***Centaurea melitensis* L.**	10.64%
Centaurea pullata L.	2.13%
Centaurium erythraea Rafn, Danm, Holst	1.06%
Centaurium pulchellum (Sw.) Druce	2.13%
Cerastium glomeratum Thuill.	2.13%
Chamaemelum fuscatum (Brot.) Vasc.	3.19%
Chamaemelum nobile (L.) All.	2.13%
Chamaesyce nutans (Lag.) Smal	1.06%
Chamaesyce prostrata(Aiton) Small	1.06%
Chenopodium album L.	8.51%
Chenopodium opulifolium Koch & Ziz	1.06%
***Chenopodium vulvaria* L.**	12.77%
***Chrozophora tinctoria* (L.) Raf.**	15.96%
***Cinchorium intybus* L.**	22.34%
Circium arvense (L.) Scop.	1.06%
Cladanthus mixtus (L.) Chevall.	4.26%
Conium maculatum L.	1.06%
Convolvulus altheoides L.	4.26%
***Convolvulus arvensis* L.**	45.74%
Conyza bonariensis (L.) Cronq.	9.57%
Conyza canadensis (L.) Cronq.	6.38%
Conyza sumatrensis (Retz.) E. Walker	8.51%
Coronilla scorpioides (L.) W. D. J. Koch	3.19%
Crepis capillaris (L.) Wallr.	1.06%
Crepis foetida L.	1.06%
***Crepis vesicaria* L.**	11.70%

Appendix B. *Continue*

Species	Frequency
Crepis sp.	2.13%
Crypsis sp	1.06%
Cuscuta campestris Yunck.	1.06%
Cynara cardunculus L.	1.06%
***Cynodon dactylon* (L.) Pers.**	52.13%
Cynoglossum creticum Mill.	1.06%
Cyperus rotundus L.	2.13%
Dactylis glomerata L.	3.19%
Datura stramonium L.	1.06%
***Daucus carota* L.**	20.21%
Diplotaxis erucoides (L.) DC.	3.19%
***Diplotaxis virgata* (Cav.) DC.**	47.87%
***Ecballium elaterium* (L.) A. Rich.**	17.02%
Echinochloa colonum (L.) Link.	1.06%
Echinops strigosus L.	2.13%
Echium arenarium Guss.	1.06%
Echium creticum L.	1.06%
***Echium plantagineum* L.**	28.72%
Echium vulgare L.	1.06%
Elymus repens (L.) Gould	3.19%
Emex spinosa (L.) Campd.	1.06%
Erodium cicutarium (L.) L'Hér.	8.51%
***Erodium malacoides* (L.) L´Hér**	12.77%
***Erodium moschatum* (L.) L'Hér.**	17.02%
Eryngium campestre L.	6.38%
***Euphorbia exigua* L.**	10.64%
Euphorbia helioscopia L.	6.38%
Euphorbia serrata L.	1.06%
Fallopia convolvulus (L.) Á. Löve	3.19%
Fedia scorpioides Dufresne	1.06%
Filago pyramidata L.	7.45%
Foeniculum vulgare Mill.	3.19%
Frankenia laevis L.	1.06%
Fumaria agraria Lag.	3.19%
Fumaria faurei (Pugsley) Lidén	1.06%
Fumaria officinalis L.	4.26%
Fumaria parviflora Lam.	3.19%
Galactites tomentosa Moench	6.38%
***Galium aparine* L.**	28.72%
Galium divaricatum Pourret ex Lam.	4.26%
Galium lucidum All.	1.06%
Galium murale (L.) All.	2.13%
***Galium parisiense* L.**	10.64%
Galium spurium L.	4.26%

Appendix B. *Continue*

Species	Frequency
Galium tricornutum Dandy	9.57%
Galium verrucosum Huds.	3.19%
Gaudinia fragilis (L.) P. Beauv	1.06%
Geranium disectum L.	4.26%
Geranium molle L.	2.13%
Glaucium corniculatum (L.) Rudolph	1.06%
***Glebionis coronaria* (L.) Spach**	50.00%
***Glebionis segetum* (L.) Fourr.**	13.83%
Hainardia cylindrica (Willd.) Greuter	3.19%
Hedera helix L.	1.06%
Hedypnois cretica (L.) Dum.–Cours.	3.19%
***Heliotropium europaeum* L.**	13.83%
***Helminthotheca echioides* (L.) Holub**	40.43%
Herniaria cinerea DC.	8.51%
***Hirschfeldia incana* (L.) Lagr. Foss.**	15.96%
Holcus lanatus L.	1.06%
Hordeum leporinum Link	1.06%
Hordeum marinum Huds.	1.06%
***Hordeum murinum* L.**	54.26%
Hypericum perforatum L.	2.13%
Juncus bufonius L.	6.38%
Kickxia spuria (L.) Dumort.	2.13%
***Lactuca serriola* L.**	31.91%
Lamarckia aurea (L.) Moench	5.32%
Lamium amplexicaule L.	4.26%
Lathyrus cicera L.	1.06%
Lathyrus hirsutus L.	1.06%
***Lavatera cretica* L.**	36.17%
Lavatera trimestris L.	6.38%
Leontodon longirrostris (Finch & P. D. Sell) Talavera	1.06%
Leontodon maroccanus (Pers.) Ball	1.06%
Linaria latifolia Desf.	4.26%
Linaria spartea (L.) Chaz.	1.06%
Linum sp.	1.06%
Linum tenue Desf.	1.06%
Lolium multiflorum Lam.	1.06%
***Lolium rigidum* Gaudin**	77.66%
Lotus subbiflorus Lag.	1.06%
Lupinus angustifolius L.	2.13%
Lythrum acutangulum Lag.	5.32%
Lythrum acutangulum Lag.	5.32%
Lythrum hyssopifolia L.	2.13%

Appendix B. *Continue*

Species	Frequency
Lythrum junceum Banks & Sol.	6.38%
Malva hispanica L.	1.06%
Malva intermedia Boreau	1.06%
***Malva nicaeensis* All.**	26.60%
***Malva parviflora* L.**	38.30%
***Malva sylvestris* L.**	18.09%
Malvella sherardiana (L.) Jaub. & Spach	1.06%
Marrubium vulgare L.	1.06%
Medicago ciliaris (L.) All.	1.06%
Medicago minima (L.) L.	2.13%
Medicago orbicularis (L.) Bartal.	1.06%
***Medicago polymorpha* L.**	**18.06%**
Medicago sativa L.	1.06%
Medicago scutellata (L.) Mill	1.06%
Medicago sp.	3.19%
Melilotus indicus (L.) All.	6.38%
Mentha suaveolens Ehrh.	1.06%
Mercurialis ambigua L.	1.06%
Misopates orontium (L.) Raf.	7.45%
Misopates sp.	1.06%
Nigella papillosa G. López	3.19%
Notobasis syriaca (L.) Cass.	1.06%
Ononis mitissima L.	7.45%
Ononis natrix L.	1.06%
Onopordum nervosum Boiss.	1.06%
Ornithogalum narbonense L.	2.13%
Ornithopus compresus L.	1.06%
Orobanche ramosa L.	1.06%
Osyris alba L.	1.06%
Oxalis corniculata L.	1.06%
Pallenis spinosa (L.) Cass.	3.19%
Papaver dubium L.	1.06%
Papaver hybridum L.	4.26%
Papaver pinnatifidum Moris	1.06%
***Papaver rhoeas* L.**	25.53%
Parapholis incurva (L.) C. E. Hubb.	1.06%
Parapholis pycnantha (Druce) C. E. Hubb.	1.06%
***Phalaris brachystachys* Link**	25.53%
Phalaris coerulescens Desf.	3.19%
***Phalaris minor* Retz.**	50.00%
***Phalaris paradoxa* L.**	47.87%
***Piptatherum miliaceum* (L.) Coss.**	17.02%

