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SPECIAL FEATURE: FUNCTIONAL DIVERSITY

Comparing functional diversity in traits and demography of Central European vegetation

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Botanical garden; Habitat filtering; LHS traits; Seed reproduction; Standardized effect size; Trait under-dispersion; Vegetative reproduction

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Abstract

Question: A major obstacle to understanding non-random patterns in plant traits (over-dispersion or under-dispersion) has been our limited knowledge of trait–demography relationships for large sets of species. Here, we suggest that some of the needed data on demographic processes can be gathered from growth records on plants in botanical gardens. We examine within-community patterns in demographic responses determined from such growth records, and ask whether they are different from patterns in plant traits.

Location: Czech Republic.

Methods: We assembled data on seed and vegetative reproduction for ca. 1000 Central European species from the Botanical Garden of Charles University in Prague. We used these data as estimates of potential vegetative and seed reproduction of individual species under favourable conditions. We linked these data with co-occurrence data from the Czech National Phytosociological Database and with data on major species traits. We examined dispersion of both species traits and garden reproduction using randomization tests on the data set as a whole and on the data stratified using EUNIS classification into seven or 32 habitat types.

Results: The patterns found for species traits and for garden reproduction are similar, with strong under-dispersion for the data set as a whole and diminishing under-dispersion in subsets of the data. Under-dispersion was much stronger for traits than for garden reproduction. No over-dispersion was detected in either trait or garden reproduction data.

Conclusions: The major source of the pattern in the data is environmental filtering. Stronger filtering for traits indicates that the linkage between environment and traits is much tighter than that between environment and demography. In ecologically homogeneous communities, reproduction parameters are closer than trait values to a random distribution, indicating that co-existence of species are not limited by either similarities or differences in their demography. These findings show that trait dispersion need not be directly related to species demography and, more generally, that correct identification of trait–demography relationships is necessary for better understanding patterns of trait dispersion.

Introduction

Investigating functional diversity of plant communities using species traits has become a major focus of research in plant ecology in the past decade, revealing several types of pattern in the distribution of trait values in plant communities. First, mean values of many traits differ across community types (e.g. Díaz et al. 2004; Messier et al. 2010). Further, trait structure within communities may also show different types of non-random pattern. Environmental filtering makes trait values of individual species within a community more similar to each other

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than would be expected from random processes ('trait under-dispersion'; Ackerly & Cornwell 2007; de Bello 2012). Trait under-dispersion may also result from selection for equalizing processes in competition (Chesson 2000; Mayfield & Levine 2010). On the other hand, trait values of individual species in a community can have values that are more dissimilar to each other than expected from a random distribution ('trait over-dispersion'); this has been ascribed to microenvironmental heterogeneity (Cornwell & Ackerly 2009), facilitation (Verdú et al. 2009) or niche differentiation (Stubbs & Wilson 2004; for a review see Götzenberger et al. 2012).

Understanding these trait patterns is contingent on understanding the links between these traits and plant performance within communities. Species values of each particular trait ('soft' traits of Lavorel & Garnier 2002) define the potential of a given plant species to perform particular ecological functions, but the actual performance of any individual involves responsive behaviour to environmental factors, both abiotic and biotic (Suding et al. 2003; McGill et al. 2006; see also Fig. 1). Relationships between organismal traits and community composition thus depend on a chain of mediating processes that include the growth, survival and reproduction (Suding et al. 2003; Clark et al. 2004; Gross et al. 2009; these processes largely correspond to the 'hard traits' of Weiher et al. 1999). Due to the high number of plant traits affecting demographic responses, there is a fair amount of arbitrariness in the choice of traits to be examined (Bernhardt-Römermann et al. 2008). In contrast, definitions of compound demographic parameters such as reproduction are much less arbitrary.

While the relationships between traits and occurrence of plants in different environments are well established for large sets of species (see e.g. Grime et al. 1997; Díaz et al. 2004), data on demographic processes are largely restricted to relatively few species (Burns et al. 2010). This makes community-wide analysis of such parameters nearly impossible. Here, we suggest that useful proxy variables for plant demographic processes for extensive sets of species can be gathered from growth records on plants in botanical gardens. Botanical gardens have been used as valuable sources of data for a number of ecological subjects (Gratani et al. 2008; Dawson et al. 2009; Primack & Miller-Rushing 2009; Ferenczy et al. 2010). They could also provide reasonable assessment of demographic processes under good or optimum conditions for large sets of species, given that species are kept in suitable environments and proper records are kept on performance of each species. Such records can provide parameters (e.g. growth and reproduction) that are more ecologically relevant than most soft traits, although they do not constitute strict 'hard' traits as they typically document performance in only a given, rather favourable, environment. While there can be a number of issues regarding data from these records (e.g. semi-quantitative data only, small sample sizes, reduced inter-specific competition, low genetic variation), these disadvantages are easily outweighed by the large number of species that can be compared.

