



Refining rare weed trait syndromes along arable intensification gradients

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Keywords

Agroecology; Arable fields; Assembly patterns; Biodiversity; Community assembly; Filters; Functional groups; Hungary; Red List

Nomenclature

Király (2009)

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Abstract

Question: How does the conservation (rarity) value of arable weed communities differ along intensification gradients? Which functional traits best distinguish the weed communities of more and less extensively managed fields? Can the same traits predict the rarity of individual weed species?

Location: Hungary.

Methods: Using relevé data from 60 cereal and 70 stubble fields, together with weed trait data, we characterized community responses to arable intensification using functional trait analyses based on trait-convergence and trait-divergence assembly patterns. We also examined how well the broad-scale rarity status of species predicts their occurrence along intensification gradients, and how it maps onto our functional classifications describing intensification responses.

Results: The response of weeds to intensification in cereal fields was best described by a functional classification based on species' flowering duration, maximum height and seed weight: weeds of extensively managed fields have short flowering seasons (2–5 mo) and particularly large or small seeds. The highest proportions of rare species also happen to be found in these groups. The rarest weeds among these species tend to be late-winter and early-summer annuals, while the rare species of stubble fields tend to be broad-leaved with low nitrogen requirements, small seeds and short height. Stubble fields showed a decline in weed cover with increasing application of fertilizer and distance from the field edge, but we could detect no strong associations of management factors with trait composition, perhaps because the intensification gradient across these fields was shorter.

Conclusions: Many rare Hungarian weeds are associated with traditional extensive farming practices. They are particularly characterized by short, mid-summer flowering periods and by preference for low nitrogen levels, but a range of trait syndromes must be considered to understand their ecology and conservation. Analyses based on trait-divergence patterns, rather than trait-convergence patterns, provide better insights into the functional composition of weed communities, emphasizing the importance of disruptive filters in weed community assembly and the need for improved methods to detect such effects.

Introduction

Rapid intensification of farming methods in industrializing countries over the last century – especially with mechanization and the advent of synthetic fertilizers and herbicides – has impoverished the weed flora of arable habitats (Hilbig & Bachthaler 1992; Robinson & Sutherland 2002; Storkey et al. 2012; Meyer et al. 2013). As a consequence, arable weed species had a high extinction rate in the

twentieth century in many rural landscapes of Europe (Van Calster et al. 2008).

Declines in weed floras have commonly been described at the level of species, but this approach does not directly shed light on the ecological processes that affect floras, nor does it readily allow generalizations about taxa or assemblages that did not occur in a given study, most notably rare species. Recent advances in multivariate techniques (Lehsten et al. 2009; Pillar et al. 2009) allow a functional

approach to arable weed ecology (Booth & Swanton 2002) that is sensitive to divergent assembly patterns as well as convergent ones (Garnier & Navas 2012). This means detecting, for example, not just changes in average community attributes, such as desiccation tolerance or nitrogen requirement, but also changes in the distribution of attributes such as germination time or seed weight. This is especially important in arable weed ecology, because many agricultural interventions impose disruptive filters that select against certain attributes – e.g. a particular germination period – rather than selecting for any particular attribute. Another advantage of multivariate techniques is their ability to detect correlative patterns of interacting attributes that may together constitute syndromes for weed persistence in the face of multi-faceted weed control regimes. There is great potential for exploring the diversity of patterns in weed functional trait responses to such management filters as the timing of interventions, levels of fertilizer, types of herbicide and depth of tillage (Storkey et al. 2010; Gunton et al. 2011; Trichard et al. 2013) – and such patterns may be intrinsic to the community assembly rules of arable vegetation.

We might expect that filters and the trait attributes they select for will co-vary along an axis of intensification. Key features of extensive cropping are high proportion of cereals in the rotation, low sowing density, use of locally saved seed, shallow tillage, limited fertilizer and no pesticide application, and late ploughing of stubble (Hofmeister 1992). Some recent studies suggest that weeds found in more extensive systems tend to be shorter plants, producing larger seeds and flowering later than species found in more intensive systems (Lososová et al. 2006; Navas 2012), while management factors in Dutch meadows had strong associations with species' seed mass and height (Jamil et al. 2013). We may also expect traits to be directly associated with species' rarity status. A 'rare weed trait syndrome' of short stature, large seeds and late flowering was identified in winter wheat fields in the UK (Storkey et al. 2010). Increasing cereal weeds in France were found to be smaller plants that also had small seeds and long germination periods (Fried et al. 2012), whereas in French sunflower fields increasing weeds were characterized by tall stature, preference for nitrogen, late germination and late flowering (Fried et al. 2009a). The most abundant arable weed species in Central Europe were found to flower in early spring, with high nutrient requirement and relative shade tolerance (Lososová et al. 2008). These studies suggest that rare and common weed trait syndromes could be crop- as well as region-specific. Alternatively, we may need to explore more general syndromes by accounting for interactions among traits and non-monotonic relationships with environmental factors.

In Hungary, a recent study found 149 weed species at risk of extinction, many of them linked to cereal ecosystems (Pinke et al. 2011a). Earlier work showed that Red List weed species occur more frequently in extensively managed cereal fields than in intensive ones, presumably because of differences in herbicide and fertilizer application (Pinke et al. 2009). Weeds in unploughed stubble can have special conservation value as food sources for insects and birds, and the early stubble ploughing that accompanies arable intensification typically prevents completion of their life cycle (Pinke & Pál 2009). A study of summer annual weed vegetation (including stubble) also found decreasing effects of intensive crop management towards the field periphery (Pinke et al. 2012).