Appendix B. *Continue*

Species	Frequency
Plantago afra L.	7.45%
Plantago albicans L.	1.06%
Plantago coronopus L.	2.13%
***Plantago lagopus* L.**	18.09%
Plantago lanceolata L	4.26%
Poa annua L.	1.06%
Polycarpon tetraphyllum (L.) L.	6.38%
***Polygonum aviculare* L.**	43.62%
Polygonum bellardii All.	1.06%
Polypogon maritimus Willd.	1.06%
***Polypogon monspeliensis* (L.) Desf.**	28.72%
Portulaca oleracea L.	4.26%
***Pulicaria paludosa* Link**	41.49%
Raphanus raphanistrum L.	6.38%
***Rapistrum rugosum* (L.) All.**	10.64%
Ranunculus arvensis L.	1.06%
Reseda luteola L.	6.38%
***Ridolfia segetum* (L.) Moris**	21.28%
Rostraria cristata (L.) Tzvelev	8.51%
Rubus ulmifolius Schott	1.06%
Rumex conglomeratus Murray	1.06%
Rumex crispus L.	3.19%
Rumex obtusifolius L.	1.06%
Rumex pulcher L.	8.51%
Sagina apetala Ard.	1.06%
Scabiosa atropurpurea L.	1.06%
Scolymus hispanicus L.	5.32%
***Scolymus maculatus* L.**	21.28%
Scorpiurus muricatus L.	1.06%
Scorpiurus sulcatus L.	4.26%
Scorpiurus vermiculatus L.	2.13%
Scorzonera laciniata L.	1.06%
Sedum sediforme (Jacq.) Pau	1.06%
Senecio vulgaris L.	1.06%
Setaria sp.	2.13%
Setaria verticillata (L.) P. Beauv.	1.06%
Setaria viridis (L.) P. Beauv.	1.06%
Sherardia arvensis L.	5.32%
Silene gallica L.	3.19%
Silene nocturna L.	1.06%
Silene stricta L.	2.13%
***Silybum marianum* (L.) Gaertn.**	30.85%
Sinapis alba L.	6.38%
Sinapis arvensis L.	3.19%

Appendix B. *Continue*

Species	Frequency
Sisymbrium officinale (L.) Scop.	1.06%
Solanum nigrum L.	2.13%
Sonchus asper (L.) Hill	5.32%
***Sonchus oleraceous* L.**	51.06%
Sonchus tenerrimus L.	4.26%
Sorghum halepense (L.) Pers.	1.06%
Spergula arvensis L.	1.06%
Spergularia bocconei (Scheele) Graebn.	1.06%
Spergularia nicaeensis Burnat	3.19%
Spergularia rubra (L.) J. Presl & C. Presl	2.13%
Spergularia sp.	1.06%
Stachys arvensis (L.) L.	3.19%
Stachys ocymastrum (L.) Briq.	2.13%
Symphyotrichum squamatum (Spreng.) G. L. Nesom	5.32%
Taraxacum officinale Weber	2.13%
Teucrium capitatum L. ^{Ch}	1.06%
Thymus vulgaris L.	1.06%
Tolpis barbata (L.) Gaertn.	1.06%
***Torilis arvensis* (Huds.) Link**	14.89%
Torilis nodosa (L.) Gaertn.	9.57%
Trachynia distachya (L.) Link	6.38%
Tragopogon crocifolius L.	1.06%
Trifolim angustifolim L.	2.13%
Trifolium campestre Schreb.	5.32%
Trifolium glomeratum L.	2.13%
Trifolium repens L.	2.13%
Trifolium resupinatum L.	1.06%
Trifolium scabrum L.	1.06%
Trifolium sp.	2.13%
Trifolium squamosum L.	1.06%
Trifolium tomentosum L.	1.06%
Trifolium vesiculosum Savi	3.19%
***Trisetaria panicea* (Lam.) Paunero**	31.91%
***Urospermun picrioides* (L.) F. W. Schmidt**	12.77%
Urtica urens L.	1.06%
Vaccaria hispanica (Mill.) Rauschert	1.06%
Verbascum sinuatum L.	3.19%
Verbena officinalis L.	1.06%
Verbena supina L.	1.06%
Veronica anagalloides Guss.	1.06%
Veronica arvensis L.	2.13%
Veronica persica Poir.	1.06%

Appendix B. *Continue*

Species	Frequency
Veronica polita Fr.	4.26%
Vicia cracca L.	1.06%
Vicia lutea L.	1.06%
Vicia sativa L.	4.26%
Vulpia ciliata Dumort.	1.06%
Vulpia geniculata (L.) Link	9.57%
Vulpia myuros (L.) C. C. Gmel.	3.19%
Xanthium spinosum L.	1.06%
Xanthium strumarium L.	4.26%

Appendix C. Functional trait values corresponding to the Q table of the 25 considered species in cereal fields in UK. See table 1b for abbreviation (chapter III).

Species	PH	SM	MFF	LF
Aethusa cynapium L.	0.49	0.99	6	therophyte
Alopecurus myosuroides Huds.	0.60	1.99	5	therophyte
Anagallis arvensis L.	0.22	0.50	6	therophyte
Anthriscus sylvestris (L.) Hoffm.	0.90	3.81	5	hemicryptophyte
Bromus sterilis L.	1.00	9.50	5	therophyte
Brassica napus L.	1.51	3.30	5	therophyte
Chenopodium album L.	0.80	0.60	7	therophyte
Cirsium arvense (L.) Scop.	0.90	1.30	7	geophyte
Epilobium angustifolium L.	1.15	0.04	7	geophyte
Fallopia convolvulus (L.) Á. Löve	1.00	5.80	7	therophyte
Galium aparine L.	0.50	8.70	6	therophyte
Geranium dissectum L.	0.45	2.24	5	therophyte
Heracleum sphondylium L.	1.32	7.30	6	hemicryptophyte
Poa annua L.	0.35	0.30	1	therophyte
Polygonum aviculare L.	0.90	1.30	5	therophyte
Senecio vulgaris L.	0.20	0.23	2	hemicryptophyte
Sinapis arvensis L.	0.40	1.90	6	therophyte
Sisymbrium officinale (L.) Scop.	0.46	0.31	5	therophyte
Sonchus oleraceus L.	0.60	0.30	1	therophyte
Stellaria media (L.) Vill.	0.22	0.40	1	therophyte
Tripleurospermum inodorum (L.) Sch. Bip.	1.25	0.37	7	hemicryptophyte
Veronica hederifolia L.	0.20	4.00	1	therophyte
Veronica persica Poir.	0.50	1.08	1	therophyte
Vicia sativa L.	1.10	34.90	5	therophyte
Viola arvensis Murr.	0.40	0.41	4	therophyte

Appendix D. Functional trait values corresponding to the Q table of the 58 considered species in the sampled cereal fields in Spain (chapter III).

