



Both farming practices and landscape characteristics determine the diversity of characteristic and rare arable weeds in organically managed fields

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Keywords

Crop edge; Farm management; Mediterranean dry-land arable fields; *Secalietalia cerealis*; Species richness

Nomenclature

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Abstract

Questions: Do both current and past (short-term) farming practices and landscape characteristics have an effect on the diversity of characteristic and rare arable plant communities in organic fields? What is the role of farm management strategies, apart from farm spatial configuration, in determining the diversity components of these species sets?

Location: Thirty-two farms scattered across NE Spain (Catalonia).

Methods: Specialist species of arable fields, belonging to the *Secalietalia cerealis* Br-Bl. 1936, were surveyed at the edges of organically managed fields. We assessed the effects of farm management and landscape characteristics at the field and farm scales on α -, β - and γ -diversity values of these characteristic arable species. Analyses were also conducted on a subset of *Secalietalia* species that are considered to be rare. Statistical analyses were performed using multimodel inference determined on the basis of all possible models from an *a priori* set.

Results: Field variables, such as years since conversion to organic management, proportion of cereal crops in the rotation and autumn sowing, had a positive effect, whereas growing non-cereal crops and fertilization had a negative effect on the richness of characteristic species. The field area had a positive effect on the species richness of characteristic and rare arable plants. At the farm level, the proportion of cereal crop fields to the total amount of fields affected both β and γ characteristic diversity. The landscape variables at the farm level only influenced the β -diversity of rare species.

Conclusions: The effects of management and landscape on arable weed diversity depended on whether the field or the farm is the focus of the analysis. Characteristic and rare arable species were more affected by factors operating at local scales. Characteristic species richness responded positively to sowing cereal crops, autumn sowing and periodic soil disturbances but was negatively affected by slurry fertilization. Thus, policies promoting some of the former practices should favour characteristic arable species and mitigate the decline of the rare arable species.

Introduction

Arable weeds have been a major concern among farmers because they are traditionally viewed as an impediment to crop production, causing crop losses of approximately 30% (Oerke 2005). Thus, weed control is a primary objective guiding crop management strategies, despite the fact that only a few weed species are problematic and cause actual

crop losses (Albrecht 2003). Given its current extent, agricultural land contributes significantly to global biodiversity (Tscharntke et al. 2005). Because of management intensification, however, agriculture is considered to be the primary agent for the decline of plant diversity. Agro-ecosystems are thus among the habitats that hold a large proportion of rare and endangered species in many European countries (Rich & Woodruff 1996; Tscharntke et al. 2005).

A particular set of specialist species of arable fields belongs to the phytosociological order *Secalietalia cerealis* Br-Bl. 1936, being characteristic arable weeds that thrive almost exclusively in arable cropping systems because of their dependence on regular disturbance (Critchley et al. 2006) and their inability to succeed in more competitive habitats (Romero et al. 2008; José-María et al. 2010). In general, characteristic and rare species of any habitat are more affected by changes in land use than generalists (Albrecht 2003). Thus, the populations of characteristic arable weeds have declined severely because of agricultural intensification (Robinson & Sutherland 2002; Albrecht 2003). This decline has been so sharp that some of them have become rare or even extinct (Baessler & Klotz 2006; Chamorro et al. 2007; Cirujeda et al. 2011). Some European countries have included arable species in Red Data Lists (Cheffings & Farrell 2005; Ture & Bocuk 2008), which is a first step in developing conservation strategies (Kleijn & Van der Voort 1997). Because characteristic arable species represent key indicators of the natural and aesthetic values of farmland, their conservation in agroecosystems can be considered as an indicator of sustainable land use (Tschardt et al. 2005; Storkey et al. 2012). The effects of agricultural intensification at field and landscape levels on the species richness of weed communities in Mediterranean dryland cereal fields have been reported extensively (Romero et al. 2008; José-María et al. 2010). Nevertheless, its effect on characteristic and rare arable weeds is still poorly understood because of their low frequency, which limits the reliability of statistical analysis. To our knowledge, this is the first study that addresses this issue by analysing the characteristic arable species present in a large sample of organic fields.