All of the above-mentioned Hungarian studies considered species as independent entities. In the present study, we characterize weed communities of Hungarian cereal and stubble fields using functional traits. We first look at the correlates of species' rarity in these surveys, comparing intensive with extensive cereal fields, and using quantitative management variables from the stubble survey to look for predictors of rare species cover. We then use some weed traits hypothesized to respond to arable intensification to compare the two types of cereal field, looking for both convergent multi-trait patterns and divergent multi-trait syndromes based on functional classification. Similarly, in the stubble data we look at the functional patterns most associated with management factors. Next, we examine the hypothesis that there are rare weed trait syndromes (Storkey et al. 2010) by exploring how weed traits may be connected to rarity status in each of our two data sets. Thus we aim to answer the following questions:

1. How does the conservation (rarity) value of weed communities differ (a) between intensively and extensively managed cereal fields, and (b) among stubble fields with varying management histories? Which management factors are most important for rarity?
2. Which traits best distinguish the weed communities of more and less extensively managed (a) cereal and (b) stubble fields?
3. Which functional traits best distinguish between common and rare weed species in (a) cereal and (b) stubble fields?

Methods

Field surveys

We used data from two different weed surveys of cereal and stubble fields, referred to below as the 'cereal' and 'stubble' data. First, 60 cereal fields were surveyed in four geographical regions of western Hungary (Fig. 1) between May and Jun 2007, at the seasonal peak of cereal weed

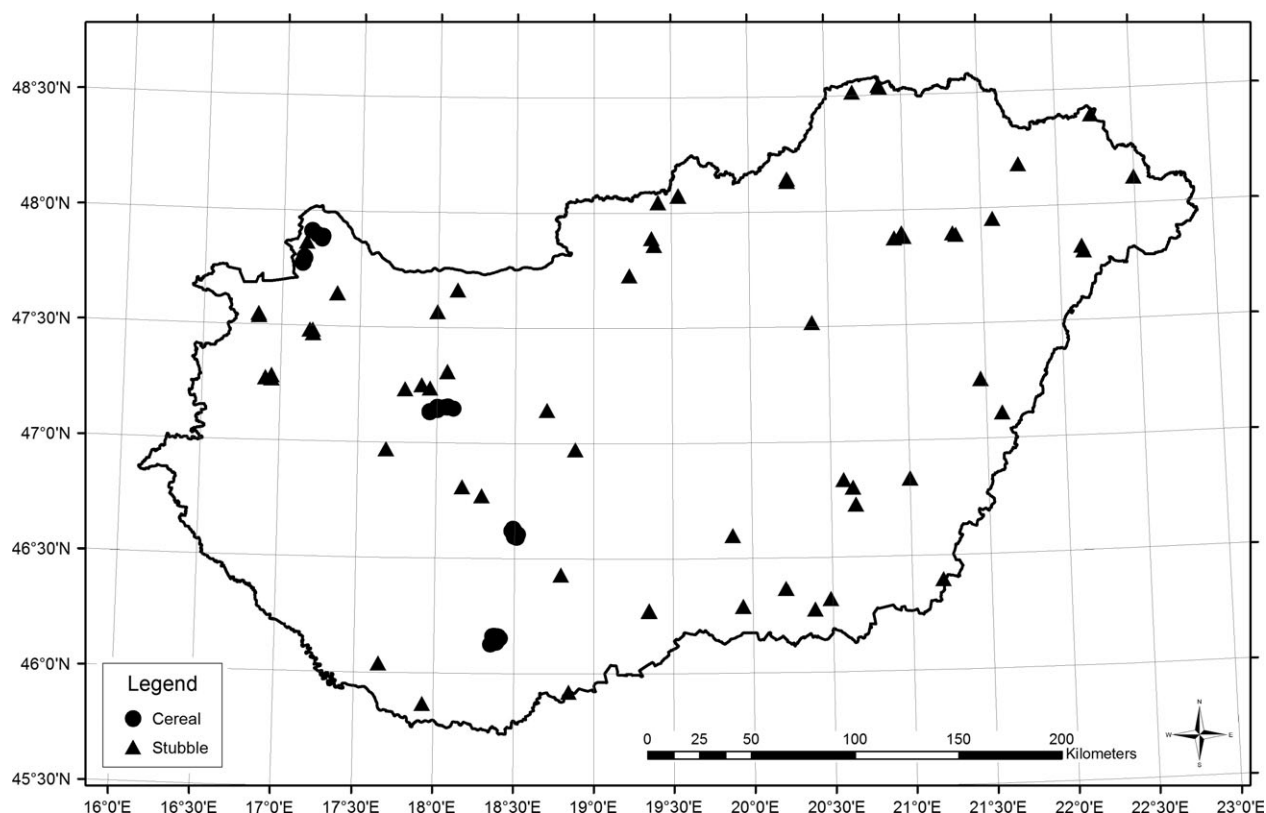


Fig. 1. Distribution of the 60 cereal (circles) and 70 stubble (triangles) fields surveyed in Hungary. For cereals, the points fall into four clusters in localities where traditional extensive farming practices survive; each cluster represents 15 fields.