Species	PH	SM	MFF	LF
Amaranthus blitoides S. Watson	0.47	0.83	4	therophyte
Anagallis arvensis L.	0.22	0.50	3	therophyte
Apera spica-venti (L.) P. Beauvois	0.40	0.10	5	therophyte
Avena sterilis L.	0.50	19.94	3	therophyte
Bromus diandrus Roth	0.35	11.24	3	therophyte
Campanula erinus L.	0.07	0.01	4	therophyte
Capsella bursa–pastoris (L.) Medik.	0.30	0.10	12	therophyte
Catapodium rigidum (L.) C. E. Hubb	0.25	0.26	4	therophyte
Centaurea diluta Aiton	0.80	3.50	5	therophyte
Centaurium pulchellum (Sw.) Druce	0.55	0.02	5	therophyte
Cerastium glomeratum Thuill.	0.25	0.05	2	therophyte
Chenopodium album L.	0.80	0.60	4	therophyte
Chenopodium vulvaria L.	0.42	0.40	4	therophyte
Chrozophora tinctoria (L.) Raf.	0.45	13.00	3	therophyte
Convolvulus arvensis L.	0.40	15.10	3	geophyte
Conyza bonariensis (L.) Cronq.	0.90	0.10	1	therophyte
Cynodon dactylon (L.) Pers.	0.20	0.20	4	hemicriptophyte
Diplotaxis virgata L.	0.30	0.23	2	therophyte
Euphorbia exigua L.	0.15	0.35	2	therophyte
Filago pyramidata L.	0.12	0.05	3	therophyte
Galium aparine L.	0.50	8.70	3	therophyte
Galium parisiense L.	0.20	0.20	4	therophyte
Glaucium corniculatum (L.) Rudolph	0.25	0.90	4	therophyte
Glebionis coronaria (L.) Spach	1.20	1.50	9	therophyte
Glebionis segetum (L.) Fourr	0.50	1.52	2	therophyte
Heliotropium europaeum L.	0.40	0.40	3	hemicriptophyte
Helminthotheca echioides (L.) Holub	0.40	1.31	4	hemicriptophyte
Herniaria cinerea DC.	0.15	0.22	2	therophyte
Hirschfeldia incana (L.) Lagr.–Foss	0.70	0.23	2	therophyte
Juncus bufonius L.	0.20	0.02	4	therophyte
Kickxia spuria (L.) Dumort.	0.30	0.41	7	therophyte
Lactuca serriola L.	0.60	0.58	4	therophyte
Lolium rigidum Gaudin	0.40	3.34	4	therophyte
Lythrum acutangulum Lag.	0.20	0.19	6	therophyte
Lythrum hyssopifolia L.	0.20	0.44	3	therophyte
Lythrum junceum Banks & Sol.	0.20	0.19	4	geophyte
Malva parviflora L.	1.00	2.22	4	therophyte
Medicago polymorpha L.	0.35	2.95	3	therophyte
Melilotus indicus (L.) All.	0.80	2.30	4	therophyte
Misopates orontium (L.) Raf.	0.25	0.12	3	therophyte
Papaver rhoeas L.	0.40	0.20	3	therophyte
Phalaris brachystachys Link	0.90	1.90	4	therophyte

Appendix D. *Continue*

Species	PH	SM	MFF	LF
Phalaris minor Retz.	0.90	1.60	4	therophyte
Phalaris paradoxa L.	0.90	1.30	5	therophyte
Polycarpon tetraphyllum (L.) L.	0.15	0.05	3	therophyte
Polygonum aviculare L.	0.90	1.30	2	therophyte
Polygonum bellardii All.	0.60	1.55	4	therophyte
Polypogon monspeliensis (L.) Desf.	1.15	0.10	4	therophyte
Portulaca oleracea L.	0.20	0.10	5	therophyte
Pulicaria paludosa Link	0.30	0.17	5	therophyte
Raphanus raphanistrum L.	0.30	23.60	1	therophyte
Ridolfia segetum (L.) Moris	1.50	0.60	4	therophyte
Solanum nigrum L.	0.70	0.70	2	therophyte
Sonchus asper (L.) Hill	0.60	0.28	2	therophyte
Sonchus oleraceus L.	0.60	0.30	1	therophyte
Torilis nodosa (L.) Gaertn.	0.45	2.30	3	therophyte
Trisetaria panicea (Lam.) Paunero	0.80	0.06	3	therophyte
Verbena officinalis L.	0.41	0.30	3	hemicriptophyte

Appendix E. List of the 88 species recorded in the cereal fields in UK and their frequency. In bold are the species included in the functional analyses (chapter III).

Species	Frequency
Acer campestre L.	0.59%
Acer pseudoplatanus L.	1.18%
***Aethusa cynapium* L.**	19.41%
Alliaria petiolata (M. Bieb.) Cavara & Grande	0.59%
***Alopecurus myosuroides* Huds.**	54.12%
***Anagallis arvensis* L.**	10%
***Anthriscus sylvestris* (L.) Hoffm.**	7.65%
Aphanes arvensis L.	4.12%
Atriplex patula L.	2.35%
Avena fatua L.	3.53%
Beta vulgaris L.	4.12%
***Brassica napus* L.**	10.59%
***Bromus sterilis* L.**	20.59%
Calystegia sepium (L.) R. Br.	0.59%
Capsella bursa–pastoris (L.) Medik.	4.71%
*Carduus crispu*s L.	1.18%
Cerastium fontanum Baumg.	0.59%
***Chenopodium album* L.**	15.88%
*Chenopodium bonus-henricu*s L.	0.59%
***Cirsium arvense* (L.) Scop.**	27.65%
Cirsium vulgare (Savi) Ten.	2.94%
Convolvulus arvensis L.	2.35%
Cornus sanguinea L.	1.76%
Coronopus didymus (L.) Sm.	1.18%
Coronopus squamatus (Forssk.) Asch.	1.76%
*Crataegus monogyn*a Jacq.	1.18%
Cynosurus cristatus L.	0.59%
Dactylis glomerata L.	1.18%
Elymus repens (L.) Gould	0.59%
***Epilobium angustifolium* L.**	8.24%
Epilobium hirsutum L.	1.76%
Equisetum arvense L.	2.35%
Euphorbia peplus L.	0.59%
***Fallopia convolvulus* (L.) Á. Löve**	18.82%
Festuca rubra L.	1.76%
Fraxinus excelsior L.	3.53%
Fumaria officinalis L.	2.94%
***Galium aparine* L.**	58.82%
***Geranium dissectum* L.**	22.35%
Geranium molle L.	2.35%
Helminthotheca echioides (L.) Holub	1.18%

Appendix E. *Continue*

Species	Frequency
***Heracleum sphondylium* L.**	8.82%
Hordeum vulgare L.	1.18%
Lamium album L.	0.59%
Lamium purpureum L.	2.35%
Lapsana communis L.	2.94%
Lathyrus pratensis L.	0.59%
Leucanthemum vulgare Lam.	1.76%
Lolium multiflorum Lam.	1.18%
Lolium perenne L.	4.71%
Matricaria recutita L.	0.59%
*Medicago sativ*a L.	0.59%
Myosotis arvensis Hill	1.76%
Papaver rhoeas L.	4.12%
*Phacelia tanacetifoli*a Benth	1.18%
Pisum sativum L	1.18%
Plantago lanceolata L.	0.59%
***Poa annua* L.**	20.59%
Poa pratensis L.	0.59%
Poa trivialis L.	1.18%
***Polygonum aviculare* L.**	12.35%
Polygonum persicaria L.	1.18%
Quercus robur L.	1.18%
*Ranunculus repen*s L.	0.59%
Rosa canina L.	2.35%
Rubus fruticosus L.	0.59%
*Rumex obtusifoliu*s L.	3.53%
Scandix pecten–veneris L.	4.71%
*Senecio jacobae*a L.	1.18%
***Senecio vulgaris* L.**	30.59%
Sherardia arvensis L.	0.59%
***Sinapis arvensis* L.**	11.18%
***Sisymbrium officinale* (L.) Scop.**	5.88%
Sonchus arvensis L.	0.59%
Sonchus asper (L.) Hill	3.53%
***Sonchus oleraceus* L.**	5.29%
***Stellaria media* (L.) Vill.**	9.41%
Taraxacum gr. officinale Weber	2.94%
Thlaspi arvense L.	0.59%
Trifolium repens L.	0.59%
***Tripleurospermum inodorum* (L.) Sch. Bip.**	21.18%
Tussilago farfara L.	0.59%
Urtica dioica L.	2.94%
***Veronica hederifolia* L.**	5.29%

Appendix E. *Continue*

Species	Frequency
***Veronica persica* Poir.**	22.35%
Vicia faba L.	0.59%
***Vicia sativa* L.**	5.29%
***Viola arvensis* Murr.**	17.65%

Appendix F. List of the 116 species recorded in the sampled cereal fields in Spain and their frequency
In bold the species included in the functional analyses (chapter III).