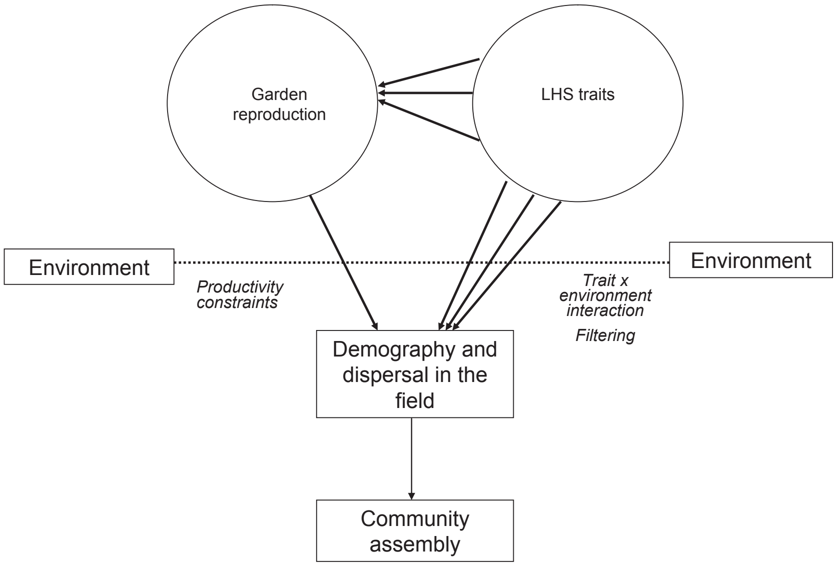

Fig. 1. Conceptual relationships between garden reproduction, LHS traits and field demography. Dotted line indicates environmental effects (filtering). Garden reproduction and LHS traits are proxies for different processes in the field, and the environment acts on each of them, although to some extent differently. Demographic processes (both in the garden and in the field) integrate effects of a number of traits into a single demographic response.

In this paper, we examine whether such data on reproduction, and relative roles of vegetative and seed reproduction, show non-random patterns similar to the patterns shown by species trait values. We hypothesize that habitat filtering will be weaker for reproductive performance than for soft traits, as reproduction values are close to the 'common currency' of ecological processes, and thus differences in overall magnitude of reproduction and preferences for either generative or vegetative reproduction will show up only in extreme environments (see e.g. Grace 1993). In contrast, habitat filtering in the LHS traits will be stronger due to the key role of environment in their action (see also Fig. 1). We further hypothesize that at the within-community level these reproduction values would tend to show similarity across co-existing species (under-dispersion or random distribution) due to the universal nature of the processes of reproduction.

We use data assembled for ca. 1000 Central European species grown in the Botanical Garden of Charles University in Prague (see also Herben et al. 2012). As the garden is rather environmentally heterogeneous, with each species maintained separately in conditions that can reasonably be assumed to be close to its natural habitat, we use these data as estimates of potential vegetative and seed reproduction of individual species under favourable conditions. We link these data with co-occurrence data from a stratified version of the Czech National Phytosociological database (Chytrý & Rafajová 2003) to obtain garden-estimated reproduction values for species that co-occur in individual database records. In addition, we link the same co-occurrence data with data on LHS traits of Westoby (1998) from the LEDA traitbase (Kleyer et al. 2008).

We examine patterns in within-sample dispersion of plant reproduction, searching separately for negative values of trait dispersion (reproduction convergence) and positive values (reproduction divergence). Detection of convergence/divergence in plant reproduction allows us to determine whether species that co-exist in the field show any non-random patterns in their reproduction (under conditions favourable for each species). We next examine the same patterns for a few key soft traits (plant height, seed mass, specific leaf area and life span), and compare these patterns with those shown by potential (i.e. garden) reproduction.

To examine the role of habitat filtering and species pool size in generating these patterns, we divide the co-occurrence data set based on major habitat types and perform the same analyses within each habitat type using only the pool of species that occur in it. We also examine whether within-community mean reproduction values show non-random patterns across habitat types (as an additional indication of habitat filtering), as differences in these means critically constrain our capacity to interpret dispersions (Ackerly & Cornwell 2007; de Bello et al. 2009).

Methods

Reproduction data from the botanical garden

The data were gathered from the native plant collection in the Central European flora of the Botanical Garden of the Faculty of Science, Charles University in Prague (http://www.bz-uk.cz). Each of the species is kept under conditions assumed to be as close to their natural conditions as possible within the garden. The habitats in the garden range in moisture from open, dry, sandy habitats and limestone, rocky habitats, through mesic, open habitats and shaded forest stands, to moist (shaded and unshaded) places. Plants are grown in open soil, with weeding done – including removal of individuals of the planted species – in order to keep stands of each species separate. For all plant species that have been growing in the garden for at least 10 yr (for the list see Herben et al. 2012), we assigned scores from 1 to 5 for vegetative and seed reproduction for that period, based on contemporaneous records. Based on these growth records and informal knowledge of the species behaviour, seed and vegetative reproduction were scored separately by one person using the same ordinal scale (Z.N.; for further details see Herben et al. 2012). Weeding/thinning visits were done on a regular basis that was the same for all species. In some plants with vigorous vegetative reproduction, assessment of seed reproduction was impossible due to seedlings being potentially mixed with the vegetative progeny. For these plants (43 species), seed reproduction is treated as a missing value. Altogether, 1013 species were scored. As the Czech flora contains ca. 2500 species (depending on taxonomic treatment), including common aliens and woody species, this constitutes over 40% of the total flora. This included 951 non-woody species, of which 823 could be matched to co-occurrence data (see below) and thus were used in the current study. Complete data (i.e. including seed reproduction) were available for 778 of these species; the rest are species for which only vegetative reproduction is known. For further information on the data set see Herben et al. (2012).

