Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits

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Summary

1. The degree of dispersion of trait values among species in a community has frequently been used to infer processes of community assembly. However, multiple assembly processes can lead to the same pattern of trait dispersion or the same process can lead to different patterns of dispersion. In particular, competitive processes can lead both to trait overdispersion (if the trait controls niche differentiation and only substantial differences allow coexistence) or to trait underdispersion (if the trait controls position in a competitive hierarchy and only similar values enhance coexistence).

2. Because different traits are likely to contribute to stabilizing (niche differentiation) and equalizing (competitive hierarchies) mechanisms of coexistence, we compare the role of dispersion of a number of individual traits for species diversity by conducting *in silico* experiments using field-parameterized spatially explicit models of communities of clonally growing plants. We manipulate both dispersion and means of different traits and examine consequent changes of species diversity in the whole community. We hypothesize that growth traits, which are directly linked to resource acquisition, are likely related to position in competitive hierarchies and thus diversity and trait dispersion will be negatively associated. In contrast, we hypothesize that architectural traits, which control spatial deployment of new plants and are thus less directly linked to resource acquisition, are more likely to be linked to niche differentiation and thus diversity and trait dispersion will be positively associated.

3. Individual traits differed considerably in effects of trait dispersion on community diversity. Specifically, increasing dispersion in growth traits often decreased diversity, presumably reflecting widening competitive differences and exclusion of weaker competitors, which is consistent with the action of equalizing mechanisms of species coexistence. In contrast, increasing dispersion in architectural traits either increased diversity or had no effect, which possibly indicates niche-based mechanisms of diversity maintenance. Changes of community-wide trait means can have large effects on diversity for a given degree of dispersion, although not usually changing the sign of the relationship.

4. *Synthesis.* These results suggest inference of community assembly processes from patterns of trait dispersion without understanding how particular traits function in community assembly may often be misleading. Effects of dispersion of traits that are likely associated with position in a competitive hierarchy are very different from those of traits associated with niche differences.

Key-words: architectural traits, clonal plants, community diversity, determinants of plant community diversity and structure, growth traits, parameterized model, process from pattern inference, trait manipulation

Introduction

Analyses of trait values have become widespread because they constitute easy-to-obtain proxy variables of functional processes in plants. Analysis of the trait structure of communities has shown that values often differ from that predicted by a random sampling process from the species pool (Götzenberger *et al.* 2011). If the variation among species in some trait is larger than random ('trait overdispersion'; Weiher & Keddy 1995), it is typically interpreted as an indication of

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competitive processes leading to divergence of trait values (see e.g. Ackerly & Cornwell 2007; Cornwell & Ackerly 2009; Götzenberger *et al.* 2011). This argument is based on the assumption that trait values are correlated with niches: the more species differ in some trait, the more likely they are to occupy a different niche and therefore be able to coexist. Such a competitive constraint on similarity in trait values ('limiting similarity' *sensu* MacArthur & Levins 1967; Meszéna *et al.* 2006) would result in communities with greater-than-random variation in trait values (Weiher & Keddy 1995), and communities with greater trait dispersion would be more diverse than those with less dispersion.

In contrast, lower variation than random ('trait underdispersion') is often taken as evidence of environmental filtering from a broader pool or, less often, facilitative effects within the community (Ackerly & Cornwell 2007; Götzenberger *et al.* 2011). However, as Ågren & Fagerström (1984) first pointed out almost 30 years ago, coexistence may also be a consequence of similarity in competitive ability, that is, there exists a 'limiting *dis*similarity', where, for a given degree of niche partitioning, only species that are not too different in competitive ability for shared resources can coexist (see also Aarssen 1983). Chesson (2000) formalized this idea by distinguishing equalizing mechanisms of coexistence, which act along with the stabilizing mechanisms of niche partitioning. Consequently, it has also been shown that evolution may favour formation of groups of similar species instead of radiating over broad niche space (Scheffer & van Nes 2006). As a consequence, underdispersion of traits related to competitive ability may reflect a strong role of competitive hierarchies in community assembly (Mayfield & Levine 2010), rather than environmental filtering. This is consistent with a number of recent empirical findings which show absent or very weak signatures of limiting similarity (e.g. Kunstler *et al.* 2012; Bennett *et al.* 2013; Price & Pärtel 2013).