Species	Frequency
Abutilon theophrasti Medik.	2.27%
Agrostis pouretti L.	4.55%
Amaranthus albus	2.27%
Amaranthus blitoides **S. Watson**	11.36%
Amaranthus retroflexus L.	2.27%
Ammi majus L.	2.27%
Anacyclus clavatus (Desf.) Pers.	4.55%
Anagallis arvensis **L.**	59.09%
Anagallis foemina Mill.	4.55%
Anchusa azurea Mill	2.27%
Anthemis arvensis L.	2.27%
Anthemis cotula L.	2.27%
Apera spica-venti **(L.) P. Beauvois**	11.36%
Apium nodiflorum (L.) Lag.	2.27%
*Arenaria leptoclado*s (Rchb.) Guss.	4.55%
Arisarum simorrhinum Durieu	2.27%
Atriplex prostrata DC.	2.27%
Avena sterilis **L.**	40.91%
Beta vulgaris L.	4.55%
Bromus diandrus **Roth**	6.82%
Bromus hordeaceus L.	2.27%
Bromus madritensis L.	2.27%
Campanula erinus **L.**	25%
Capsella bursa–pastoris **(L.) Medik.**	11.36%
Catapodium rigidum **(L.) C. E. Hubb**	11.36%
Centaurea diluta **Aiton**	6.82%
Centaurea melitensis L.	2.27%
Centaurium pulchellum **(Sw.) Druce**	9.09%
Cerastium glomeratum**Thuill.**	9.09%
Chenopodium album **L.**	9.09%
Chenopodium murale L.	2.27%
Chenopodium vulvaria **L.**	9.09%
Chrozophora tinctoria **(L.) Raf.**	11.36%
Convolvulus arvensis **L.**	56.82%
Conyza bonariensis **(L.) Cronq.**	29.55%
Conyza canadensis (L.) Cronq.	2.27%
Cynodon dactylon **(L.) Pers.**	6.82%
Cyperus rotundus L.	2.27%

Appendix F. *Continue*

Species	Frequency
Daucus carota L.	2.27%
***Diplotaxis virgata* L.**	18.18%
Ecballium elaterium (L.) A. Rich.	4.55%
Eruca vesicaria (L.) Cav.	2.27%
***Euphorbia exigua* L.**	6.82%
Filago pygmaea L.	2.27%
***Filago pyramidat*a L.**	9.09%
Fumaria parviflora Lam.	4.55%
***Galium aparine* L.**	22.73%
Galium minutulum Jord.	2.27%
***Galium parisiense* L.**	13.64%
Galium tricornutum Dandy	4.55%
Galium verrucosum Huds.	2.27%
***Glaucium corniculatum* (L.) Rudolph**	6.82%
***Glebionis coronaria* (L.) Spach**	20.45%
***Glebionis segetum* (L.) Fourr**	22.73%
***Heliotropium europaeum* L.**	18.18%
***Helminthotheca echioides* (L.) Holub**	18.18%
***Herniaria cinerea* DC.**	6.82%
***Hirschfeldia incana* (L.) Lagr.–Foss**	6.82%
Hordeum murinum L.	2.27%
***Juncus bufonius* L.**	22.73%
***Kickxia spuria* (L.) Dumort**	6.82%
***Lactuca serriola* L.**	11.36%
Lamium amplexicaule L.	4.55%
Lavatera cretica L.	2.27%
Linaria latifolia Desf.	4.55%
Lolium multiflorum Lam.	4.55%
***Lolium rigidum* Gaudin**	50%
***Lythrum acutangulum* Lag.**	13.64%
***Lythrum hyssopifolia* L.**	6.82%
***Lythrum junceum* Banks & Sol.**	11.36%
Lythrum thymifolia L.	2.27%
Lythrum tribracteatum Spreng.	2.27%
Malva intermedia Boreau	2.27%
Malva nicaensis All.	4.55%
***Malva parviflora* L.**	9.09%
***Medicago polymorpha* L.**	11.36%
***Melilotus indicus* (L.) All.**	6.82%

Appendix F. *Continue*

Species	Frequency
***Misopates orontium* (L.) Raf.**	9.09%
***Papaver rhoeas* L.**	22.73%
Parentucellia viscosa (L.) Caruel	2.27%
***Phalaris brachystachys* Link**	27.27%
***Phalaris minor* Retz.**	38.64%
***Phalaris paradoxa* L.**	52.27%
Plantago afra L.	2.27%
Poa annua L.	4.55%
***Polycarpon tetraphyllum* (L.) L.**	9.09%
***Polygonum aviculare* L.**	68.18%
***Polygonum bellardii* All.**	6.82%
***Polypogon monspeliensis* (L.) Desf.**	22.73%
***Portulaca oleracea* L.**	6.82%
***Pulicaria paludosa* Link**	54.55%
***Raphanus raphanistrum* L.**	13.64%
Reseda lutea L.	4.55%
***Ridolfia segetum* (L.) Moris**	6.82%
Rumex pulcher L.	2.27%
Sagina apetala Ard.	2.27%
Scolymus maculatus L.	2.27%
Scorpiurus vermiculatus L.	2.27%
Silene gallica L.	4.55%
Silene nocturna L.	2.27%
Sinapis alba L.	4.55%
***Solanum nigrum* L.**	9.09%
Sonchus asper (L.) Hill	6.82%
***Sonchus oleraceus* L.**	34.09%
Sorghum halepense (L.) Pers	4.55%
Stellaria media (L.) Vill.	4.55%
Torilis arvensis (Huds.) Link	4.55%
***Torilis nodosa* (L.) Gaertn.**	11.36%
***Trisetaria panicea* (Lam.) Paunero**	13.64%
***Verbena officinalis* L.**	9.09%
Verbena supina L.	2.27%
Veronica anagalloides Guss.	2.27%
Veronica hederifolia L.	2.27%
Veronica polita Fr.	4.55%
Vicia sativa L.	4.55%
Vulpia myuros (L.) C. C. Gmel.	2.27%

Appendix G. Functional trait values corresponding to the Q table of the 77 considered species in the seed bank of sampled cereal fields in Andalusia (chapter IV).