Organic farming systems, which are usually less intensively managed than conventional ones, have been found to enhance the abundance and richness of arable species (José-María et al. 2010; Ponce et al. 2011). However, large variations in management intensity among organic farms affect weed diversity (Clough et al. 2007; Armengot et al. 2011). Hence, certain current management practices might better explain the observed changes in the extant populations of weed flora than the overall intensification indicators. Because the persistence of characteristic arable weeds largely depends on their ability to remain viable in the soil seed bank, recent/past management could also help explain the diversity of weeds occurring in a given field. In addition to management, weed diversity is also negatively affected by landscape intensification (Gabriel et al. 2005; Baessler & Klotz 2006; José-María et al. 2010). Landscape intensification increases the proportion of arable habitat but also involves landscape simplification by decreasing habitat diversity and quality because of intensive field management, which is an important driver of biodiversity

loss (Robinson & Sutherland 2002; Tschardt et al. 2005).

This study aims to assess the effects of farming on characteristic weed diversity in Mediterranean dry-land organic arable fields and farms. Thus, we intend to disentangle the effects of particular management strategies that, independently of landscape characteristics, may benefit these species. We analysed characteristic arable species diversity at the field and farm (defined as the set of fields scattered in a specific area managed by the same farmer) levels. We focused on characteristic arable species, which are very specific to arable land and have suffered from recent land-use changes and may therefore have conservation value. In this way, we avoided having to include common species that also occur in neighbouring non-cropped and disturbed habitats. We surveyed organic fields from farms placed in a gradient of landscape complexity and interviewed farmers to obtain information on management practices. Specifically, we (1) assessed the effects of both current and past (in the last 5 yr) farming practices, field size and shape and landscape complexity on the species richness of characteristic and rare arable weed species in organically managed fields; and (2) evaluated the effects of farm management, apart from surrounding landscape variables, on the β - and γ -diversity values of these species sets.

Methods

Study area

Sampling was conducted in 2011 in Catalonia (41°22'–42°06' N, 0°59'–2°12' E) within an area spanning 100 km × 80 km (Fig. 1) with an average (\pm SE) altitude of 558 \pm 30 m a.s.l. (min = 95 m, max = 871 m). The climate is Mediterranean, with mean annual temperatures of 12.6 \pm 0.2 °C (min = 10.5 °C, max = 14.9 °C) and average annual precipitation of 637 \pm 21 mm (from 416 to 868 mm). The whole area lies on marls and calcareous sandstones, which create basic soils.

All of the organically managed fields from 32 farms sown with the annual crops usually included in a crop rotation of winter cereals (cereals, legumes, ryegrass and mixtures containing cereals and legumes) were surveyed. A total of 304 fields were inventoried, with an average (\pm SE) of 9.50 \pm 0.47 fields per farm. The farms were located in landscapes of different degrees of complexity according to their percentage of arable land (PAL); PAL is a widely used estimator of agricultural landscape simplification (Roschewitz et al. 2005; Gabriel et al. 2006). These landscapes ranged from structurally simple with a high PAL (ca. 97% within a circular area with a radius of 1 km around sampled fields; see Landscape characteristics below) to complex landscapes with a high percentage of