vegetation (Pinke et al. 2009). These four regions are important centres of traditional farming methods that are now in decline, allowing us to select 20 fields that were extensively managed according to the criteria of Hofmeister (1992) and general socioeconomic context (Márkus 1994). Alongside these we selected 40 intensively managed fields, giving two contrasting field types that were evenly distributed among the regions, all cropped with wheat (*Triticum aestivum*), triticale (*Triticale rimpau*) or barley (*Hordeum vulgare* and *H. distichon*). The extensively managed fields were small (<1.8 ha) and had not been treated with herbicides in the 5–10 yrs before the survey, as indicated by regular observations over 1993–2006, and no signs of spraying machinery or weed injury were detected. The intensively managed fields, by contrast, ranged in size from 0.18 to 200 ha (median: 11 ha) and were characterized by annual herbicide applications in recent years. In most cases it was not possible to find and interview the landowners of extensive fields, so we simply used the management type as a predictor variable. Weed vegetation in the fields was assessed in ten randomly located 1-m² quadrats located just inside the outermost seed drill line, by a field edge that bordered on grassland. The minimum distance between

quadrats was 3 m, and all quadrats fell within a maximum distance of 150 m. Percentage ground cover of each non-crop plant species was estimated visually and then averaged across the ten quadrats for each field.

Second, 70 stubble fields were surveyed across the whole of Hungary (Fig. 1) between Jul and Aug 2009 at the seasonal peak of summer annual weed vegetation (Pinke et al. 2012). The crop species included the above cereals plus rye (*Secale cereale*), oat (*Avena sativa*) and oil-seed rape (*Brassica napus*). Weed vegetation was generally more patchy here and was sampled in four randomly located 50-m² quadrats within each field: one at a field edge, another towards the centre, up to 300 m away, and the remaining two quadrats arbitrarily spaced between these. Percentage ground cover of each weed species was again assessed, for each quadrat. For each field, data for four management factors were obtained directly from the farmers: sowing date (22 Aug–10 Apr), tillage depth (range 0–50 cm), amount of nitrogen fertilizer (range 0–261 kg·ha⁻¹) and total amount of active herbicide ingredients (range 0–1425 g·ha⁻¹). We thus used five predictor variables, all related to intensification: fertilizer and herbicide input, which each have direct effects on weed growth

and on weed–crop competition; sowing date, which is a major determinant of weed community composition (Fried et al. 2008; Gunton et al. 2011; Pinke et al. 2011b); tillage depth, related to weed regeneration niche and intensification (Hofmeister 1992; Hunyadi 2011); and distance from the nearest field edge, which tends to magnify the effects of intensification (Pinke et al. 2012).

Trait selection

We obtained species-specific data for weed traits deemed to be most relevant to crop intensification. Plant stature, seed weight and flowering period are attributes of the ‘rare weed trait syndrome’ proposed by Storkey et al. (2010), and we obtained data on maximum plant height, month of first flowering and flowering duration from Király (2009), while seed weights were sourced from the Seed Information Database at the Royal Botanic Gardens Kew (2008). Ellenberg indicator values for light and nitrogen, as rescaled for the Hungarian Flora (Borhidi 1993), may indicate the viability of weed species experiencing competition in fertilized crops (Kleijn & vanderVoort 1997). The life-form classification of Raunkiaer has been extended by Ujvárosi (1973) with four therophyte categories: early-winter, late-winter, early-summer and late-summer annuals, according to the duration and peak month of germination period. This classification reflects phenology, suggesting whether species can regenerate following various sowing and cultivation operations and herbicide applications (Fried et al. 2012); it also reflects mode of perennation, which may determine resilience to tillage to varying depths (Hunyadi et al. 2011). This gave seven functional traits: six quantitative and one categorical. Finally, we also used the classical distinction between broad-leaf and grass weeds (hereafter termed ‘the grass indicator’), which may be strongly connected to tolerance to the herbicides used in cereal crops (Novák et al. 2011). (We attributed the pteridophyte *Equisetum arvense* as ‘grass’ for this purpose, since it is generally susceptible only to broad-spectrum herbicides, like grass weeds in cereal crops.) This binary trait may be considered as quantitative for describing the mean proportion of grass weeds at a site, as well as providing an *a priori* categorical dichotomy in any functional grouping.

We obtained data for species’ broad-scale rarity status in Hungary, beginning with the Hungarian Red List species (Király 2007). Cereal fields contained 11 and stubble fields just two Red List species, so for increased statistical power we also considered species listed in Király (2009) as rare, sporadic or declining in all regions of Hungary. Combining these three categories with the Red List species gave 39 and 33 ‘rare’ species for the cereal and stubble data sets, respectively.

Statistical analysis

Numbers in this section relate to the three questions raised in the Introduction.

1. We first looked at total weed cover and proportional cover of rare species for each survey unit (cereal field, or quadrat in a stubble field). In the cereal field survey data, we compared each of these variables between intensively and extensively managed fields using one-way ANOVA for each variable. Total weed cover was log-transformed to give normal residuals; proportion of rare species was arcsine square root-transformed and, because 15% of fields had no rare species, significance was assessed using a randomization test (999 permutations of the field type indicator). Similarly, for the stubble data, we modelled the same variables in response to the four management factors and the distance of quadrats from the field edge (using square-root transformations of distance, fertilizer and herbicide). This required multi-level models: the management factors were specified for each field, so field was modelled as a random factor, with the effect of distance from the field edge allowed to vary among fields (which improved model fits). Weed cover did not require transformation in this case, but for proportion of rare species, 64% of the data were zero so, as before, we used the arcsine square root transformation and assessed the significance of *t*-statistics for the coefficient of each predictor using randomization tests (permuting the quadrats to test the distance effect, and permuting whole fields to test the other effects).