Trait data

The following trait data were taken from the LEDA traitbase (Kleyer et al. 2008), with the number of species for which the trait data were available provided in parentheses: specific leaf area (SLA; 1253 species), maximum height (1794 species) and seed mass (1131 species). Records were taken from the whole LEDA database (i.e. including records not from Central Europe); the number of records varying considerably among species as they ranged from one to 24 (for SLA) and one to 50 (for seed mass). If several records were available for one species, the simple (unweighted) arithmetic mean value was used. Plant height data missing from LEDA and life span data (annual/perennial; 1974 species) were taken from Kubát et al. (2002); mean plant height values were used.

Species co-occurrence data

Species co-occurrence data were taken from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). A stratified subset of the database containing 20 468 plots sampled after 1970 was used (see Chytrý et al. 2005 for the stratification procedure). We refer to these units as 'plots' or 'communities' (using these terms here interchangeably).

Before stratification, the set was standardized with respect to plot sizes separately for each major vegetation type; plots were 50–500 m^2 for woodland habitats, 10–100 m^2 for scrub, 4–100 m^2 for grassland, wetland and aquatic habitats, and 1–50 m^2 for low-growing vegetation in stressed or disturbed habitats. These size differences make comparison of trait dispersion across habitats less reliable, but we believe that this allows a qualitative correction for different mean sizes of plant individuals. The plot sizes used are too small to include large-scale environmental gradients (e.g. in wetness or productivity) even in large forest plots, while even the smallest ones are large enough to include sufficiently high numbers of plant individuals to avoid data distortion due to constraints on number of individuals.

The plots were assigned to seven major EUNIS habitat types (see Chytrý et al. 2005): grasslands (6702 plots), forests (3391 plots), scrub and heathlands (354 plots), water habitats (4173 plots), rocky habitats (286 plots), peatlands and mires (531 plots), and synanthropic habitats (5030 plots). These are further referred to as EUNIS-7 habitat types. Plots not assigned to any EUNIS habitat type by Chytrý et al. (2005) were omitted from any analysis using EUNIS classification. Further, all plots were assigned to 32 small EUNIS habitat types (see Chytrý et al. 2005), further referred to as EUNIS-32 habitat types.

Data analysis

We represented reproduction in the garden using four parameters. In addition to vegetative and seed reproduction scores, we calculated *total reproduction* as the sum of both values, and *prevalence of vegetative reproduction* as the difference between vegetative and reproductive scores. We refer to all four values as garden reproduction parameters. For each plot, we calculated unweighted mean values and SD for each of these four measures for all species present in the plot for which the information was available (use of cover-weighted means and SD yielded qualitatively similar results, not shown here). Unless otherwise stated, results for only non-woody species (herbaceous species and dwarf shrubs) are shown in the paper. Because the taxonomic concept used for the co-occurrence data was different from that for the garden collections, only a subset of species scored in the garden could be matched. Plots in which <50% of the species present were scored were discarded; this yielded 13 828 plots with sufficient garden reproduction data available. In a similar fashion, we calculated unweighted mean value and SD of log values of SLA, height and seed mass. Because life span had only two states (annual, perennial), we used the proportion of annual plants as a measure of central tendency and the Simpson diversity index as a measure of dispersion

$$\mathrm{D} = \frac{1}{\left[\left(\frac{n_\mathrm{A}}{n_\mathrm{A}+n_\mathrm{P}}\right)^2 + \left(\frac{n_\mathrm{P}}{n_\mathrm{A}+n_\mathrm{P}}\right)^2\right]}$$

where n_A is the total number of annual species and n_P is the total number of perennial species. Plots in which <50% of the species present were scored were discarded, yielding the following number of plots with sufficient trait data available: SLA (18 211 plots), seed mass (17 832 plots), height (18 378 plots) and life span (18 396 plots).

Values for each garden reproduction parameter and trait were averaged over the whole set of plots to yield a mean value of the plot-wise means

$$(M = \frac{1}{n}\sum_i \frac{1}{S_i}\sum_j x_{ij})$$

and a mean value of the plot-wise SD

$$(D = \frac{1}{n}\sum_i \sqrt{\frac{1}{S_i - 1}\sum_j (x_{ij} - \bar{x}_i)^2}),$$

where n is the number of plots, S_i is the number of species in the plot i, and x_{ij} is the trait value of species j in plot i. (Slightly modified formulas were used for life span.)

We examined these values by a randomization procedure in which we randomized garden reproduction parameters and LHS traits by randomly assigning each plant species in the data set a value randomly drawn from the pool of all species, while keeping the lists of co-occurring species for each plot intact (Stubbs & Wilson 2004; Schamp et al. 2008). We chose this approach because it does not require additional assumptions about how the community structure is generated, and it examines only the non-randomness of the trait–species relationship. Species with missing values were not included in the randomization (i.e. if a plot had the information available for <100% of its species, only known values were randomized). This randomization process was done 1000 times. We used the randomization procedure to determine the significance of trait mean and trait dispersion for individual garden reproduction parameters and traits, and to calculate standardized effect sizes (SES), defined as

$$\mathrm{SES} = \frac{X_{\mathrm{obs}} - X_{\mathrm{exp}}}{s_X},$$

where X_{obs} is the true value of the parameter, X_{exp} and s_X are its mean and SD after randomization.