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Amaranthus blitoides S. Watson	therophyte	0.47	4	8	dicot	0.83	autog	barochory
Amaranthus retroflexus L.	therophyte	0.75	5	3	dicot	0.40	autog	barochory
Anagallis arvensis L.	therophyte	0.22	3	7	dicot	0.50	ent-anem	barochory
Avena sterilis L.	therophyte	0.50	3	3	monocot	19.94	anem	zoochory
Bromus madritensis L.	therophyte	0.80	3	3	monocot	3.33	anem	anemochory
Calendula arvensis L.	therophyte	0.60	1	12	dicot	5.20	ent-anem	zoochory
Campanula erinus L.	therophyte	0.07	4	6	dicot	0.01	anem	anemochory
Capsella bursa–pastoris (L.) Medik.	therophyte	0.30	12	8	dicot	0.10	entom	barochory
Centaurium erythraea Rafn	hemicryptophyte	0.80	5	2	dicot	0.016	entom	anemochory
Centaurium pulchellum (Sw.) Druce	therophyte	0.55	5	1	dicot	0.02	ent-anem	anemochory
*Cerastium glomeratum*Thuill.	therophyte	0.25	2	4	dicot	0.05	anem	barochory
Chamaesyce prostrata (Aiton) Small	therophyte	0.30	4	6	dicot	0.14	entom	barochory
Chenopodium album L.	therophyte	0.80	4	8	dicot	0.60	anem	barochory
Chenopodium murale L.	therophyte	0.60	1	12	dicot	0.55	anem	barochory
Chenopodium vulvaria L.	therophyte	0.42	4	6	dicot	0.40	anem	barochory
Chrozophora tinctoria (L.) Raf.	therophyte	0.45	3	5	dicot	13.00	anem	barochory
Cichorium intybus L.	hemicryptophyte	1.00	4	7	dicot	5.50	entom	barochory
Cladanthus mixtus (L.) Chevall.	therophyte	0.70	4	3	dicot	1.99	entom	barochory
Convolvulus arvensis L.	geophyte	0.40	3	7	dicot	15.10	entom	barochory
Conyza bonariensis (L.) Cronq.	therophyte	0.90	1	12	dicot	0.10	entom	anemochory
Conyza canadensis (L.) Cronq.	therophyte	1.30	2	8	dicot	0.07	entom	anemochory
Conyza sumatrensis (Retz.) E. Walker	therophyte	2.00	1	12	dicot	0.05	entom	anemochory
Cynodon dactylon (L.) Pers.	hemicryptophyte	0.20	4	8	monocot	0.20	anem	barochory
Cyperus rotundus L.	geophyte	0.40	5	9	monocot	0.25	anem	barochory

Appendix G. *Continue*

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Diplotaxis virgata (Cav.) DC.	therophyte	0.30	2	4	dicot	0.23	entom	barochory
Ecballium elaterium (L.) A. Rich.	hemicryptophyte	1.50	1	12	dicot	12.10	entom	barochory
Echium plantagineum L.	therophyte	0.80	2	6	dicot	4.30	entom	barochory
Filago pyramidata L.	therophyte	0.12	3	4	dicot	0.05	entom	anemochory
Fumaria agraria Lag.	therophyte	1.50	2	4	dicot	1.99	autog	barochory
Galium aparine L.	therophyte	0.50	3	7	dicot	8.70	autog	zoochory
Galium parisiense L.	therophyte	0.20	4	3	dicot	0.20	autog	zoochory
Galium verrucosum Huds.	therophyte	0.43	5	2	dicot	4.42	entom	barochory
Glaucium corniculatum (L.) Rudolph	therophyte	0.25	4	3	dicot	0.90	entom	barochory
Glebionis coronaria (L.) Spach	therophyte	0.50	2	4	dicot	1.52	entom	barochory
Glebionis segetum (L.) Fourr.	therophyte	1.20	9	8	dicot	1.50	entom	anemochory
Heliotropium europaeum L.	hemicryptophyte	0.40	3	6	dicot	0.40	entom	barochory
Helminthotheca echioides (L.) Holub	hemicryptophyte	0.40	4	6	dicot	1.31	entom	anemochory
Herniaria cinerea DC.	therophyte	0.15	2	5	dicot	0.22	entom	anemochory
Hordeum murinum L.	therophyte	0.40	5	1	monocot	10.50	autog	zoochory
Juncus bufonius L.	therophyte	0.20	4	3	monocot	0.02	anem	anemochory
Kickxia spuria (L.) Dumort.	therophyte	0.30	7	3	dicot	0.41	autog	barochory
Lactuca serriola L.	therophyte	0.60	4	6	dicot	0.58	autog	anemochory
Lamium amplexicaule L.	therophyte	0.20	1	5	dicot	0.60	autog	barochory
Lolium rigidum Gaudin	therophyte	0.40	4	2	monocot	3.34	anem	anemochory
Lythrum acutangulum Lag	therophyte	0.20	6	4	dicot	0.19	entom	barochory
Lythrum hyssopifolia L.	therophyte	0.20	3	3	dicot	0.44	entom	barochory
Lythrum junceum Banks & Sol.	geophyte	0.20	4	7	dicot	0.19	entom	barochory
Malva nicaensis All.	therophyte	0.60	5	2	dicot	8.60	entom	barochory

Appendix G. *Continue*

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Malva sylvestris L.	therophyte	1.00	4	3	dicot	2.95	entom	barochory
Misopates orontium (L.) Raf.	therophyte	0.25	3	3	dicot	0.12	entom	barochory
Papaver rhoeas L.	therophyte	0.40	3	3	dicot	0.20	entom	barochory
Phalaris brachystachys Link	therophyte	0.90	4	2	monocot	1.90	anem	barochory
Phalaris minor Retz.	therophyte	0.90	4	2	monocot	1.60	anem	barochory
Phalaris paradoxa L.	therophyte	0.90	5	2	monocot	1.30	anem	barochory
Phleum paniculatum Huds.	therophyte	0.45	5	1	monocot	0.09	anem	barochory
Piptatherum miliaceum (L.) Coss.	hemicryptophyte	1.00	4	7	monocot	1.99	anem	barochory
Poa annua L.	therophyte	0.35	4	6	monocot	0.30	autog	anemochory
Polycarpon tetraphyllum (L.) L.	therophyte	0.15	3	4	dicot	0.05	ent-anem	anemochory
Polygonum aviculare L.	therophyte	0.90	2	10	dicot	1.30	autog	barochory
Polygonum bellardii All.	therophyte	0.60	4	4	dicot	1.55	autog	barochory
Polypogon monspeliensis (L.) Desf.	therophyte	1.15	4	3	monocot	0.10	anem	anemochory
Portulaca oleracea L.	therophyte	0.20	5	5	dicot	0.10	autog	barochory
Pulicaria paludosa Link	therophyte	0.30	5	6	dicot	0.17	entom	anemochory
Rapistrum rugosum (L.) All.	therophyte	1.50	2	5	dicot	2.90	entom	barochory
Ridolfia segetum (L.) Moris	therophyte	1.50	4	3	dicot	0.60	entom	barochory
Rumex crispus L.	hemicryptophyte	1.20	3	9	dicot	1.50	anem	anemochory
Setaria viridis (L.) P. Beauv.	therophyte	0.60	7	3	monocot	1.00	anem	barochory
Silene gallica L.	therophyte	0.60	2	4	dicot	0.30	ent-anem	barochory
Solanum nigrum L.	therophyte	0.70	2	9	dicot	0.70	entom	anemochory
Sonchus asper (L.) Hil	therophyte	0.60	2	8	dicot	0.28	entom	anemochory
Sonchus oleraceus L.	therophyte	0.60	1	12	dicot	0.30	entom	anemochory
Spergula arvensis L.	hemicryptophyte	0.35	2	3	dicot	0.30	entom	barochory
Spergularia rubra (L.) J. Presl & C. Presl	hemicryptophyte	0.13	3	5	dicot	0.06	entom	anemochory

Appendix G. *Continue*

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Symphyotrichum squamatum (Spreng.) G. L. Nesom	therophyte	1.00	5	4	dicot	0.10	entom	anemochory
Trisetaria panicea (Lam.) Paunero	therophyte	0.80	3	7	monocot	0.06	anem	barochory
Veronica officinalis L.	hemicryptophyte	1.00	3	7	dicot	0.14	entom	barochory
Veronica polita Fr.	therophyte	0.30	1	9	dicot	0.35	autog	barochory

monocot= monocotyledon, dicot=dicotyledon , anem=anemogamous, autog= autogamous, entom= entomogamous, ent-anem=entomogamous/anemogamous.

Appendix H. Functional trait values corresponding to the Q table of the 62 considered species in the seed bank of the sampled cereal fields in Catalonia. (chapter IV).