2. We then characterized weed responses to management variables using functional trait analyses based on trait-convergence and trait-divergence assembly patterns with the method of Pillar et al. (2009). This method is based on Mantel correlations (congruences) of multivariate distance matrices describing the variation among quadrats. Distances are based on (1) mean values of traits of the species found in each quadrat; (2) abundance of certain functional types in each quadrat; and (3) values of specified environmental variables (in our case, field management variables) associated with each quadrat. Trait-convergence assembly patterns (TCAPs) are simply assessed using the congruence between the trait means distance matrix (1) and the environmental distance matrix (3); they are most appropriate for quantitative traits and can reveal associations of local (field-level) mean trait values with certain environmental variables. Trait-divergence assembly patterns (TDAPs), on the other hand, concern how syndromes of functional traits (categorical as well as quantitative) are related to the environment. TDAPs consider trait variation within a local community (quadrat), rather than trait means, and must be based on classifications of species into functional groups. Thus a TDAPs method uses the relative local

abundances of functional groups (in each quadrat) to compute a compositional distance matrix (2) to compare with the environmental distance matrix (3). Unless a classification is pre-defined, an iterative procedure is used, based on a standard classification algorithm and specification of a range of degrees of grouping, to compare a wide range of functional classifications. Following Gunton et al. (2011), we used an agglomerative clustering algorithm, compared numbers of groups between three and eight (classifications with two groups risk conflating TDAPs with TCAPs), and tested all possible combinations of traits. Partial matrix correlation was used to remove the influence of trends in trait mean values before computing congruences with the environmental distance matrix (Pillar et al. 2009).

For the cereal data, we applied the TCAPs algorithm iteratively to seek an optimal set of the six quantitative traits plus the grass indicator, such that their mean values could resolve differences between intensive and extensive fields. Similarly, we applied the TDAPs algorithm iteratively to these traits plus the life-form classification, to find an optimal functional classification that could resolve differences between the two field types. For each analysis, we compared the best congruence values obtained for each number of traits against corresponding values derived from repeating the whole TCAPs or TDAPs procedure on 999 sets of randomized trait data. This stratified randomization approach allowed the best congruence values for each number of traits to be corrected by subtracting the median of corresponding maximum values obtained from randomized data and re-scaling the result between 0 and 1. The maximum of these corrected values (which would be negative if out-performed by more than 50% of randomized data sets) identified the best model. The original congruence value for this model was then compared to the 999 comparable randomized values to find its quantile and thus assess its overall statistical significance, accounting for the iterative selection procedure ('data dredging'), giving a conservative test of a null hypothesis of no association. For the stubble data, we investigated functional differences among fields with differing management regimes in the same way, but using mean cover values of each weed species calculated across the four quadrats from each field (and dropping field edge distance from the analyses, after it was found to be unimportant in preliminary analyses). We compared each of the management variables alone and then proceeded to combine variables that gave the strongest congruences.

To achieve more even distributions of the traits for all these analyses, seed weight and maximum height were each transformed by taking natural logarithms. The highest correlations between pairs of quantitative traits were between flowering start time and flowering duration in the stubble species ($\rho = -0.53$), and between flowering start

time and maximum height in the cereal species ($\rho = 0.48$). Other correlations were no higher than ± 0.35 . Spatial autocorrelation could also affect our tests for statistical significance, so where significant results were found, we plotted empirical variograms to check this (see Results for details).

3. Finally, to examine rare weed syndromes, we analysed our species trait tables to look for direct relationships between species rarity status and their traits, without using relevé data. Separate analyses were performed for the species found in the cereal survey and for those found in the stubble survey. We looked for correlational patterns using the TCAPs algorithm, and for syndromes using the TDAPs algorithm, with species' rarity status providing the 'environmental' table and a dummy diagonal matrix in place of the relevé table. For the cereal species, the environmental table comprised two columns, one for overall rarity and one for Red List status; for the stubble species, we simply used overall rarity status, as there were only two Red List species. Corrections and tests based on 999 randomizations were performed as before.

Statistical modelling was performed in the software R v 2.11.1 (R Foundation for Statistical Computing, Vienna, AT; <http://www.r-project.org>). The multilevel models were fitted using the R package lme4 (<http://cran.r-project.org/web/packages/lme4/index.html>) while the TCAPs and TDAPs analyses were performed using an R package written by Gunton et al. (2011). It should be noted that our randomization tests were based on randomizing trait attributes among species, since they concerned the significance of associations of traits (and trait-derived functional types) with predictor variables, rather than species with sites.

Results

A total of 219 species were encountered in the cereal fields, and 193 species in the stubble fields, with 143 species in common. The species are listed in App. S1 and further details are given in Pinke et al. (2009, 2012). Bracketed numbers below relate to the three questions raised in the Introduction; for trait-convergence and trait-divergence analyses, *C* indicates corrected congruence values, and *P* the significance of departure from a null hypothesis of no association. Models with congruences within 0.05 of the best one are also summarized.