The same analyses were done for each of the seven EUNIS habitat types separately. In this case, we calculated *M* and *D* values by averaging plot-wise values only over plots in each habitat type. Significance and SES values were calculated by randomly assigning to each species in each plot a value (for garden reproduction parameters and LHS traits) drawn only from the pool of species that occur within the habitat type in which the given plot belongs; values of remaining species were treated as missing values. The species pool for a habitat type was defined as all species with frequency >1% in that habitat type. This yielded the following numbers of plots with sufficient (>50% species) trait data: scrub and heathlands (278 for garden parameters, 232 for garden parameters of herbs only, 194–310 for measurable trait data), forests (2928, 2556, 2290–3231), grasslands (5962, 5930, 6093–6309), peatbogs and mires (438, 408, 489–522), rocky habitats (217, 214, 155–235), synanthropic habitats (1626, 1511, 4359–4716) and water habitats (970, 953, 2476–2552).

Finally, the same set of analyses was repeated separately for individual habitat types from the 32 EUNIS habitat type classification. Only habitat types with more than 380 plots were analysed, comprising the following 15 habitat types: C1, Standing waters; C3, Littoral zone; D2, Poor fens and transition mires; E1, Dry grasslands; E2, Mesic grasslands; E3, Wet grasslands; E5.2, Woodland fringes; E5.6, Anthropogenic tall-forb stands; G1, Broad-leaved woodland; G3, Coniferous woodland; G4, Mixed woodland; G5, Forest clearings; H5.6, Trampled areas; I1, Arable land; J6, Waste deposits.

All calculations were done in R ver. 2.8.1 (R Foundation for Statistical Computing, Vienna, AT).

Results

In the analysis across the whole data set, three out of four garden reproduction parameters (vegetative reproduction, total reproduction and prevalence of vegetative reproduction) showed significantly higher mean plot values than expected by random sampling of the species pool (Table 1). Dispersion at the plot level for all four garden reproduction parameters was negative (Table 1). Values of all the traits tested had significantly non-random means: lower than expected in life span and seed mass, and higher than expected in SLA. Dispersion values in all traits tested were negative (Table 1).

Table 1. Tests of non-randomness of trait means (*M*) and dispersions (*D*) over the whole data set. Values in the table are standardized effect sizes.

Trait	Mean	Dispersion
Garden reproduction		
Seed reproduction	0.644	**−2.208***
Vegetative reproduction	**4.973****	**−2.338****
Prevalence of vegetative reproduction	**3.133****	**−1.905***
Total reproduction	**5.24****	**−1.907***
LHS traits		
Life span	**−2.74****	**−6.449****
Height	−1.644	**−6.675****
SLA	**2.668****	**−4.563****
Seed mass	**−3.787****	**−6.851****

$^*P < 0.05$, $^{**}P < 0.01$. Significant values are in bold. SES calculation and significance tests are based on 1000 randomizations.

The separate analyses of the seven EUNIS-7 habitat types (i.e. with smaller subsets used as the reference pool for randomization) showed only a few significant values of means: total reproduction in grasslands and water habitats, prevalence of vegetative reproduction in water and synanthropic habitats (positive), and seed reproduction (negative) in synanthropic habitats. Significantly non-random dispersions were more common, but not universal; all of them were negative, indicating convergence (Table 2). Differences among habitat types were highly significant (Table 1). Peatbogs and water habitats showed the highest prevalences of vegetative reproduction, whereas rocky habitats and grasslands showed the lowest prevalences of vegetative reproduction (Fig. 2). Total reproduction was highest in water habitats and lowest in scrublands and rocky habitats. For all four reproduction parameters, differences among EUNIS-7 habitats were highly significant using one-way ANOVA (Fig. 2).

Trait means in the separate analyses of the seven EUNIS-7 habitats were quite often non-random (Table 2). Heights were less than expected (on the basis on the species pool of the given habitat type) in all habitat types except for grasslands and synanthropic habitats. SLA was higher than expected in forest and rocky habitats, and seed mass lower than expected in scrub, forests and rocky habitats. The proportion of annual species was higher than expected in synanthropic habitats, and lower in grasslands and peatbogs. Differences between mean trait values among individual EUNIS habitat types were highly significant (not

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Table 2. Tests of non-randomness of trait means and dispersions for the seven EUNIS habitat types. Values in the table are standardized effect sizes.