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Amaranthus blitoides S. Watson	therophyte	0.47	6	6	dicot	0.83	autog	barochorus
Anagallis arvensis L.	therophyte	0.22	3	3	dicot	0.50	ent-aut	barochorus
Anthemis arvensis L.	therophyte	0.40	4	3	dicot	0.67	insect	barochorus
Aphanes arvensis L.	therophyte	0.20	4	4	dicot	0.23	ent-aut	barochorus
Atriplex patula L.	therophyte	0.80	5	5	dicot	1.39	ent-ane	barochorus
Atriplex prostrata DC.	therophyte	1.00	5	6	dicot	4.00	ent-ane	barochorus
Avena sterilis L.	therophyte	0.50	5	3	monocot	19.94	anem	zoochorus
Bromus diandrus Roth	therophyte	0.35	4	3	monocot	11.24	anem	zoochorus
Buglossoides arvensis (L.) I. M. Johnston	therophyte	0.50	3	7	dicot	5.44	entom	barochorus
Capsella bursa–pastoris (L.) Medik.	therophyte	0.30	1	12	dicot	0.10	entom	barochorus
Centaurium pulchellum (Sw.) Druce	therophyte	0.55	5	5	dicot	0.02	ent-aut	anemochorus
*Cerastium glomeratum*Thuill.	therophyte	0.25	4	2	dicot	0.05	autog	anemochorus
Chaenorhinum minus (L.) Lange	chamaetophyte	0.50	5	5	dicot	0.10	autog	barochorus
Chamaesyce prostrata (Aiton) Small	therophyte	0.30	5	2	dicot	0.14	entom	barochorus
Chenopodium album L.	therophyte	0.80	7	6	dicot	0.60	anem	barochorus
Chenopodium vulvaria L.	therophyte	0.42	5	6	dicot	0.40	anem	barochorus
Convolvulus arvensis L.	geophyte	0.40	3	4	dicot	15.10	entom	barochorus
Conyza bonariensis (L.) Cronq.	therophyte	0.90	7	3	dicot	0.10	entom	anemochorus
Conyza canadensis (L.) Cronq.	therophyte	1.30	7	5	dicot	0.07	entom	anemochorus
Conyza sumatrensis (Retz.) E. Walker	therophyte	2.00	7	4	dicot	0.05	entom	anemochorus
Diplotaxis erucoides (L.) DC.	therophyte	0.8	3	7	dicot	0.20	entom	barochorus

Appendix H. *Continue*

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Eleusine tristachya (Lam.) Lam.	therophyte	0.6	4	5	monocot	0.62	anem	barochorus
Filago pyramidata L.	therophyte	0.12	5	3	dicot	0.05	entom	anemochorus
Fumaria officinalis L.	therophyte	0.80	2	7	dicot	3.24	autog	barochorus
Galium parisiense L.	therophyte	0.20	5	1	dicot	0.20	ent-aut	zoochorus
Galium tricornutum Dandy	therophyte	0.85	2	4	dicot	10.60	ent-aut	zoochorus
Heliotropium europaeum L.	hemicryptophyte	0.40	6	5	dicot	0.40	entom	barochorus
Herniaria cinerea DC.	therophyte	0.15	3	4	dicot	0.22	autog	anemochorus
Hypecoum procumbens L.	therophyte	0.20	4	2	dicot	17.60	entom	barochorus
Hypericum perforatum L.	hemicryptophyte	0.95	5	3	dicot	0.20	ent-aut	barochorus
Dittrichia viscosa (L.) Greuter	chamaetophyte	1.50	6	2	dicot	0.30	entom	anemochorus
Juncus bufonius L.	therophyte	0.20	6	8	monocot	0.02	anem	anemochorus
Kickxia spuria (L.) Dumort.	therophyte	0.30	6	4	dicot	0.41	autog	barochorus
Lactuca serriola L.	therophyte	0.60	6	3	dicot	0.58	autog	anemochorus
Lamium amplexicaule L.	therophyte	0.20	3	7	dicot	0.60	autog	barochorus
Lolium rigidum Gaudin	therophyte	0.40	5	4	monocot	3.34	anem	anemochorus
Malcolmia africana (L.) R. Br.	therophyte	0.40	3	2	dicot	0.30	entom	barochorus
Malva sylvestris L.	therophyte	1.00	4	4	dicot	2.95	entom	barochorus
Medicago lupulina L.	therophyte	0.50	3	3	dicot	1.60	ent-aut	barochorus
Medicago polymorpha L.	therophyte	0.35	2	6	dicot	2.95	autog	zoochorus
Oxalis corniculata L.	therophyte	0.20	1	12	dicot	0.20	autog	barochorus
Papaver hybridum L.	therophyte	0.35	3	4	dicot	0.12	autog	barochorus
Papaver rhoeas L.	therophyte	0.40	3	4	dicot	0.20	entom	barochorus
Phragmites australis (Cav.) Steud.	hemicryptophyte	0.40	6	6	monocot	1.50	anem	anemochorus
Poa annua L.	therophyte	0.35	1	12	monocot	0.30	autog	anemochorus

Appendix H. *Continue*

Species	LF	PH	MFF	FD	GF	SM	PT	DT
Polygonum aviculare L.	therophyte	0.90	4	5	dicot	1.30	autog	barochorus
Portulaca oleracea L.	therophyte	0.20	5	5	dicot	0.10	autog	barochorus
Roemeria hybrida (L.) DC.	therophyte	0.47	4	2	dicot	0.20	entom	anemochorus
Setaria adhaerens (Forssk.)Chiov.	therophyte	0.70	6	5	monocot	1.00	anem	zoochorus
Setaria pumila (Poir.) Roem. & Schult.	hemicryptophyte	0.75	7	2	monocot	1.32	anem	zoochorus
Setaria verticillata (L.) P. Beauv.	therophyte	0.90	6	4	monocot	0.70	anem	zoochorus
Setaria viridis (L.) P. Beauv.	therophyte	0.60	6	3	monocot	1.00	anem	barochorus
Sonchus oleraceus L.	therophyte	0.60	1	12	dicot	0.30	entom	anemochorus
Stellaria media (L.) Vill.	therophyte	0.40	3	4	dicot	0.40	entom	barochorus
Sisymbrium irio L.	therophyte	0.50	4	2	dicot	0.10	entom	barochorus
Verbena officinalis L.	hemicryptophyte	1.00	4	3	dicot	0.14	entom	barochorus
Veronica arvensis L.	therophyte	0.30	3	9	dicot	0.12	entom	barochorus
Veronica hederifolia L.	therophyte	0.20	2	8	dicot	4.00	entom	barochorus
Veronica persica Poir.	therophyte	0.50	2	10	dicot	1.10	entom	barochorus
Veronica polita Fr.	therophyte	0.30	3	7	dicot	0.35	autog	barochorus
Viola arvensis Murr.	therophyte	0.20	5	3	dicot	0.90	ent-aut	barochorus
Vulpia unilateralis (L.) Stace	therophyte	0.40	4	3	monocot	0.41	anem	zoochorus

monocot= monocotyledon, dicot=dicotyledon, anem=anemogamous, autog= autogamous, entom= entomogamous, ent-aut=entomogamous/autogamous, ent-ane=entomogamous/anemogamous.

Appendix I. List of the 175 species recorded in the seed bank of sampled cereal fields in Andalusia and their frequency. In bold are the species included in the functional analyses (chapter IV).