Cereal fields

(1a) In the cereal survey, total weed cover was on average six times higher in extensively than intensively managed fields, and the mean proportion of rare species was 0.22 and 0.009, respectively (Fig. 2). (2a) The trait-convergence method did not reveal any significant associations once the

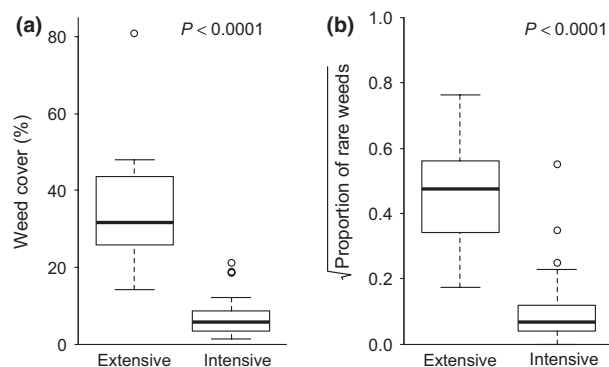


Fig. 2. Characteristics of weed vegetation in extensively and intensively managed cereal fields: (a) total weed cover; (b) the proportion of weeds classified as rare, square root-transformed to reveal detail at the lower end of the scale. Each box shows a median (thick line) and interquartile range, with whiskers spanning all outliers within 1.5 times the box height. P = significance for a null hypothesis of no difference between extensive and intensive fields.

correction for data dredging was made. The trait-divergence method, however, yielded a classification into eight groups based on species flowering duration, maximum height and seed weight (Fig. 3a; $C = 0.32$, $P = 0.04$; next best classification: $C = 0.22$). Four groups are mostly responsible for the differences between field types (Fig. 3b): groups 1 and 2 are much more abundant in extensive fields, while groups 5 and 8 are much more abundant in intensive fields. Groups 1 and 2 have the shortest flowering duration (range: 2–5 mo); group 1 also has the highest seed weight (10–310 mg), whereas group 2, which is actually the most abundant type in extensive fields, has one of the lowest seed weights (≤ 1.3 mg). Among the groups associated with intensive management,

group 5 has the greatest maximum height (100–300 cm), while group 8 has the longest flowering duration (8–12 mo) combined with one of the smallest maximum heights (10–60 cm). Species rarity was not used in this analysis, so it is notable that groups 1 and 2 also contain the highest proportions of rare species, and groups 5 and 8 the lowest (Fig. 3c).

To check whether spatial autocorrelation might be interfering with our significance tests, we plotted variograms of the abundance of each of the functional types for each field type. There were no general patterns of increased similarity among closer fields in either case (App. S2).

Stubble fields

(1b) The linear model for weed cover showed negative effects of distance from the field edge (ca. $0.08\% \text{ m}^{-1}$; $P < 0.001$) and of nitrogen fertilizer level (ca. $0.12\% \text{ kg}^{-1} \cdot \text{ha}^{-1}$; $P = 0.03$), while the model for the proportion of rare weeds showed a slight negative response to fertilizer ($0.02\% \text{ kg}^{-1} \cdot \text{ha}^{-1}$; $P = 0.01$; Fig. 4). (2b) The trait-convergence and trait-divergence analyses exploring all response traits in the stubble fields did not yield significant associations with any management variable. The strongest result was for the divergence analysis, with a classification based on maximum height and nitrogen and light indicator values responding to sowing season and tillage depth ($C = 0.05$, $P = 0.2$).

Species analyses

Our search for relationships between species rarity status and functional traits, for all species found in each survey,

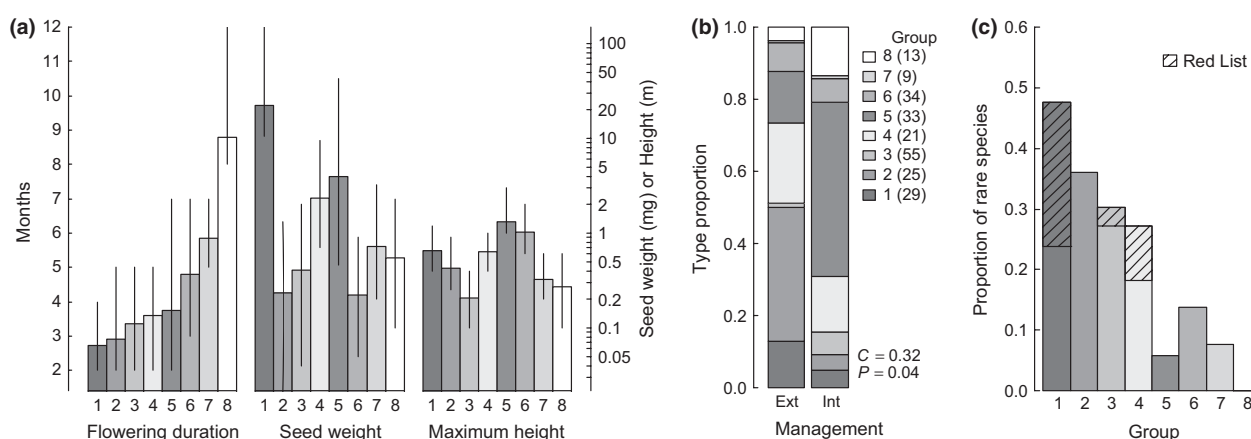


Fig. 3. A functional type classification derived for cereal weed communities with respect to field management system. (a) The eight functional groups described by mean values for the three traits used, with lines spanning the ranges found in each group. (b) The proportions of the groups in the extensively (Ext) and intensively (Int) managed fields, with C = corrected congruence value according to the trait-divergence pattern analysis and P = significance for a null hypothesis of no association; numbers of species in each group are indicated in brackets in the key. (c) Proportions of rare and Red List (hatched) species within each group.