These theoretical considerations suggest that inference of community processes such as niche partitioning, competitive exclusion or habitat filtering from patterns of trait dispersion should depend on the role of the traits in the community, rather than putting all traits into the same analysis with the same expectations. Although the literature contains relatively little discussion as yet on generalities concerning which traits are associated with which community processes, several examples of disparate patterns among different traits already exist (Swenson & Enquist 2009; Spasojevic & Suding 2012). Rather than being problematic, however, the differences in patterns for different traits could provide insights into the multiple processes that contribute to assembly of real communities. If so, then the critical next step is to understand which traits are relevant to which community processes and the extent to which these associations are general. That is, are traits relevant to niche partitioning (α diversity *sensu* Ackerly & Cornwell 2007) consistently different from traits relevant to competitive dominance?

In this paper, we examine the assertion that more dispersed trait values would be associated with more diverse communities assembled from a given species pool if limiting similarity

processes operate for that trait, but be associated with less diverse communities if competitive hierarchies regulate community assembly relative to that trait. We hypothesize that traits directly linked to rates of resource acquisition or use, such as maximum potential relative growth rate (RGRmax) or maximum plant size, are related to position in competitive dominance hierarchies, and hence, increasing dispersion will be associated with lower diversity. In contrast, we hypothesize that traits more related to spatial deployment of new plants are related to division of niche space by allowing spatial segregation, and thus, increasing dispersion of these traits will be associated with higher diversity.

To test these hypotheses, we manipulate dispersion of individual trait values in two virtual communities of field-parameterized 'species' and examine the community response using the resulting change in species diversity as an indicator of the processes that lead to species coexistence. We thus use *in silico* manipulations of values of traits around the baseline observed values for all species in the community to mechanistically examine the effects of trait structure on community diversity in a way that can never be attained in a field system (see e.g. Pacala, Canham & Silander 1993; Rees, Grubb & Kelly 1996; Peck 2004; Marks & Lechowicz 2006; Turnbull *et al.* 2007; Wildová *et al.* 2007). By examining a number of different traits for the full set of coexisting species in two different communities, we test for generality in linkages between levels of trait dispersion and community processes. In addition to manipulation of trait dispersion, we also manipulated the community-wide trait mean because extent and effects of trait dispersion may be contingent on mean values of that trait (see Ricotta & Moretti 2011), which, in turn, is often determined by the environment (Díaz *et al.* 2004). To simplify the analysis of the demographic consequences of effect of dispersion of trait values, we ran the simulations in a homogenous environment without any external source of heterogeneity. Thus, environmental filtering is excluded as a possible source of patterns in trait dispersion, and we focus on interpretations related to limiting similarity and competitive hierarchies.

We simulated two different field-parameterized systems to attain greater generality: (i) a four-species mountain grassland in Central Europe parameterized by Herben & Wildová (2012) and (ii) a five-species fen community in Michigan parameterized by Wildová *et al.* (2007); (see also Yu *et al.* 2012). In both cases, the parameterized species used in simulations represent all the common species from the community. At the same time, both these communities have species coexisting at a scale of several centimetres, which enabled us to assess changes in fine-scale species richness as the result of manipulation of functional diversity. As are almost all perennial herbaceous communities, both these systems are dominated by clonal plants, making it possible to examine the consequences of architectural traits that determine spatial deployment of ramets, as well as the more commonly analysed traits related to growth rates. In a previous simulation study (Wildová, Goldberg & Herben 2012), we showed that equalizing mechanisms likely contributed to coexistence in

this system, but did not manipulate degree of trait dispersion to test the linkage between dispersion and diversity.