	Trait	Scrub	Forests	Grasslands	Peatbogs	Rocky	Synanthropic	Water
Mean	Seed reproduction	−0.174	−0.445	0.912	−0.409	−0.816	**−2.589****	0.128
	Vegetative reproduction	0.609	1.643	1.584	−0.183	0.084	**2.09***	**1.833***
	Prevalence of vegetative reproduction	0.696	1.426	0.458	0.463	0.709	**2.887****	1.398
	Total reproduction	0.398	1.208	**1.938***	−0.019	−0.485	0.348	**2.706****
Dispersion	Seed reproduction	**−1.813***	−1.546	0.249	−0.813	−1.067	−0.531	−0.831
	Vegetative reproduction	−1.637	−1.18	−1.513	−0.772	**−2.303****	−1.07	**−2.598****
	Prevalence of vegetative reproduction	**−2.86****	**−1.645***	−0.005	−0.686	**−2.571****	−0.447	**−2.313****
	Total reproduction	0.206	−0.614	**−1.734***	−0.514	0.467	−1.313	0.339
Mean	Life span	−0.175	1.182	**−2.945****	**−1.382***	−0.116	**3.334****	1.325
	Height	**−5.473****	**−4.609****	−1.065	**−2.256****	**−3.152****	−1.354	0.781
	SLA	1.108	**4.69****	0.783	0.159	**1.925***	1.467	−0.791
	Seed mass	**−4.49****	**−2.562****	−1.339	−0.097	**−3.217****	**−1.657***	−0.115
Dispersion	Life span	0.088	0.806	**−3.18****	−1.135	−0.926	**−5.099****	−1.589
	Height	**−4.884****	**−5.851****	**−3.669****	**−2.554****	**−3.323****	**−3.414****	−0.026
	SLA	**−1.48***	**−1.613***	**−2.794****	−0.002	−0.756	**−2.399****	−1.209
	Seed mass	**−4.54****	**−4.379****	**−3.096****	−1.491	**−2.971****	**−2.639****	−1.256

*$P < 0.05$, **$P < 0.01$. Significant values are in bold. SES calculation and significance tests are based on 1000 randomizations.

shown). Trait dispersions, if significant, were invariably negative (Table 2, Fig. 3). The only positive dispersion value found was dispersion of height in forests, calculated from the data on all species (including woody species).

Patterns at the level of narrower habitat types (classification into 32 EUNIS habitat types) showed non-random patterns in means and dispersions of garden reproduction in few habitat types (two to five out of 15 examined; see also Fig. 3). All significant dispersions were negative. Traits showed more pronounced patterns. In approximately half (six to seven) of the habitat types, trait means were significant (with the exception of SLA, which was significant in only three habitat types); trait dispersions where significant and negative in eight out of ten of the habitat types for all traits. There were no significant positive dispersions.

Discussion

Habitat filtering and dispersion in garden reproduction and LHS traits

The results show strong non-random structure of within-community dispersions and community-level means in both garden reproduction data and LHS traits. On a gross level, the patterns found for LHS traits and for garden reproduction data are quite similar, with strong under-dispersion for the data set as a whole and diminishing degrees of under-dispersion in subsets of the data. With one exception, no over-dispersion was detected in the data. While differences in mean trait values across habitat types are well known (see e.g. van Groenendael et al. 1996; Díaz et al. 2004; Klimešová et al. 2011; Rusch et al. 2011; Gough et al. 2012), and demographies of species are known to be environmentally dependent (e.g. Dahlgren & Ehrlén 2011), to our knowledge this is the first demonstration of non-random within-community patterns of a demographic parameter.

The prevalence of under-dispersion observed in analyses across the entire data set (i.e. not broken down by individual habitat types) is clearly due to environmental filtering of the species pool (Colwell & Winkler 1984; Kraft et al. 2007; de Bello 2012). Indeed, in all the analyses, the existence and intensity of under-dispersion in the data strongly depended on the species pool used for randomization. Narrower species pools invariably reduced under-dispersion both in the LHS traits and in garden reproduction. The strong role of habitat filtering is further supported by fact that means of both LHS traits and garden reproduction differ among individual EUNIS-7 habitat types.

However, the nature of the habitat filtering differs between garden reproduction and LHS traits. For the LHS traits, strong differences in mean trait values from individual habitat types result from different trait values maximizing fitness in different environmental conditions (e.g. high SLA in forests vs low in peatbogs, scrublands and grasslands). Due to non-negligible habitat heterogeneity even within the rather narrowly defined habitat types, changes in trait values thus simply reflect these gradients with different trait values, maximizing fitness in different environmental conditions. In contrast, reproduction is a property that must be maximized in any environment within the constraints imposed by habitat productivity and species' environmental tolerances. Therefore, it is much less likely to show strong differences within broadly defined individual habitat types, leading to only a few cases of under-dispersion, either at the EUNIS-7 or EUNIS-32 level. The filtering effect in the garden reproduction data is thus confined mainly to the extremes of environmental