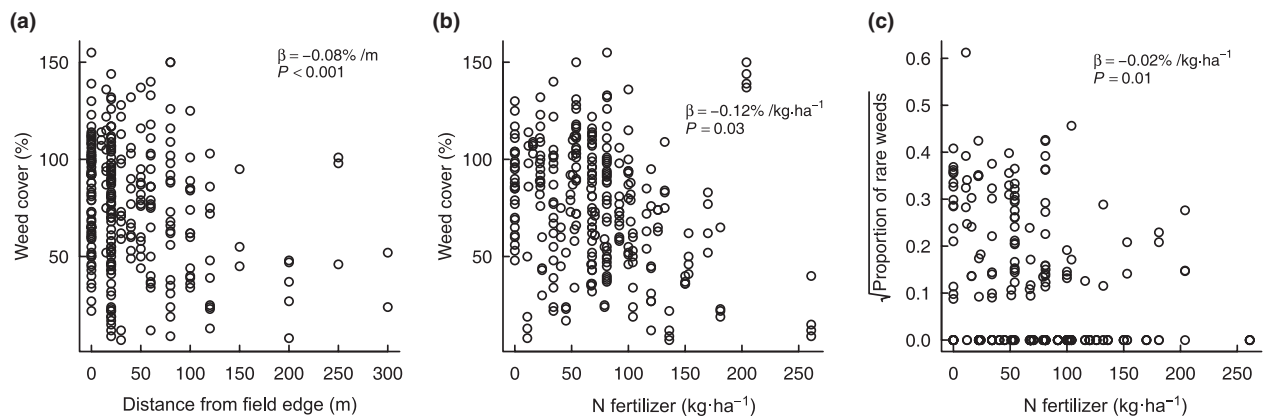


Fig. 4. Total weed cover in stubble fields against (a) distance from the field edge, (b) N fertilizer application, and (c) proportion of rare weeds against N fertilizer application. Each point represents one quadrat. Coefficients (β) for the plotted predictors from general multilevel models are plotted with P = significance for a null hypothesis of zero partial correlation.

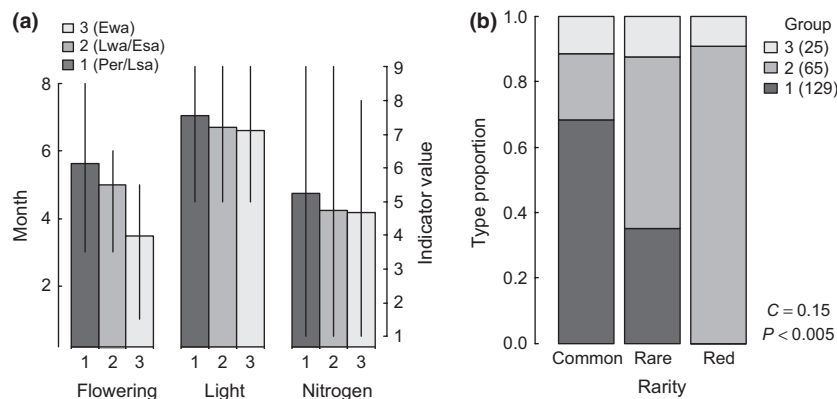


Fig. 5. Functional trait syndromes related to species rarity in the early-summer weed flora inventory of extensive and intensive cereal fields. (a) Mean values of the three quantitative traits (month of first flowering, light and N indicator values) in each of the three groups, with lines spanning the ranges found in each group, and (inset) the life-form composition of the groups ('Per'=perennials, 'Lsa'=Late-summer annuals, 'Lwa'=late-winter annuals, 'Esa'=early summer annuals, 'Ewa'=early winter annuals). (b) The proportions of each group among the common, rare (not Red List) and Red List species, with C = congruence value according to the trait-divergence pattern analysis and P = significance for a null hypothesis of no association. The number of species in each group is indicated in brackets in the key to the groups.

yielded only weak trait-convergence patterns but strong trait-divergence patterns. (3a) The best classifications of the cereal species all had three groups; the best model ($C = 0.15$, $P < 0.005$) was based on a combination of life form, time of first flowering and nitrogen and light indicator values (Fig. 5). A total of 15 other models had congruences within 0.05 of the best model, of which the next three ($C = 0.12$ – 0.13) all used subsets of the same traits, along with flowering duration and maximum height plus the grass indicator in one case and seed size in another. In all these four classifications, Red List and rare species dominate group 2, which contains predominantly or entirely late-winter annuals, flowering from spring onwards. In the best classification (Fig. 5a), group 2 species begin flowering from Mar to Jun, group 1 species, which are

predominantly common, tend to be perennials and late-summer annuals with flowering onset from Mar to Aug, and group 3 species, which have minimal association with rarity status, comprise early-winter annuals.