Materials and methods

THE MODEL

We used a spatially explicit, individual-based model that simulates vegetative growth of clonal plants, with the nodes and internodes that form horizontally growing rhizomes, and above-ground shoots (ramets) that are borne by the nodes as the basic units in the model (Fig. 1; see also Wildová *et al.* 2007; Wildová, Goldberg & Herben 2012). It incorporates competitive processes between ramets through density-dependent resource uptake and accumulation. The resource is not specified but could be any resource limiting to population growth. This resource is accumulated by ramets (shoots), and its amount is used for decisions for further growth of the rhizome by adding further nodes, internodes and ramets. When new nodes are formed, part of the resource remaining at the mother node is put into the new node; translocation between older established nodes is not modelled. Further, it incorporates an architectural model of growth of clonal plants that simulates development of branched rhizome patterns and ramets borne by them based on the resource available to the ramets and a set of species-specific architectural rules. For structural assumptions and formulas used in the model, see the Appendix S1 and Wildová *et al.* (2007).

The model runs on a continuous simulation plane with toroidal boundaries. The simulation plane is defined as homogeneous; any heterogeneity is generated by the ramets themselves. Model parameters include both ramet growth traits and architectural traits such as allocation to new ramets, spacers between ramets, and rhizome architecture (see Wildová *et al.* 2007; Yu *et al.* 2012; and Herben & Wildová 2012 for a complete list of parameters and their values in the two field systems).

PARAMETERIZATION AND CALIBRATION

For the Central European mountain grassland model, we parameterized the four dominant species that characterize ca. 90% (median value over plots and years) of the total biomass of the community, *Anthoxanthum alpinum* Á. Löve et D. Löve, *Deschampsia flexuosa* (L.) Trin., *Festuca rubra* L. and *Nardus stricta* L. The model was parameterized primarily from direct measurements in the field; two parameters were estimated indirectly by a gradient descent estimation based on the best fit to an 8-year time series of fine-scale field data (see Herben & Wildová 2012 for details). As intraspecific variation in ramet sizes in all species is rather small in this system (unpubl. data),
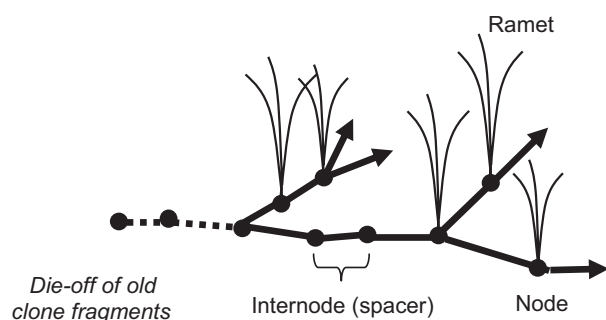
the system was parameterized assuming that ramets attain their maximum size during one time step (15 days). The parameterized model correctly predicted the time course of ramet numbers and, to a lesser degree, also spatial pattern in the community over 18 years of simulation (the length of time for which field data are available).

For the Michigan fen model, we parameterized the five dominant species that characterize 75% of the biomass, *Carex lasiocarpa* Ehrh., *C. sterilis* Willd., *Cladium mariscoides* (Muhl.) Torr., *Carex stricta* Lam. and *Schoenoplectus pungens* (Vahl) Palla; no other species constitutes > 5% of the biomass. These species span a range of growth forms from tussock-forming to runners and are described in detail in Wildová *et al.* (2007) and Yu *et al.* (2012). The model was parameterized primarily using direct estimation from measurements of plants either collected in fens in south-eastern Michigan, USA, or grown in a short-term (90 days) garden experiment (see Wildová *et al.* 2007 for details). Two parameters were estimated indirectly by testing a broad range of trait value combinations and then finding the best fit with data from a separate 300-day experiment conducted by Hershock (2002). Due to intraspecific variation in ramet sizes, this system was parameterized to take account of ramet growth over time and hence variable ramet sizes. Comparison of model simulations with other data from the 300-day pot experiment suggests that, despite the necessary structural simplifications made in the model, it seems to capture the major processes accounting for growth and competition of these plants (Yu *et al.* 2012).