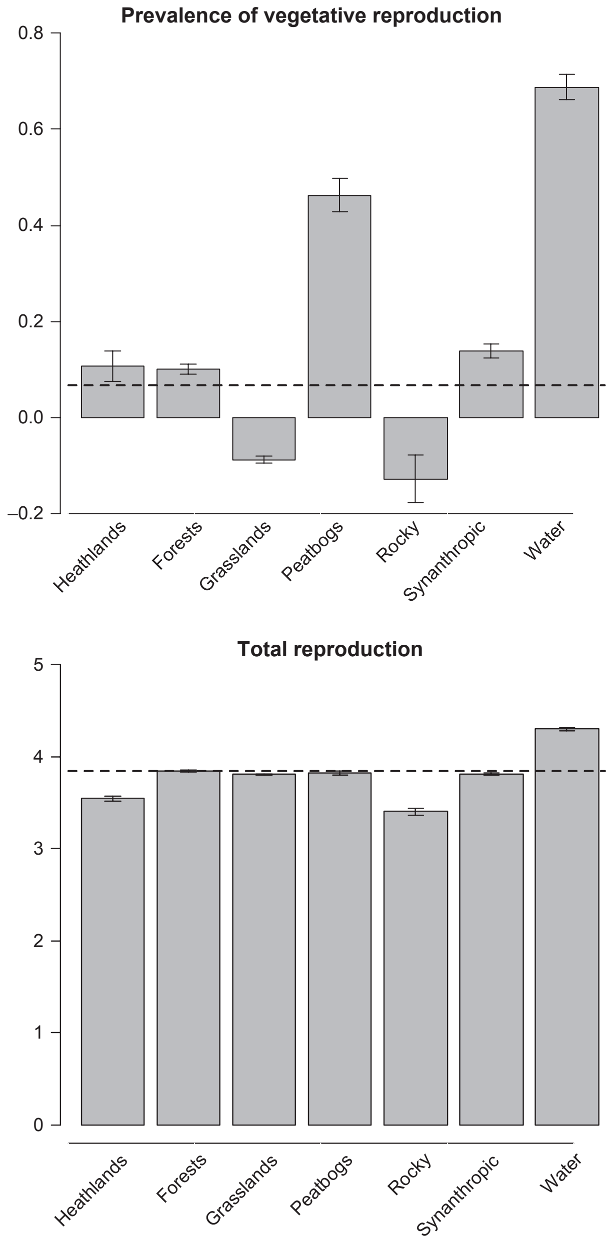

Fig. 2. Differences among the EUNIS-7 habitat types in prevalence of vegetative reproduction and in total reproduction of non-woody plants. Differences among habitat types are significant using one-way ANOVA (Prevalence of vegetative reproduction: $F = 274.4$, $df = 6$, 13 097, $P < 0.001$; Total reproduction: $F = 242.4$, $df = 6$, 13 097, $P < 0.001$). Bars indicate SE. Dashed line indicates grand mean.

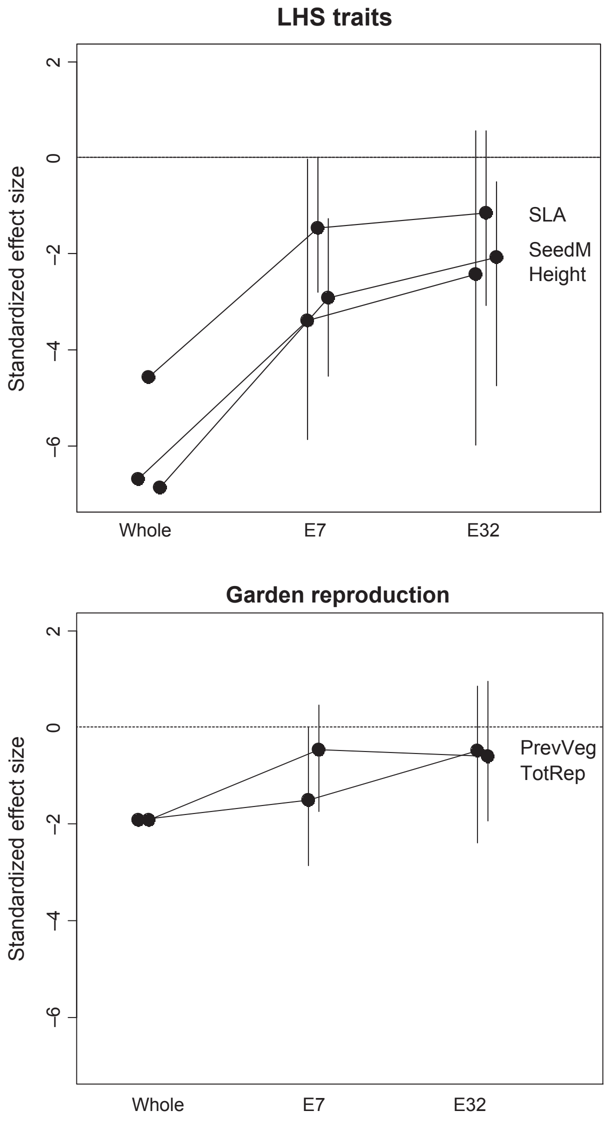

Fig. 3. Standardized effect sizes for dispersion of garden reproduction and LHS traits across the whole data set, and using EUNIS-7 and EUNIS-32 habitat type classifications. Negative values of SES (below the dotted line) indicate under-dispersion, positive values indicate over-dispersion. Dots indicate means, with vertical lines connecting minimum and maximum values for the given habitat type classification. Data for EUNIS-32 habitat types are calculated from the 15 types with a sufficiently high number of samples (see Methods for details). SeedM – seed mass, PrevVeg – prevalence of vegetative reproduction, TotRep – total reproduction.

gradients, such as water availability or temperature; in such habitats, generative reproduction can be hindered and therefore vegetative reproduction becomes dominant (Grace 1993). Indeed, garden reproduction shows higher under-dispersion in more extreme habitats (such as scrublands, peatbogs and water habitats), indicating that, in these habitat types, differences (e.g. in water availability) are steep enough to bring about differences in mean potential reproduction (see also, e.g. Sosnová et al. 2010). Further, this difference between distributions of LHS traits and garden reproduction could have been augmented by the ordinal nature of the garden reproduction data (only five values) in comparison with the LHS traits (quantitative data for three traits).