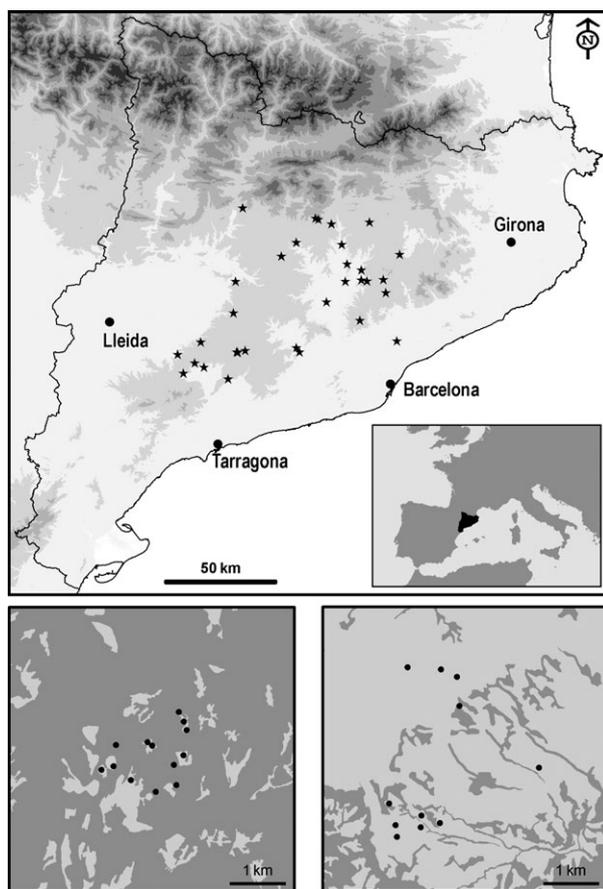


Fig. 1. Location of the 32 farms within Catalonia (NE Spain) above (grey tones indicate elevation every 500 m). Fields sampled in two farms taken as examples of complex (left) and simple (right) landscapes. Light grey represents arable habitats while dark grey includes natural and semi-natural habitats.

natural and semi-natural habitats (ca. 92%). Natural habitats in the studied area included pine (*Pinus halepensis* Mill. and *P. nigra* Arnold) and oak (*Quercus ilex* L. and *Q. faginea* Lam.) woodlands as well as scrub, small stands of perennial-dominated grasslands and riverine vegetation.

Plant species survey

The survey was conducted during May and June 2011, corresponding to the phenological optimum of weeds in the Mediterranean. The weed survey was restricted to field edges, defined as the first two cultivated meters adjacent to the margins (Marshall & Moonen 2002), to maximize the detection of characteristic arable weeds (cf. José-María et al. 2010; Kovács-Hostyánszki et al. 2011). On the edge of each field, depending on its size, a minimum of three and a maximum of ten

2 m × 5 m plots (80 m apart) were established. We used rarefaction to compensate for differences in the sampling effort between fields.

Within each plot, we only recorded arable species characteristic of the phytosociological order *Secalietalia cerealis* Br.-Bl., 1936, i.e. communities of dryland arable fields under Mediterranean climate on basic soils (see Appendix S1). These species were also identified as characteristic or obligate arable weeds by Albrecht (2003), Romero et al. (2008) and José-María et al. (2010). Characteristic arable weeds do not include species frequently occurring outside of the fields. Some characteristic arable species have severely declined in abundance over the last decades and are now considered regionally rare (Chamorro et al. 2007; Cirujeda et al. 2011; Solé-Senan et al. 2014). We took the subset of these characteristic species that are considered rare according to de Bolòs et al. (2005) for the analyses (see Appendix S1). Nevertheless, these rare arable species are not included in the Red Data List of the area surveyed (Sáez et al. 2011). The nomenclature of plant species and phytosociological adscription also follows that of de Bolòs et al. (2005). Within each plot, the percentage of crop cover was assessed.

Farming management

Farmers were interviewed to obtain information about their farming practices on each sampled field and on the entire farm during the 5 yr prior to sampling. (see Tables 1, 2, respectively). The selected variables reflect historical field management (years since the conversion to organic farming and the cereal ratio, which is the proportion of cereal crops in the 5-yr rotational schemes), and current management during the 2010–2011 period (remaining variables) of each field and farm.

Landscape characteristics

We measured the perimeter and area of each field, determined its shape (perimeter/area), and computed the PAL around it using ArcGIS 9.0 (ESRI, Redlands, CA, US). The landscape around each field was characterized within a circular area of a 1-km radius using Catalan Habitats Cartography (Carreras & Diego 2004). The mean PAL around the fields and the mean distance between the fields of each farm were considered to be the landscape metrics at the farm level.

Plant diversity

In-field characteristic and rare species diversity were evaluated as the number of *Secalietalia* species recorded in each field. The farm diversity of characteristic weeds was

Table 1. Characterization of farming practices and landscape characteristics of the fields (304) surveyed. Mean and range (in brackets) of continuous variables and proportion of fields and farms with the stated practices for the categorical variables. On the right, model-averaged estimate \pm unconditional SE (UnSE) for the explanatory management and landscape variables at the field scale on characteristic and rare species richness. Asterisks indicate an effect for which the 95% CI did not include zero.