Species	Frequency
Amaranthus albus L.	2.90%
***Amaranthus blitoides* S. Watson**	68.11%
***Amaranthus retroflexus* L.**	11.59%
Amaranthus viridis L.	1.45%
Ammi majus L.	2.90%
Anacyclus clavatus (Desf.) Pers.	1.45%
Anacyclus radiatus Loisel.	1.45%
***Anagallis arvensis* L.**	59.42%
Anagallis foemina Mill.	1.45%
Anchusa azurea Mill.	1.45%
*Andryala integrifoli*a L.	2.90%
Anthemis arvensis L.	2.90%
Anthemis cotula L.	4.35%
Apium nodiflorum (L.) Lag.	2.90%
Arenaria leptoclados (Rchb.) Guss.	2.90%
Arisarum simorrhinum Durieu	1.45%
Atriplex patula L.	4.35%
Atriplex prostrata DC.	1.45%
***Avena sterilis* L.**	30.43%
Beta vulgaris L.	4.35%
Bromus diandrus Roth	1.45%
Bromus hordeaceus L.	2.90%
***Bromus madritensis* L.**	14.49%
***Calendula arvensis* L.**	5.80%
***Campanula erinus* L.**	43.48%
***Capsella bursa–pastoris* (L.) Medik.**	10.14%
Cardamine hirsuta L.	2.90%
Cardaria draba (L.) Desv.	1.45%
Catapodium rigidum (L.) C. E. Hubb	1.45%
***Centaurium erythraea* Rafn**	21.74%
***Centaurium pulchellum* (Sw.) Druce**	8.70%
Cerastium fontanum Baumg	1.45%
***Cerastium glomeratum*Thuill.**	7.25%
Chamaemelum fuscatum (Brot.) Vasc.	2.90%
Chamaesyce canescens (L.) Prokh.	2.90%
Chamaesyce nutans (Lag.) Small	2.90%
***Chamaesyce prostrata* (Aiton) Small**	14.49%
***Chenopodium album* L.**	60.87%
***Chenopodium murale* L.**	15.94%
Chenopodium opulifolium Koch & Ziz	4.35%

Appendix I. *Continue*

Species	Frequency
Chenopodium vulvaria **L.**	10.14%
Chrozophora tinctoria **(L.) Raf.**	24.64%
Cichorium intybus **L.**	7.25%
Cladanthus mixtus **(L.) Chevall.**	5.80%
Coleosthephus myconis (L.) Cass.	1.45%
Convolvulus arvensis **L.**	13.04%
Conyza bonariensis **(L.) Cronq.**	75.36%
Conyza canadensis **(L.) Cronq.**	8.70%
Conyza sumatrensis **(Retz.) E. Walker**	42.03%
Coronopus didymus (L.) Sm.	2.90%
Coronopus squamatus (Forssk.) Asch.	1.45%
Cuscuta campestris Yunck.	1.45%
Cynodon dactylon **(L.) Pers.**	21.74%
Cyperus rotundus **L.**	15.94%
Datura innoxia Mill.	2.90%
Daucus carota L.	2.90%
Diplotaxis virgata L.	39.13%
Diplotaxis catholica (L.) DC.	1.45%
Ecballium elaterium **(L.) A. Rich.**	7.25%
Echinochloa crus–galli (L.) P. Beauv.	4.35%
Echium plantagineum **L.**	7.25%
Eleusine indica (L.) Gaertn.	1.45%
Erodium moschatum (L.) L'Hér.	1.45%
Euphorbia helioscopia L.	2.90%
Filago pyramidata **L.**	5.80%
Fumaria agraria **Lag.**	7.25%
Fumaria officinalis L.	1.45%
Galium aparine **L.**	11.59%
Galium murale (L.) All.	1.45%
Galium parisiense **L.**	17.39%
Galium spurium (L.) Simonk	2.90%
Galium verrucosum **Huds.**	10.14%
Geranium dissectum L.	1.45%
Glaucium corniculatum **(L.) Rudolph**	10.14%
Glebionis coronaria **(L.) Spach**	20.29%
Glebionis segetum **(L.) Fourr**	13.04%
Heliotropium europaeum **L.**	68.12%
Helminthotheca echioides **(L.) Holub**	15.94%
Herniaria cinerea **DC.**	8.70%
Hordeum leporinum (Link) Arcan	2.90%
Hordeum marinum Huds.	1.45%
Hordeum murinum **L.**	5.80%
Juncus bufonius **L.**	53.62%

Appendix I. *Continue*

Species	Frequency
***Kickxia spuria* (L.) Dumort.**	10.14%
***Lactuca serriola* L.**	11.59%
***Lamium amplexicaule* L.**	11.59%
Lavatera cretica L.	2.90%
Linaria latifolia Desf.	1.45%
Lolium multiflorum Lam.	1.45%
***Lolium rigidum* Gaudin**	56.52%
***Lythrum acutangulum* Lag.**	5.80%
Lythrum borysthenicum (Schrank) Litv	1.45%
***Lythrum hyssopifolia* L.**	30.43%
***Lythrum junceum* Banks & Sol.**	11.59%
Malva neglecta Wallr.	4.35%
***Malva nicaensis* All.**	5.80%
Malva parviflora L.	4.35%
***Malva sylvestris* L.**	13.04%
Medicago lupulina L.	2.90%
Medicago polymorpha L.	1.45%
Melilotus indicus (L.) All.	2.90%
Mentha suaveolens Ehrh.	2.90%
***Misopates orontium* (L.) Raf.**	17.39%
Oxalis corniculata L.	1.45%
Oxalis pes–caprae L.	1.45%
Pallenis spinosa (L.) Cass.	1.45%
Papaver hybridum L.	1.45%
***Papaver rhoeas* L.**	14.49%
Parapholis incurva (L.) C. E. Hubb.	1.45%
Parentucellia viscosa (L.) Caruel	1.45%
***Phalaris brachystachys* Link**	31.88%
***Phalaris minor* Retz.**	40.58%
***Phalaris paradoxa* L.**	36.23%
***Phleum paniculatum* Huds.**	10.14%
***Piptatherum miliaceum* (L.) Coss**	7.25%
Plantago afra L.	2.90%
Plantago coronopus L.	1.45%
Plantago lagopus L.	2.90%
***Poa annua* L.**	20.29%
Poa infirma Kunth	2.90%
***Polycarpon tetraphyllum* (L.) L.**	20.29%
***Polygonum aviculare* L.**	42.03%
***Polygonum bellardii* All.**	7.25%
***Polypogon monspeliensis* (L.) Desf.**	56.52%
***Portulaca oleracea* L.**	34.78%
***Pulicaria paludosa* Link**	53.62%

Appendix I. *Continue*

Species	Frequency
Raphanus raphanistrum L.	2.90%
Rapistrum rugosum (L.) All.	8.70%
Reseda lutea L.	2.90%
***Ridolfia segetum* (L.) Moris**	7.25%
Rostraria cristata (L.) Tzvelev	4.35%
***Rumex crispus* L.**	5.80%
Sagina apetala Ard.	1.45%
Salsola kali L.	1.45%
Scleranthus annuus L.	2.90%
Scolymus maculatus L.	2.90%
Sedum rubens L.	1.45%
***Setaria viridis* (L.) P. Beauv.**	7.25%
Sherardia arvensis L.	1.45%
***Silene gallica* L.**	10.14%
Silybum marianum (L.) Gaertn.	4.35%
Sinapis alba L.	4.35%
***Solanum nigrum* L.**	15.94%
***Sonchus asper* (L.) Hill**	10.14%
***Sonchus oleraceus* L.**	63.77%
Sorghum halepense (L.) Pers	1.45%
***Spergula arvensis* L.**	7.25%
***Spergularia rubra* (L.) J. Presl & C. Presl**	5.80%
Spergularia salina J. Presl & C. Presl,	1.45%
Stachys arvensis (L.) L.	1.45%
Stachys ocymastrum (L.) Briq.	1.45%
Stellaria media (L.) Vill.	2.90%
***Symphyotrichum squamatum* (Spreng.) G. L. Nesom**	21.74%
Torilis arvensis (Huds.) Link	4.35%
Torilis nodosa (L.) Gaertn.	2.90%
Trifolium glomeratum L.	1.45%
Trifolium lappaceum L.	1.45%
Trifolium pratense L.	1.45%
Trifolium repens L.	4.35%
Trifolium resupinatum L.	2.90%
***Trisetaria panicea* (Lam.) Paunero**	8.70%
Urospermum picroides (L.) F. W. Schmidt	1.45%
Urtica urens L.	2.90%
Verbena supina L.	2.90%
Veronica arvensis L.	4.35%
Veronica catenata Pennell	1.45%
Veronica hederifolia L.	1.45%
***Veronica officinalis* L.**	5.80%
Veronica persica Poir.	1.45%