MANIPULATING TRAITS TO CHANGE TRAIT DISPERSION

To examine consequences of trait dispersion on community richness, we identified six traits for the Central European mountain grassland species from Herben & Wildová (2012), and six traits for the Michigan fen species from Wildová *et al.* (2007); see Table 1. These traits were selected using the following criteria: (i) they approximate traits that are used in trait-based studies of community, (ii) they differ among species in the community, and (iii) their estimates are reliable and have been estimated independently of other traits. As parameterizations of these two systems were done in a slightly different fashion, use of these criteria produced different subsets from the total number of traits used in the model (see Table 1; for observed spacing of trait values see Fig. S1).

We used maximum ramet growth rate (growth rate) and maximum ramet size (ramet size), ramet life span and internode cost as traits directly related to species growth rate. The first two traits are related to two of the three key traits in the LHS scheme of Westoby (1998); (Westoby *et al.* 2002). While ramet growth rate is rarely measured in community analyses, the other leaf-related traits more often used in community-trait analyses (e.g. specific leaf area, SLA, of the LHS system) are often considered a proxy for growth rate based on their strong correlations (Reich, Walters & Ellsworth 1992; Wright & Westoby 1999; Shipley *et al.* 2005; Poorter *et al.* 2008; Donovan *et al.* 2010). The other two growth-related traits in our analyses are rarely measured or used in community analyses, but nevertheless have strong connections to potential productivity and competitive dominance for clonal plants. Longer-lived ramets can continue to produce new ramets with the same initial investment, thus also increasing clonal growth rate. Internode cost represents the cost in resources to make rhizomes or stolons connecting ground ramets and thus, increasing values reduces new ramet production.

Seed traits are often included in trait-based community analyses to represent dispersal or colonization ability. We do not include any seed traits in this analysis because we work with clonally growing plants

Fig. 1. Basic elements of the clonal plant growth in the model.

Table 1. Traits used in the analysis. Empty cells mean that the trait was not manipulated in the given system

| | Trait values in individual species | | | | | | | | | |
| | Mountain grasslands | | | | Fens | | | | | |
Trait	DF	FR	NS	AA	CL	CI	CE	CM	SP	Comment
Ramet growth rate [g day^{-1}]					0.052	0.088	0.112	0.031	0.065	
Ramet initial size [g]					0.04	0.09	0.01	0.029	0.09	Ramet size at the time step when it is formed
Ramet life span [days]	556	253	132	75						
Internode cost [g]	0.0023	0.0078	0.015	0.0026	0.050	0.037	0.033	3.18	1.18	Biomass of the internode (energetic investment needed for clonal spreading)
Internode length [cm]	0.15	0.27	0.19	0.10	0.26	0.16	0.16	0.63	1.52	NB. In some species, there are several internodes between two neighbouring ramets
Ramet replacement probability	0.28	0.46	0.001	0.06						Probability that the mother shoot will not die when a new rhizome is formed.
Probability of terminal branching	0.288	0.247	0.181	0.138						Probability that a plant could branch at each node if it had enough resources
Probability of branching from a dormant bud					0.095	0.09	0.005	0.02	0.065	Probability that non-terminal node initiates a new rhizome branch
Branching angle [deg]	15	27	49	33	46	44	40	55	34	Angle between the daughter rhizome and the mother rhizome

DF, *Deschampsia flexuosa*; FR, *Festuca rubra*; NS, *Nardus stricta*; AA, *Anthoxanthum alpinum*; CL, *Carex lasiocarpa*; CI, *Carex stricta*; CE, *Carex sterilis*; CM, *Cladium mariscoides*; SP, *Schoenoplectus pungens*.

for which vegetative spread is the major component of their space-encroaching behaviour (Zobel, Moora & Herben 2010). Instead, we use architectural traits that describe patterns of spatial expansion, such as branching probability and angle or internode length (Table 1), to capture the wide range of growth strategies and associated traits exhibited by clonal plants (Klimešová & de Bello 2009).