	Mean [range]/Proportion	Characteristic Arable Weeds	Rare Arable Weeds Subset
		Estimate \pm UnSE	Estimate \pm UnSE
Years from Conversion to Organic Farming	9.67 [1, 25]	0.078 \pm 0.027*	0.012 \pm 0.012
Cereal Ratio [†]	0.56 [0, 1]	0.272 \pm 0.099*	0.155 \pm 0.056*
Soil Tillage			
Inversion Tillage (vs No Till and No Inversion Tillage)	105 (199)	-0.038 \pm 0.034	-0.009 \pm 0.028
Current Crop			
Mixed (vs Cereal)	87 (170)	0.004 \pm 0.078	0.032 \pm 0.050
Legume (vs Cereal)	17 (170)	-0.161 \pm 0.119	-0.056 \pm 0.075
Ryegrass (vs Cereal)	30 (170)	-0.548 \pm 0.110*	-0.271 \pm 0.074*
Seed Origin			
Reuse Seeds (vs Purchased)	192 (112)	-0.085 \pm 0.031*	-0.070 \pm 0.028*
Sowing Time			
Spring Sowing (vs Autumn Sowing)	58 (246)	-0.187 \pm 0.069*	-0.052 \pm 0.026*
Sowing Density (kg·ha ⁻¹)	154.81 [16.5, 384]	0.068 \pm 0.025*	0.026 \pm 0.011*
Type of N Inputs			
Fertilization (vs No Fertilization)	185 (119)	-0.031 \pm 0.011*	-0.017 \pm 0.006*
Slurry (vs Manure)	18 (167)	-0.151 \pm 0.029*	-0.097 \pm 0.014*
Amount of N Inputs (kg·ha ⁻¹)	47.44 [0, 600]	-0.001 \pm 0.006	-0.019 \pm 0.010
Mean Crop Cover (%)	51.16 [0, 95]	0.056 \pm 0.020*	0.099 \pm 0.028*
Amount of N Inputs \times Crop Cover		-0.043 \pm 0.015*	-0.056 \pm 0.021*
Weed Control			
Control (vs No Control)	128 (176)	0.026 \pm 0.009*	0.002 \pm 0.004
Tillage (Pre-sowing Control) [vs Harrowing (Post-sowing)]	89 (39)	0.110 \pm 0.024*	0.043 \pm 0.010*
Animal Husbandry			
Grazing (vs No Grazing)	91 (213)	-0.138 \pm 0.050*	-0.068 \pm 0.026*
Percentage of Arable Land (PAL)	46.58 [6.83, 100]	-0.039 \pm 0.016*	0.025 \pm 0.013*
Field Area (m ²)	15374.54 [1629.99, 150415.50]	0.046 \pm 0.017*	0.065 \pm 0.023*
Field Shape (Perimeter/Area)	0.06 [0.01, 0.19]	-0.034 \pm 0.013*	-0.014 \pm 0.009

[†]Calculated as the proportion of cereal crops in the 5-yr rotation scheme of each field.

Table 2. Characterization of farming practices and landscape characteristics of the farms (32) surveyed. Mean and range (in brackets) of continuous variables and proportion of fields and farms with the stated practices for discrete variables.

Farm Type	
Crop Specialized Farm	11/32
Mixed Farm	21/32
Ratio of Cereal Crop Fields	0.50 (0, 1)
Mean PAL	47.94 (8, 96.67)
Mean Field Distance (m)	669.87 (242.57, 3940.62)

partitioned considering the multiplicative relationship between γ species richness (total number of characteristic species in the farm) and β -diversity (accounting for the among-field community composition differentiation or within-farm heterogeneity; calculated as $\beta = \gamma/\alpha$, where α is the mean species richness per field; Whittaker 1960). The relative contributions of each fraction allowed assessment of the effects of the variables on the arable species at the farm scale.

In-field diversity analysis

As we surveyed a different number of plots in each field depending on field area, the in-field species richness was rarefied. Rarefaction provides an estimate of the expected species richness for a given number of samples. For each field, we estimated the expected number of species in three plots because this was the minimum number of plots surveyed per field.