Appendix I. *Continue*

Species	Frequency
***Veronica polita* Fr.**	7.25%
Vicia sativa L.	1.45%
Vulpia ciliata Dumort.	1.45%
Vulpia myuros (L.) C. C. Gmel.	1.45%
Xanthium spinosum L.	1.45%
Xanthium strumarium L.	1.45%

Appendix J. List of the 116 species recorded in the seed bank of sampled cereal fields in Catalonia and their frequency. In bold are the species included in the functional analyses

Species	Frequency
Ailanthus altissima (Mill.) Swingle	1.39%
Alopecurus myosuroides Huds.	2.78%
***Amaranthus blitoides* S. Watson**	48.61%
Amaranthus retroflexus L.	2.78%
Anacyclus clavatus (Desf.) Pers.	4.17%
***Anagallis arvensis* L.**	25.00%
***Anthemis arvensis* L.**	9.72%
***Aphanes arvensis* L.**	6.94%
*Arenaria serpyllifoli*a L.	2.78%
***Atriplex patula* L.**	5.56%
***Atriplex prostrata* DC.**	5.56%
***Avena sterilis* L.**	12.50%
Bassia scoparia (L.) Voss	2.78%
***Bromus diandrus* Roth**	13.89%
***Buglossoides arvensis* (L.) I. M. Johnston**	6.94%
Calendula arvensis L.	1.39%
Campanula erinus L.	1.39%
***Capsella bursa–pastoris* (L.) Medik.**	25.00%
Cardaria draba (L.) Desv.	2.78%
Centaurea solstitialis L.	1.39%
***Centaurium pulchellum* (Sw.) Druce**	8.33%
***Cerastium glomeratum* Thuill.**	6.94%
***Chaenorhinum minus* (L.) Lange**	16.67%
***Chamaesyce prostrata* (Aiton) Small**	36.11%
***Chenopodium album* L.**	27.78%
***Chenopodium vulvaria* L.**	30.56%
Cirsium arvense (L.) Scop.	1.39%
***Convolvulus arvensis* L.**	18.06%
***Conyza bonariensis* (L.) Cronq.**	59.72%
***Conyza canadensis* (L.) Cronq.**	13.89%
***Conyza sumatrensis* (Retz.) E. Walker**	45.83%
Coronilla scorpioides (L.) W. D. J. Koch	2.78%
Crepis bursifolia L.	1.39%
Crepis sancta (L.) Bornm.	1.39%
Cynodon dactylon (L.) Pers.	1.39%
Descurainia sophia (L.) Prantl	1.39%
Digitaria sanguinalis (L.) Scop.	2.78%
***Diplotaxis erucoides* (L.) DC.**	44.44%
***Dittrichia viscosa* (L.) Greuter**	6.94%
Echium vulgare L.	2.78%

Appendix J. *Continue*

Species	Frequency
***Eleusine tristachya* (Lam.) Lam.**	5.56%
Elymus pungens (Pers.) Melderis	2.78%
Eragrostis barrelieri Daveau	2.78%
Erophila verna (L.) Chevall.	2.78%
Erucastrum nasturtiifolium (Poir.) O.E.Schulz	2.78%
Euphorbia falcata L. subsp.falcata	1.39%
Euphorbia helioscopia L.	1.39%
Fallopia convolvulus (L.) Á. Löve	4.17%
Ficus carica L.	1.39%
***Filago pyramidata* L.**	36.11%
***Fumaria officinalis* L.**	13.89%
Galium aparine L.	4.17%
***Galium parisiense* L.**	15.28%
Galium spurium (L.) Simonk	4.17%
***Galium tricornutum* Dandy**	5.56%
Geranium molle L.	1.39%
***Heliotropium europaeum* L.**	45.83%
***Herniaria cinerea* DC.**	47.22%
***Hypecoum procumbens* L.**	8.33%
***Hypericum perforatum* L.**	11.11%
***Juncus bufonius* L.**	16.67%
***Kickxia spuria* (L.) Dumort.**	25.00%
***Lactuca serriola* L.**	6.94%
***Lamium amplexicaule* L.**	5.56%
Legousia hybrida (L.) Delarbre	4.17%
Linaria supina Chaz.	4.17%
***Lolium rigidum* Gaudin**	76.39%
***Malcolmia africana* (L.) R. Br.**	6.94%
***Malva sylvestris* L.**	6.94%
Matricaria chamomilla L.	2.78%
***Medicago lupulina* L.**	6.94%
***Medicago polymorpha* L.**	15.28%
Melilotus officinalis (L.) Pall.	1.39%
Minuartia hybrida (Vill.) Schischk.	2.78%
Misopates orontium (L.) Raf.	4.17%
***Oxalis corniculata* L.**	19.44%
***Papaver hybridum* L.**	9.72%
***Papaver rhoeas* L.**	86.11%
Phleum paniculatum Huds.	1.39%
***Phragmites australis* (Cav.) Steud.**	34.72%
Piptatherum miliaceum (L.) Coss	2.78%
Plantago coronopus L.	1.39%
Plantago lanceolata L.	2.78%

Appendix J. *Continue*

Species	Frequency
***Poa annua* L.**	11.11%
Poa pratensis L.	1.39%
Polycarpon tetraphyllum (L.) L.	1.39%
***Polygonum aviculare* L.**	48.61%
Polypogon monspeliensis (L.) Desf.	1.39%
***Portulaca oleracea* L.**	23.61%
Reseda phyteuma L.	1.39%
***Roemeria hybrida* (L.) DC.**	11.11%
Rostraria cristata (L.) Tzvele	2.78%
Rumex crispus L.	2.78%
Scandix pecten–veneris L.	1.39%
Senecio vulgaris L.	4.17%
***Setaria adhaerens* (Forssk.)Chiov.**	11.11%
***Setaria pumila* (Poir.) Roem. & Schult.**	8.33%
***Setaria verticillata* (L.) P. Beauv.**	12.50%
***Setaria viridis* (L.) P. Beauv.**	5.56%
Silene nocturna L.	1.39%
***Sisymbrium irio* L.**	11.11%
Solanum nigrum L.	4.17%
Sonchus asper (L.) Hill	2.78%
***Sonchus oleraceus* L.**	31.94%
Sonchus tenerrimus L.	1.39%
***Stellaria media* (L.) Vill.**	9.72%
Torilis arvensis (Huds.) Link	1.39%
Trigonella monspeliaca L.	1.39%
***Verbena officinalis* L.**	19.44%
***Veronica arvensis* L.**	15.28%
***Veronica hederifolia* L.**	22.22%
***Veronica persica* Poir.**	16.67%
***Veronica polita* Fr.**	8.33%
***Viola arvensis* Murr.**	8.33%
Vulpia ciliata Dumort.	2.78%
***Vulpia unilateralis* (L.) Stace**	11.11%