Functional differentiation within communities

Over-dispersion, i.e. higher differences among co-existing species than expected by random sampling from the species pool, was never observed in the data on non-woody species, either in the LHS traits or in the growth data. The only case of over-dispersion was for height in forest communities (EUNIS-7 habitat type forest, and several forest EUNIS-32 habitat types), using the data set of all plants (i.e. including woody species). Thus, the only over-dispersion in the LHS traits is due to vertical stratification of forests. However, neither LHS traits nor garden reproduction data would seem to be good *a priori* candidates to show over-dispersion. All the traits considered are related to competitive processes, in which co-existence would be more favoured by species similarity (equalizing mechanisms, see Mayfield & Levine 2010) than by differentiation in the trait values, and show strong habitat filtering effects.

It is conceivable that a community could be composed of species with different reproduction patterns (e.g. different proportions of vegetative and seed reproduction), which would freely co-exist, but there is no indication of any instances of this. Although the species data indicate the existence of a trade-off between vegetative and seed reproduction in the garden (Herben et al. 2012; see also e.g. Reekie & Bazzaz 1987; Chaloupecká & Lepš 2004), the distribution of different reproduction modes in the field is nevertheless driven mainly through filtering in extreme habitats.

Use of garden reproduction as a proxy for species demography in the field

The validity of our inferences rests upon the degree to which garden reproduction serves as a reliable indicator of field reproduction. Reproduction of a population in the field depends both on the potential reproduction of the species (i.e. reproduction in optimal conditions) and on the actual environmental conditions of the field site, where the population may be occurring in suboptimal conditions. Thus, our approach relies on two assumptions: (1) that in the garden all the study species have been maintained in conditions reasonably close to their optima (enabling valid estimation of the heights of the bell-shaped fundamental niche-response curves), and (2) that proportions of optimum and suboptimum habitats in the field are similar in all species (see also Fig. 4).

We believe that there is no major difficulty with the first assumption, as the garden's environmental heterogeneity, coupled with the siting of species within it, generally enables the species to grow in rather favourable habitats. While some species may be more easily 'domesticated' than others, there is no indication that any particular ecological group of species has been performing poorly relatively to others. On the other hand, the second assumption is less supported, as realized niches often differ from fundamental niches and this relationship differs among species (Wisheu & Keddy 1992). Differences between fundamental and realized niches in the field are largely driven by competition with other species, which is not accounted for in garden reproduction, with this effect likely to differ both across species and the different communities that include the species. If a species generally occurs only or primarily in suboptimal habitat (typically due to competitive exclusion from part of its fundamental niche), using a garden proxy for its reproduction in the field is much less reliable than in a species that typically occurs close to its optimum conditions or has a flat response curve (Fig. 4). Temporal variation in habitat quality can impose similar limitations on the applicability of garden data as a proxy for field performance.

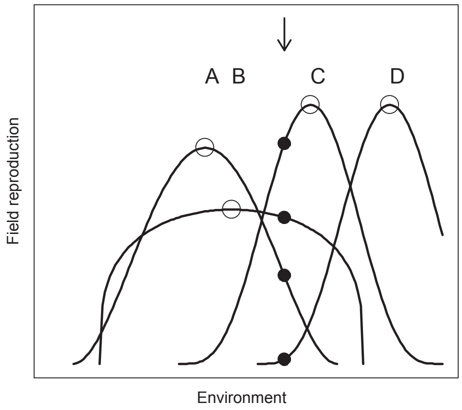

Fig. 4. Conceptual issues in assigning the garden reproduction values to vegetation records from the field. Lines show field reproduction environmental responses of four species. The arrow indicates the position of a vegetation record from one field site; open circles show reproduction values in an optimum environment (garden reproduction) of the species found at that site; full circles show true reproduction values in the habitat conditions at that site. The difference between the value of reproduction in optimum conditions and in the site's conditions depends on the shape of the response of reproduction to habitat conditions as well as the location of the species' optimum along the environmental gradient. It increases with the proportion of suboptimal conditions in which the species occurs. The difference is small in species B, which has a flat response, more pronounced in species A, and strongest in species D. Species C is little affected because the site conditions are close to its optimum.

Finally, it must be stressed that, for perennials, reproduction is only one of the two key components of demography. Although mortality is typically less environmentally dependent (i.e. survival environmental responses are typically wider than reproduction responses), this is not necessarily true universally. Additionally, mortality may be correlated with reproduction via density-dependent mechanisms or life-history patterns (e.g. in monocarpic plants).

Conclusion

Comparative analysis of dispersion in LHS traits and garden reproduction shows that, in spite of weak correlations between these two sets of species parameters, their dispersions within communities are rather similar to each other. This is at least partly due to the predominant effect of environmental filtering, both on trait values and reproduction parameters. However, at the finer level, reproduction parameters are closer than trait values to random patterns, indicating that co-existence of species is not limited by similarities or differences in their reproduction parameters. There is also no indication in the data that species with different reproduction modes (vegetative vs seed) would be more likely to co-exist than species randomly selected from the species pool.

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References

Ackerly, D.D. & Cornwell, W.K. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135–145.

Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W. & Stadler, J. 2008. On the identification of the most suitable traits for plant functional trait analyses. *Oikos* 117: 1533–1541.

Burns, J.H., Blomberg, S.P., Crone, E.E., Ehrlen, J., Knight, T.M., Pichancourt, J.-B., Ramula, S., Wardle, G.M., Buckley, Y.M. 2010. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *Journal of Ecology* 98: 334–344.