The effects of landscape and management variables at the field scale (Table 1) on species richness were analysed using mixed effect models, which account for the hierarchically nested design. We included the farm as a random factor. Because rarefied species richness behaves nearly as a count process but its values can be fractional, we used a Gaussian model on the log-transformed values to stabilize the relationship between the variance and the mean. Due to the interaction between the amount of nitrogen input and the mean crop cover in each field detected in the preliminary analyses, this interaction was also included in the

models as a new variable. This interaction variable was obtained from the product of these two variables to ensure its inclusion in the models despite the absence of main effects (Hector et al. 2010). We standardized (mean equal to 0 and SD equal to 1) all continuous explanatory variables. This approach homogenized their ranges and facilitated comparison of their effects based on regression coefficients.

Statistical analyses were performed using the multi-model inference method (Burnham & Anderson 2002). This method allows inference to be made on the basis of all models from an *a priori* set rather than based only on the best estimated model. There were 65 535 possible combinations of all of the explanatory variables. However, only 49 151 models were evaluated because we excluded models that considered the type and the amount of nitrogen inputs at the same time because of the moderate correlation between them.

Models were compared using the adjusted Akaike information criterion (AIC) (Burnham & Anderson 2002). This method allows direct comparison of the information loss of each model in relation to the estimated best model, which has the minimum AIC ($\Delta_i = AIC_i - AIC_{\min}$). Afterwards, the Akaike weight (w_i) was calculated for each model. To assess the effect of each variable, multi-model inference from the entire set of models was used, which provides the model-averaged parameter estimates and their unconditional SE weighted by their Akaike weights. The 95% confidence intervals were also computed to evaluate the breadth of the likely magnitude of their contributions. All analyses were also conducted for the in-field species richness of the rare weeds subset.

Farm γ - and β -diversity analysis

The number of fields surveyed per farm differed according to the number of organic fields managed by a farmer. Therefore, because the number of plots per field also differed, the γ - and β -diversity values at the farm level were estimated by means of a double rarefaction, selecting four random fields per farm and three random samples per field. As no hierarchical design is present at the farm level, a linear model with a Gaussian error distribution was used after confirming the normality and homoscedasticity of the residuals. Continuous explanatory variables were standardized (see In-field diversity analysis).

The process of re-sampling and fitting the models was repeated 10 000 times. We evaluated the effect of each variable on the γ - and β -diversity values of each set of species by the density distribution of the estimated coefficients for each variable. We considered that a variable might have a relevant effect when the distribution of its estimated coefficients is not centred at zero, and thus, the dis-

tribution is clearly biased towards either positive or negative values.

Statistical analyses were performed using R 3.0.0 (R Foundation for Statistical Computing, Vienna, AT) with the lme4 package (<http://CRAN.R-project.org/package=lme4>) for mixed-effects models.

Results

Characteristic and rare arable weed communities: overview

Overall, we recorded 65 characteristic arable weed species, 46 of which are considered rare (Appendix S1). Only 183 sampled plots (9.37%) did not contain any characteristic arable species. We found at least one rare species in 1162 sampling plots. The most frequent characteristic species, recorded in >30% of the plots, were *Papaver rhoeas* L. and *Polygonum convolvulus* L. However, many of the species recorded (47 of 65) were present in <5% of the plots. Our results showed that some species that are not considered rare in local flora (de Bolòs et al. 2005) were recorded less frequently than some of these rare species. This is the case for species such as *Anchusa italica* Retz. (0.25% of plots), *Galeopsis ladanum* L. subsp. *angustifolia* (Her. ex Hoffm.) Gaudin (0.25%) and *Ranunculus arvensis* L. (2.30%). Among the species considered rare, the most frequent were *Kickxia spuria* (L.) Dumort and *Galium aparine* L. subsp. *spurium* (L.) Simonk, but they were recorded in <16% of the total plots. Therefore, despite sampling only those areas preferred by characteristic and rare weed species, these species were found to be uncommon in Mediterranean dryland arable fields. The mean (\pm SE) characteristic species richness per field (in three plots) estimated by rarefaction was 5.93 ± 0.17 , and that of rare weed species was 1.79 ± 0.07 . At the farm level, the mean (\pm SE) characteristic γ species richness was 12.34 ± 0.64 , estimated by rarefaction, and that of rare weed species was 4.68 ± 0.30 .

