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

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ABSTRACT

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

1. Introduction

Agricultural landscapes are characterized by a mosaic of habitats where the range of hosted plant species are affected by the spatio-temporal disturbances featuring agricultural intensification (AI) such as pesticides and fertilizers inputs, tillage operations and plant biomass removal (Tscharntke et al., 2005). Since species richness does not always adequately reflect the overall diversity, it is likely that the impacts of AI on plant communities are better reflected by functional traits (Storkey et al., 2013; Armengot et al., 2016). As functional diversity refers to the ecological roles that species have in their community and how their traits influence composition and ecosystem functioning, the response-effect trait framework can be used for predicting the impact of environmental changes on ecosystem services (ESs) delivery in multi-trophic systems (Gaba et al., 2017; Solé-Senan et al., 2017). The framework integrates plant traits, divided into response traits that govern how plants respond to different environmental filters and effect traits that determine how plants affect their environment (Lavorel and Garnier, 2002). There is agreement that effect traits cause a response from other organisms driving the ESs (e.g. floral traits to pollinator traits). Therefore, dealing with functional traits instead of species richness helps to predict the role of plant species in providing ESs (Lavorel and Grigulis, 2012). In agroecology, pollination is one of the most studied ES because it entails the maintenance of plant communities and agricultural productivity (Le Féon et al., 2010; Potts et al., 2010). Furthermore, trait syndromes, which are correlative patterns of interacting functional traits, can be used to predict the identity of flower visitors (Ricou et al., 2014). In this context, understanding how floral trait syndromes change in an agricultural landscape will be ground-breaking to underpin the provisioning of resources for pollinators.

The additive partitioning approach disentangles diversity patterns across multiple spatial scales (Wagner et al., 2000). Total diversity in a location (γ-diversity) can be partitioned into two components; α-diversity (the diversity within a given sampling unit) and β-diversity (the turnover of diversity between sampling units). This approach has been

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applied to the analysis of plant species richness in different habitats (Wagner et al., 2000) and along gradients of landscape complexity across field positions in arable fields (Solé-Senan et al., 2014). Furthermore, the additive partitioning can similarly be applied to species richness (S) and measures of functional diversity such as Rao's Quadratic entropy (Q) (Rao, 1982; de Bello et al., 2009). However, we are not aware of any published studies partitioning both S and Q (response against effect traits) in Mediterranean arable plant communities.

This study is aimed at understanding how AI drives changes in plant species richness and plant functional assemblages in agricultural landscapes, while also considering the detail at which habitats within mosaic landscapes should be classified and sampled in order to provide useful information on functional diversity. More specifically, we aim to determine how the provisioning of resources for pollinators depends on AI. We hypothesized that the different levels of AI at which habitats are subjected are likely to enhance a diversity of trait syndromes along those habitats. A landscape with a higher diversity of effect trait syndromes should provide more resources for different pollinator species than a landscape dominated by habitats providing low trait syndrome diversity. Furthermore, we suspect that habitats subjected to low AI provide resources to specialized pollinators, whereas habitats subjected to high AI will select for plant species with trait syndromes for generalist pollinators (Juárez-Escario et al., 2017; Solé-Senan et al., 2017). We hypothesize that the species diversity turnover along spatial scales will not be concomitant to a shift in terms of functional diversity, highlighting that a pool of plant species with the same traits are filtered together. Hence, AI can be used as the main driver of the spatio-temporal patterns of species and functional diversity in agricultural landscapes. The questions forming the basis for the analysis conducted address: (1) how habitats and levels of AI affect plant species and functional assemblages (2) how AI variability affects the provision of resources for pollinators, (3) how the contributions of α-diversity and β-diversity-to γ-diversity differ between species and functional diversity and (4) what vegetation types should be promoted to support pollinating insects. Our study is aimed at disentangling the relationships between patch disturbances and the provisioning of floral resources eventually available for insects, thus providing guidance for diversity maintenance in agricultural mosaic landscapes.

2. Material and methods

2.1. Study area and plant survey

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

We checked the spatial autocorrelation in species assemblages along the surveyed patches with the Mantel test (Bray-Curtis distance for species assemblages, Euclidean distance for geographic distance for patches and based on Spearman correlation with 999 permutations) (Legendre and Legendre, 1998). No spatial autocorrelation effect was found (all patches, $R = -0.019$, p-value = 0.782; abandoned fields, $R = 0.101$, p-value = 0.162; alfalfa edges, $R = -0.012$, p-value = 0.512; inner alfalfa fields, $R = -0.108$, p-value = 0.899; boundaries, $R = -0.098$, p-value = 0.891; cereal edges, $R = -0.118$, p-value = 0.918; inner cereal fields, $R = 0.038$, p-value = 0.328; roadverges, $R = -0.016$, p-value = 0.534). To test differences in species assemblages between years, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) on the mean frequency of each species per patch assuming the factor "year" as a qualitative variable. No differences in species assemblages between years were found ($F = 3.02$, $R^2 = 0.02$, p-value > 0.05). Species accumulation curves with first-order jack-knife estimates of total species richness of each habitat were calculated to check the adequacy of the sampling effort, ranging from 92.5% (abandoned fields) to 97.5% (inner cereal fields) (Supplementary Appendix A). Both analyses were conducted using the vegan package (Oksanen et al., 2013) in R (R Developement Core Team, 2008).

2.2. Levels of agricultural intensification

We considered a farmer-subjective score of the intensity of the farming management practices at patch scale based on interviews with farmers (Table 1). Only patches in which the management fits in terms of the levels exposed in Table 1 were surveyed. It included disturbance indicators that are known to influence plant diversity such as mean fertilizer and herbicide inputs (Kleijn and van der Voort, 1997), belowground disturbances and vegetation removal (Kühner and Kleyer, 2008). The score provided a proxy of the level of agricultural intensification (AI) intensity, namely: (1) Low (Low_{AI}): intensification shared in abandoned fields, boundaries and roadverges; (2) Medium ($Medium_{AI}$): intensification shared between field edges and inner alfalfa fields; (3) High ($High_{AI}$): intensification shared between field edges and inner cereal fields.

2.3. Functional traits

Although a same trait could be both a response and an effect trait (Gaba et al., 2017, Solé-Senan et al., 2017), for each encountered species, we defined five response and four effect traits based on our hypotheses. Response traits such as growth form (GF) (Juárez-Escario et al., 2016, Juárez-Escario et al., 2017), plant height (H) (Fried et al., 2012; Storkey et al., 2013), onset of flowering (OF) (Fried et al., 2012; Juárez-Escario et al., 2013; Robleño et al., 2017) specific leaf area (SLA) and seed mass (SMass) (Storkey et al., 2013) have been related not only to the disturbance response caused by AI, but also to species persistence

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

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

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