(3b) The best classifications of species from the stubble weed inventory again all had three groups; the best model ($C = 0.18$, $P < 0.005$) was based on a combination of duration of flowering period, nitrogen indicator value, seed weight, maximum height and the grass indicator (Fig. 6), while the next best ($C = 0.17$) dropped seed weight and used time of first flowering instead of flowering duration, and the third ($C = 0.13$) used both flowering period traits along with nitrogen indicator value and maximum height. In all these classifications, the proportion of rare (including Red List) species was highest in a group that had the lowest

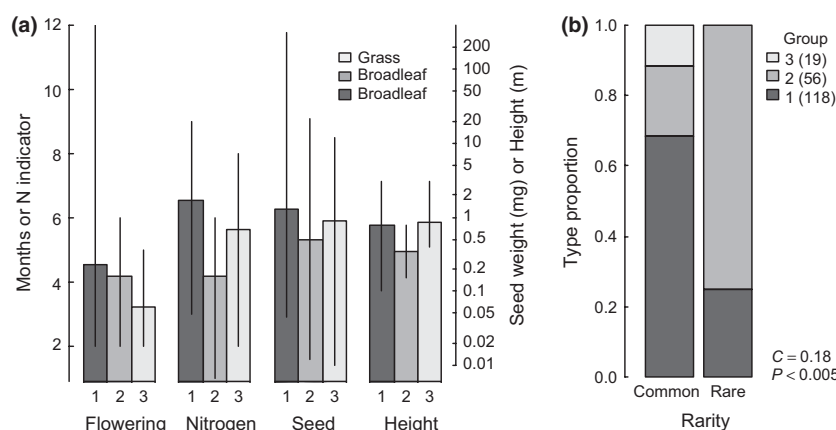


Fig. 6. Functional trait syndromes related to species rarity ('Rare' here includes Red List species) in the late-summer weed flora inventory of stubble fields. **(a)** Mean values of the four quantitative traits (duration of flowering period, N indicator value, seed weight and maximum height) in each of the three groups, with lines spanning the ranges found in each group, and (inset) the grass indicator. **(b)** The relative contribution of each group to the sets of common and rare species, with C = congruence value according to the trait-divergence pattern analysis and P = significance for a null hypothesis of no association. The number of species in each group is indicated in brackets in the key to groups.

nitrogen indicator value. In the best classification (Fig. 6a), this group 2 comprises broad-leaf species with the lowest nitrogen requirements (indicator values 1–6), smallest stature (15–80 cm) and relatively small seeds (0.01–22 mg). Most of the common species are recruited from group 1, characterized by the highest nitrogen requirement, and group 3, which contains all the grass weeds, none of which are classed as rare.

Discussion

Extensive vs intensive cereal fields

Our finding of higher proportions of rare and Red List species in extensively managed fields concurs with studies from other countries. Higher diversity of weeds in extensively managed fields (Hawes et al. 2010; José-María et al. 2010; Armengot et al. 2012; Kolárová et al. 2013) is generally attributed to a lack of herbicide application and reduced amounts of fertilizer (Cirujeda et al. 2011; Rassam et al. 2011; Andreassen & Stryhn 2012; Pál et al. 2013; Salonen et al. 2013), and our results emphasize the value of such systems for rare and threatened arable weed species in Hungary. Only a few traditional extensively managed small fields remain in Hungary, and they are continuously being abandoned or intensified, making the persistence of these valuable habitats uncertain (Pinke et al. 2009).

The communities of our extensive and intensive cereal fields were distinguished by a range of trait syndromes, which suggests some disruptive filters in community assembly. In the intensive communities, for example, longer potential flowering periods were typical, allowing a range of phenologies to cope with management interventions such as herbicide application, as also found by Fried

et al. (2012). Also, the mixture of short (<60 cm) and tall (>100 cm) species could reflect competitive exclusion of weeds of similar height to cereal crops. The communities of extensive fields, meanwhile, had divergent seed weights (mostly <1.3 mg and >10 mg), which probably become less viable under the competitive conditions of sustained intensive arable management. Larger seed weight may be disadvantageous because it entails production of fewer seedlings, and whatever advantages are conferred on these by being initially larger do not pertain under herbicide spraying (Navas 2012). In addition, seed size is negatively correlated with persistence in the seed bank (Thompson et al. 1993), so large-seeded species quickly disappear under unfavourable conditions, while they are also excluded by seed cleaning technologies (Hilbig & Bachthaler 1992). Small seeds are also selected against by modern seed cleaning, and we note that the range of seed size in the two groups associated with intensive fields (0.1–43 mg) spans the seed size range of cereals cropped in the fields. There may also be a tendency for small-seeded species to disperse into extensively managed fields from the more natural dry meadows that are often nearby.

Overall, our results partially agree with trends previously reported for weeds associated with more extensive management, such as larger seed size and late flowering (Lososová et al. 2006; Navas 2012), but we believe that our use of a method sensitive to trait-divergence assembly patterns allowed us to detect more complex patterns.

It is particularly interesting that the two groups associated with extensive cereal fields contained the highest proportions of rare and Red List species, while the groups most associated with intensive fields contained fewest – in spite of the groups being defined purely by functional response

traits. The group with medium stature, the largest seeds and the shortest flowering duration (group 1 in Fig. 3) can be identified as a particular conservation concern and includes many of the most threatened and declining arable weed species in Hungary (e.g. *Agrostemma githago*, *Caucalis platycarpus*, *Galium tricornutum*, *Ranunculus arvensis*, *Turgenia latifolia*, *Melampyrum arvense*, *M. barbatum*; App. S1). This shows some congruence with the rare weed trait syndrome of short stature, large seeds and late flowering proposed by Storkey et al. (2010) – more than our explicit functional analysis of species rarity (see below).