Field diversity

Overall, the in-field species richness of characteristic arable weeds was influenced by farming practices, field physical characteristics and PAL (Table 1). However, based on the magnitude of their effects, management variables had a much stronger effect on these species than the landscape descriptors.

Regarding past (short-term) field management, years since conversion to organic farming positively affected the richness of characteristic arable species, and fields with a high proportion of cereal crops in the rotation (cereal ratio) harboured more characteristic and rare species (Table 1).

Regarding current management, the variables that had the strongest effect based on their estimated coefficients were the crop type and sowing period, type of fertilization, weed control and animal grazing. In contrast, the type of tillage did not influence richness of either characteristic or rare species (Table 1). The characteristic and rare species richness were negatively affected by sowing of annual ryegrass compared with cereal-sown fields, as well as by spring crops compared with winter crops. Fertilizer application reduced the weed diversity of these species, but primarily when slurry was applied. Although the amount of nitrogen input affected neither the characteristic arable species nor the rare species, its interaction with the crop cover had a negative effect on both groups of species. Weed control favoured the richness of characteristic species compared with lack of weed control. Among the fields with weed control, pre-sowing tillage had a positive effect on characteristic and rare arable weeds compared with harrowing. Grazing negatively affected the richness of characteristic and rare weed species. Although the magnitude of the effect was much lower than the above-mentioned variables, we also found a positive effect of crop cover on the species richness, perhaps biased by the effect of interaction with the amount of nitrogen input. Higher PAL and perimeter/area ratio were related to lower species richness of characteristic species; however, larger fields promoted richness.

Farm diversity

The γ -diversity of characteristic species richness was affected by farm management but not by landscape simplification or inter-field distances (Fig. 2). The only factor determining total characteristic species richness at the farm level was the ratio of cereal crop fields within a farm. The γ -diversity of rare arable species richness was not influenced by factors operating at the farm scale.

The farm β -diversity was favoured by mixed farming compared to farms without stock. The number of cereal crops sown in a farm had a negative effect on the β -diversity of characteristic species, but was not affected by the landscape variables. However, the β -diversity of the subset of rare weeds was positively affected by the distance between fields; resulting in highly variable assemblages when more distant fields were considered.

Discussion

Characteristic and rare arable weeds surveyed

Due to the large number of fields surveyed in this study, and because the study focused exclusively on crop edges of organic fields where most characteristic arable weeds thrive, we found more characteristic weeds (65) than other