Chaloupecká, E. & Lepš, J. 2004. Equivalence of competitor effects and tradeoff between vegetative multiplication and generative reproduction: case study with *Lychnis flos-cuculi* and *Myosotis nemorosa*. *Flora - Morphology, Distribution, Functional Ecology of Plants* 199: 157–167.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Chytrý, M. & Rafajová, M. 2003. Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. *Preslia* 75: 1–15.

Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. 2005. Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia* 77: 339–354.

Clark, J.S., LaDeau, S. & Ibanez, I. 2004. Fecundity of trees and the colonization–competition hypothesis. *Ecological Monographs* 74: 415–442.

Colwell, R.K. & Winkler, D.W. 1984. A null model for null models in biogeography. In: Strong, D.R. Jr, Simberloff, D., Abele, L.G. & Thistle, A.B. (eds.) *Ecological communities: conceptual issues and the evidence*, pp. 344–359. Princeton University Press, Princeton, NJ, US.

Cornwell, W.K. & Ackerly, D.D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.

Dahlgren, J.P. & Ehrlén, J. 2011. Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos* 120: 1183–1190.

Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. 2009. Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions* 15: 141–147.

de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? *Global Ecology and Biogeography* 21: 312–317.

de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., Sebastià, M.-T. & Lavorel, S. 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science* 20: 475–486.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295–304.

Ferenczy, A., Eppich, B., Varga, R.D., Bíró, I., Kovács, A., Petrányi, G., Hirka, A., Szabóki, C.S., Isépy, I., Priszter, S.Z., Türei, D., Gimesi, L., Garamvölgyi, Á., Homoródi, R. & Hufnagel, L. 2010. Comparative analysis of the relationship between phenological phenomena and meteorological indicators based on insect and plant monitoring. *Applied Ecology and Environmental Research* 8: 367–376.

Götzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K. & Zobel, M. 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews* 87: 111–127.

Gough, L., Gross, K.L., Cleland, E.E., Clark, C.M., Collins, S.L., Fargione, J.E., Pennings, S.C. & Suding, K.N. 2012. Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition. *Oecologia* 169: 1053–1062.

Grace, J.B. 1993. The adaptive significance of clonal reproduction in angiosperms – an aquatic perspective. *Aquatic Botany* 44: 159–180.

Gratani, L., Crescente, M.F., Varone, L., Fabrini, G. & Digiulio, E. 2008. Growth pattern and photosynthetic activity of different bamboo species growing in the Botanical Garden of Rome. *Flora - Morphology, Distribution, Functional Ecology of Plants* 203: 77–84.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259–281.

Gross, N., Kunstler, G., Liancourt, P., de Bello, F., Suding, K.N. & Lavorel, S. 2009. Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology* 23: 1167–1178.

Herben, T., Nováková, Z., Klimešová, J. & Hrouda, L. 2012. Species traits and plant performance: functional trade-offs in a large set of species in a botanical garden. *Journal of Ecology* 100: 1522–1533.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96: 1266–1274.

Klimešová, J., Doležal, J. & Sammul, M. 2011. Evolutionary and organismic constraints on the relationship between spacer length and environmental conditions in clonal plants. *Oikos* 120: 1110–1120.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist* 170: 271–283.

Kubát, K., Hrouda, L., Chrtek, J. jun, Kaplan, Z., Kirschner, J. & Štěpánek, J. 2002. *Klíč ke Květeně České republiky (Key to the Flora of the Czech Republic)*. Academia, Praha, CZ.

Lavorel, S. & Garnier, E. 2002. Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

Mayfield, M.M. & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.

Messier, J., McGill, B.J. & Lechowicz, M.J. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13: 838–848.

Primack, R.B. & Miller-Rushing, A.J. 2009. The role of botanical gardens in climate change research. *New Phytologist* 182: 303–313.

Reekie, E.G. & Bazzaz, F.A. 1987. Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *The American Naturalist* 129: 907–919.

Rusch, G.M., Wilmann, B., Klimešová, J. & Evju, M. 2011. Do clonal and bud bank traits vary in correspondence with soil properties and resource acquisition strategies? Patterns in alpine communities in the Scandian mountains. *Folia Geobotanica* 46: 237–254.

Schamp, B.S., Chau, J. & Aarssen, L.W. 2008. Dispersion of traits related to competitive ability in an old-field plant community. *Journal of Ecology* 96: 204–212.

Sosnová, M., van Diggelen, R. & Klimešová, J. 2010. Distribution of clonal growth forms in wetlands. *Aquatic Botany* 92: 33–39.

Stubbs, W.J. & Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. *Journal of Ecology* 92: 557–567.

Suding, K.N., Goldberg, D.E. & Hartman, K.M. 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.

van Groenendael, J.M.V., Klimeš, L., Klimešová, J. & Hendriks, R.J.J. 1996. Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society. B, Biological Sciences* 351: 1331–1339.

Verdú, M., Rey, P.J., Alcántara, J.M., Siles, G. & Valiente-Banuet, A. 2009. Phylogenetic signatures of facilitation and competition in successional communities. *Journal of Ecology* 97: 1171–1180.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.

Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.

Wisheu, I.C. & Keddy, P.A. 1992. Competition and centrifugal organization of plant-communities – theory and tests. *Journal of Vegetation Science* 3: 147–156.

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