Intensification in stubble fields

Which features of extensive field management are most important? Our study of stubble fields considered four of Hofmeister's (1992) characteristics: sowing season, tillage depth, fertilizer application and herbicide application, and found negative effects of fertilizer on overall weed cover and the proportion of rare species, yet no strong effects of any factor on functional composition. Negative effects of nitrogen fertilizer on the species richness and abundance of rare weeds in crops are well known (Kleijn & van der Voort 1997; Kovács-Hostyánszki et al. 2011), and Storkey et al. (2012) found that the proportion of arable weed species in different threat categories among European countries could be explained by average rates of fertilizer and (to a lesser extent) herbicide application. Although fertilization effects may persist longer after harvest than earlier filters, such as tillage and herbicide, the lack of functional responses is probably due to the effective intensification gradient being much shorter (less extreme) in our stubble data set. Moreover, it is possible that our results partly reflect the remedial actions of farmers in response to soil conditions and weed floras, rather than direct vegetation responses. The amount of fertilizer application may therefore be negatively correlated with background field fertility levels, as well as positively correlated with additional variables relating to intensification, such as expenditure on herbicides and farm machinery (José-María et al. 2010; Armengot et al. 2011).

Our finding of decreased weed cover in stubble fields with increasing distance from the field edge concurs with other studies (Wilson & Aebischer 1995; Fried et al. 2009b), which argues that field edges are generally less affected by herbicide and fertilizer application, and that light conditions may also be more favourable than in the inner parts of the fields dominated by the crop.

Rare weed trait syndromes

Our direct attempt to find rare weed trait syndromes showed the importance of life form (either Raunkiaer's or

a grass/broad-leaved distinction) and of short flowering periods and low nitrogen requirements, which were common to the classifications of both sets of species (partly reflecting the overlap in species lists). Our classifications show little relationship to the 'rare weed trait syndrome' of Storkey et al. (2010), except in the tendency for rare stubble species to be short, or to the 'decreasing cereal weeds' pattern found by Fried et al. (2012), except in the association with nitrogen; apparently those patterns rather emerged from our data when actual abundances of weeds in extensive vs intensive fields were considered, and it is notable that we failed to find any convergent effects. The importance of short or later flowering periods corresponds with our classifications based on weed abundances in extensive cereal fields, but the other traits are different. The discrepancies may be due partly to the nature of the sources used for attributing species as 'rare', which represent a national perspective. Thus some non-threatened species of semi-natural habitats are actually very rare as arable weeds, and *vice versa* – raising the question of the relative importance of conserving species vs (arable) communities (Moonen & Barberi 2008). As for the discrepancies from published rare weed trait syndromes, we argue that trait-divergence assembly patterns potentially constitute better 'syndromes' than trait-convergence patterns. The latter are commonly used in functional trait analyses – e.g. Kimberley et al. (2013) showed that plant species associated with ancient woodland in the UK were almost exclusively short and usually had large seeds, while Gabrielová et al. (2013) found a short flowering period to be one of the most important features of critically endangered species in the Czech Republic. Our analyses, in contrast, are able to implicate intermediate values of some traits and interactions between them.

Thus, synthesizing our analyses, we tentatively suggest that farmers and policy-makers with an interest in conserving Hungarian arable communities consider management techniques that promote species similar in height to cereal crops, especially those with seeds >10 mg, while conservationists interested in broad-scale species conservation might consider ways to promote broad-leaved annuals with low nitrogen requirements. Special attention should be given to the attribute of short, relatively late-flowering periods, which emerges from both analyses as well as from studies reviewed above (Introduction).

We were interested in the proportions of life forms because Raunkiaer's scheme, and extensions of it, capture a variety of functional trait information and are widely used. Our results suggest that the extension of Ujvárosi (1973) to cover a range of germination periods can provide a useful *a priori* classification for distinguishing rare and common weeds. Over half of the rare species and 90% of the Red List species from cereal fields were late-winter or

early-summer annuals – indeed, life form seems the most important feature of the classification, since the quantitative traits involved do not show strong differentiation among the three groups (Fig. 5). An additional analysis using life forms alone ($P = 0.08$, $C = 0.31$; App. S3) also suggested a higher abundance of late-winter and early-summer annuals in extensively managed fields. These patterns may relate to the susceptibility of such species to the timing of herbicide application in intensive cereal farming, which usually occurs during the peak of their vegetative growth. Late-summer annuals and perennials, by contrast, are able to germinate or resprout after early-season herbicide applications, while many early-winter annuals can germinate during later stages of the season (Ujvárosi 1973; Holzner et al. 1982). Of course, the timing of our surveys may have affected the abundance of life forms detected with respect to their phenology, so additional work over a wider time-frame or seed bank studies would be useful.

Conclusion

We found that extensively managed Hungarian cereal fields harbour more rare weed species than intensively managed fields, and that rates of nitrogen fertilizer application help explain the abundance of rare weeds in stubble. Functional trait analyses based on trait-divergence patterns, rather than convergence patterns, provided insights into these trends: species associated with extensively managed cereal fields had short flowering durations and either large or small seeds, although we were unable to detect functional trends along gradients defined by specific management factors in stubble fields. We also found that rare Hungarian cereal weed species tend to have low nitrogen requirements and to be late-winter or early-summer annuals, again with shorter flowering periods. All of these attributes should be considered in attempts to secure the conservation of threatened arable floras, both in Hungary and elsewhere.

We hope that future work will elucidate the attributes of declining species and look at weed trait-divergence patterns in a wider range of crops, survey dates and regions. Indeed, it should be possible to develop more general arable weed assembly rules by considering cropping conditions as quantitative predictor variables, including the functional traits of crop plants (Gunton et al. 2011), as well as a wide range of environmental factors.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Rarity status and classification of species.

Appendix S2. Variograms of the abundances of functional types identified in the analysis of weeds from cereal fields.

Appendix S3. Graphs of a functional classification of weed species differing between extensive and intensive cereal fields, based on life form alone.