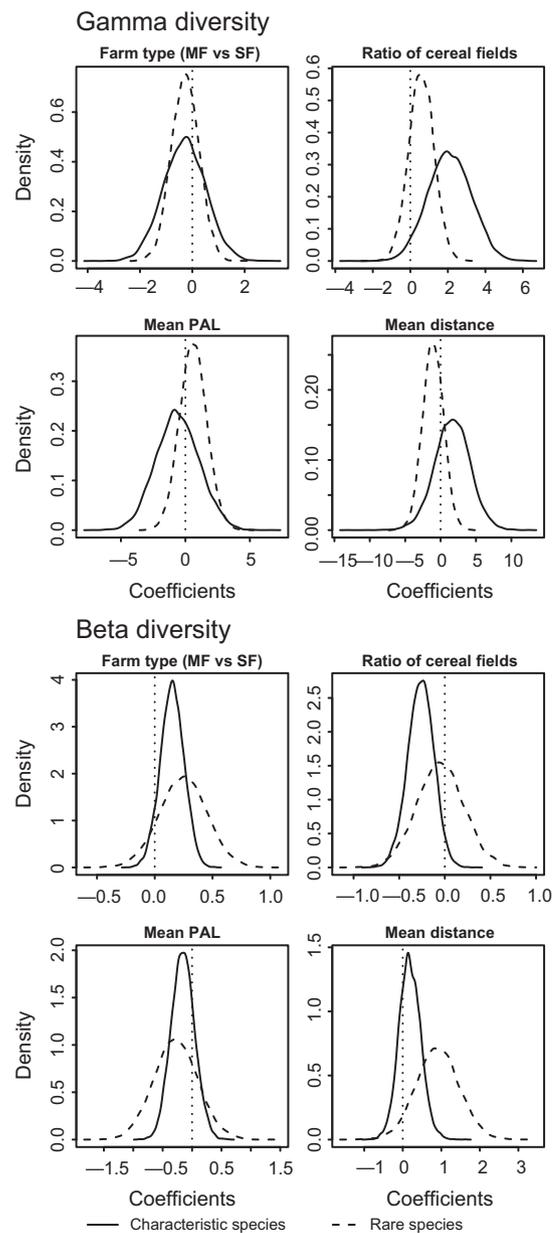


Fig. 2. Density distribution of estimated coefficients for each farm-level explanatory variable. The distribution of coefficients results from fitting the models for γ - and β -diversity of characteristic and rare weeds to 10 000 random subsets of data, and indicates the probability of a variable having an effect of a given magnitude. Farm type represents the magnitude of the difference between mixed farms (MF) and farms without stock (SF). Ratio of cereal fields, PAL (percentage of arable land) and mean distance (mean distance between fields of a farm) represent the magnitude of the slope in relation to the dependent variable.

studies from the same area (Romero et al. 2008; José-María et al. 2010). However, most of these species were found in very few samples: more than 70% of characteristic arable weeds had frequencies <5%, including some that

are not considered rare by de Bolòs et al. (2005). This indicates the vulnerability of these species, which are very scarce even in those habitats found to be most appropriate for their growth (José-María et al. 2010).

Effects of management on in-field species richness

Most management variables affected the in-field arable species richness. Although above-ground weed flora depends largely on the specific conditions generated by the standing crop (Hawes et al. 2010), our results show that the flora was also influenced by short-term historical management. For instance, old organically managed fields harbour a higher number of characteristic weed species compared with recently converted fields. Thus, despite variation in the intensity of its practices (Clough et al. 2007; Armengot et al. 2011), organic farming seems to mitigate the decline of characteristic weed populations. A high proportion of cereals in the rotational scheme promoted the occurrence of these weeds, as previously noted (Kolářová et al. 2013), because this cropping system provides the conditions to which they are adapted. For instance, most characteristic species germinate in autumn, which matches the typical cycle of winter arable crops (Satakamp et al. 2011). Thus, ploughing before spring sowing removes the emerged seedlings (Critchley et al. 2006), leading to a decrease in the total diversity of characteristic weeds, as observed here.

Arable weeds and crop species compete for the same resources and, hence, tend to be exclusive (Ponce et al. 2011). Characteristic arable species are usually less competitive than crops (Critchley et al. 2006), and thus, we found that they are negatively affected by farming practices favouring crop growth. This is illustrated in our study by the negative effect of fertilization on characteristic species richness, as previously described (Gabriel et al. 2005; Storkey et al. 2012). This effect is even stronger when slurry is applied because slurry generally contains higher and more labile forms of nitrogen than other fertilizer sources (Romanyà et al. 2012). The negative effect of fertilization on weed species is usually indirect because fertilizer stimulates crop growth, thus reducing light penetration and consequent weed growth (Pyšek & Leps 1991).

At the edges of fields, where we performed our surveys, sowing is less homogenous than in the centre (Romero et al. 2008). Thus, crop cover represents the actual amount of the cereal crop competing with the weeds. Its effect on characteristic and rare species richness was modulated by its interaction with the amount of available nitrogen. While this interaction is significant, the main effects of the variables involved (amount of nitrogen and crop cover) are of little interest. This significant interaction

indicated that at high values of crop cover, weed species richness declined as fertilizer levels increased because some characteristic weeds are out-competed by the crop (Pyšek & Leps 1991). However, under low crop cover, characteristic and rare species are favoured by the improved resource availability without being subject to competitive pressure from the crop.

Not all management practices aimed at improving crop conditions have consistently negative effects on characteristic species. Pre-sowing weed control, such as tillage practices, favoured characteristic species richness, contrary to some findings (Santín-Montanyá et al. 2013). Our study focused on characteristic arable species adapted to annual soil disturbance (Critchley et al. 2006) and not on overall weed diversity, which may respond differently. In contrast, post-emergence mechanical weed control reduces species richness because it directly affects the established community. Similarly, characteristic species were negatively affected by animal grazing, which might represent a change to the disturbance regime other than ploughing or harvesting (Critchley et al. 2006).

Effects of landscape on in-field species richness

Despite the significant influence of landscape variables on characteristic and rare species richness, effects of such variables were of minor importance. Moreover, patterns in the response of species richness in both sets of species in relation to landscape simplification differed slightly. Simple landscapes (with high PAL) had a negative effect on characteristic species richness, but benefited the rare weeds subset. This effect on weed species richness has previously been reported (Gabriel et al. 2005; Roschewitz et al. 2005; José-María et al. 2010) and related to the relevance of alternative habitats in the surrounding landscape as a refuge for weed species, which would not be the case for characteristic weeds that preferentially thrive in arable habitats. Rare species at the crop edges were favoured by more available habitat (higher PAL), contrary to evidence from other studies (Kovács-Hostyánszki et al. 2011; Solé-Senan et al. 2014). Our results indicate that characteristic arable weeds, especially rare weeds, respond more to local conditions and thus depend more on the fields themselves than on landscape characteristics.

At the field level, larger fields held more characteristic and rare weed species, even when the effect of increased sample size was removed through rarefaction. Larger fields might support a more diverse weed flora by containing a broader range of microenvironments while still enabling intra-field exchange of diaspores. Moreover, large fields are often created from the historical amalgamation of smaller fields, which may enlarge local species pools (Marshall 2009). Nevertheless, some authors found either

no effect of area on species richness (Marshall 2009) or even a negative effect (Gaba et al. 2010). These characteristic weed species thrive preferentially on field edges; thus we expected higher characteristic species richness in fields with a higher perimeter/area ratio (Gabriel et al. 2005). However, our data support the opposite effect, most likely due to the strong positive effect of area.

Effects of farming and landscape on farm diversity

A higher number of cereal crop fields within a farm led to more homogenous management among fields, which reduced the β -diversity of characteristic species richness. However, total species richness (γ -diversity) was higher in farms with a higher proportion of cereal fields. These results indicate that the higher γ -diversity was a result of higher in-field diversity found in the cereal fields instead of differences between weed communities in the fields. Regarding the different purpose of crops (e.g. hay, silage, seeds), farming practices in mixed farms are usually more heterogeneous than in farms without stock, which was reflected in the higher β -diversity for both characteristic and rare species. However, the γ -diversity of mixed farms remains equivalent to that of farms without stock.

In contrast to other studies (Baessler & Klotz 2006; Gabriel et al. 2006; Solé-Senan et al. 2014), our results showed that landscape simplification at the farm level did not have an effect on either γ - or β -diversity. This result indicates that characteristic and also rare arable species were not only more sensitive to landscape variables at the field than at the farm level but were even more sensitive to specific management practices. The β -diversity of rare arable species depended on the distance between fields. Rare weed species appear under certain local conditions, which depend on small-scale effects and on the history of the fields.

Implications for conservation

Our results show that most characteristic species are very uncommon in the sampled fields, despite being surveyed only in their preferred areas. Most species were found in very few samples, including some species that are not considered regionally rare (de Bolòs et al. 2005); therefore, the rarity of characteristic species should be revised to determine appropriate conservation strategies. Management pressure imposed on agricultural land, even under organic systems, affected characteristic arable species richness similarly to the effect on rare weeds. Implementation and maintenance of organic management guidelines could lead to the preservation of characteristic and rare arable species at field edges. However, organic farming is currently insufficient to counteract the current critical conservation status of rare weeds. Thus, it is necessary to adopt

specific management practices, in addition to encouraging conversion to organic farming. As our results show, the promotion of cereal crops should be encouraged, particularly autumn-sown varieties, and slurry fertilisation and grazing should be limited to benefit both characteristic and rare species in organically managed fields.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristic arable species recorded.