For trait dispersion, we manipulated the standard deviation of a single trait at a time across species, keeping unchanged the mean over all species and relative spacing of individual species' trait values. All other traits except the one manipulated were kept at their baseline values in all species for a given simulation. As the traits we work with are either multiplicative constants or have potentially log-normally-distributed values such as biomasses or growth rates, we manipulated trait dispersion after log transformation and back-transformed the values after manipulation (see also Mason *et al.* 2003; Lepš *et al.* 2006). Trait dispersion was manipulated by multiplying the standard deviation of log-transformed trait values by a set of multipliers (see Table S1) and recalculating new trait values with the same mean and relative spacing, but different standard deviation. To examine how the effect of trait dispersion depends on the mean value of the trait in the community, we also shifted the mean of each trait by adding/subtracting constants to the log-transformed values of the mean (Table S1). We examined all combinations of multiplicative changes in standard deviation and additive changes in the mean. For each trait, the range over which standard deviation and mean were changed was decided upon using pilot simulations to define the range within which the diversity response of the resulting community was approximately monotonic. We examined a broader region for the internode cost in

the mountain grassland system, where diversity seemed to peak at intermediate parameter values. We used the community with field-parameterized values for each species as a baseline with which the simulations with altered parameter values were compared.

In a separate set of simulation experiments, we examined the effect of spacing of trait values while keeping the range unchanged. To accomplish this, we changed the inner two (in the mountain grassland system) or three (in the fen system) values of each trait to make the trait spacing regular (in logarithmic space). This procedure also changes the mean and standard deviation, but those changes are small in relation to the manipulations above. Species diversity in the systems with regular spacing were compared with that in the community with baseline values (i.e. spaced as in the field) for each species.

SIMULATION EXPERIMENTS

For each trait, we assessed the effect of dispersion and mean on species diversity and total biomass in simulations of all the species in a given community (four in the mountain grassland, five in the fen). Following Herben & Wildová (2012), simulations of the mountain grassland species were run on a toroidal plane corresponding to an area of 77 × 77 cm, initialized by the abundance and spatial structure recorded in plots of the same size in the field (for details, see Herben & Wildová 2012). The time step of the simulation corresponded to 15 days (i.e. 10 steps per growing season), and the simulations were run for 18 years. For this time period, the model is known to approximate field data well and largely stable species composition is reached in the field parameter combination, although it is not a full equilibrium

(Herben & Wildová 2012). We do not run the system to the full equilibrium as the time period required to do so (100+ years in the model; unpubl. data) is longer than the stability of the field conditions assumed for the parameterization. The initial density and spatial arrangement of plants followed the spatial arrangement of ramets in a field plot (for details, see Herben & Wildová 2012).

Simulations of the fen community were run on a toroidal plane corresponding to an area of 52.5 × 52.5 cm, which is based on the size of mesocosm experiments performed by Hershock (2002); (see also Wildová *et al.* 2007). The time step of the simulation was defined to correspond to 1 day (150 steps per growing season), and the simulations were run for eight years to account for faster dynamics in this system relative to the mountain grassland. After this interval, a fairly stable species composition is reached in the baseline (non-manipulated) parameter combination. The initial density and spatial arrangement of plants in the simulation was arbitrary and is based on (but not identical to) mesocosm experiments performed by Hershock (2002). The three clumper species (*C. lasiocarpa*, *C. stricta* and *C. sterilis*) were planted in five randomly positioned clumps of 6 × 6 cm with nine ramets each; the two remaining runner species were distributed randomly (45 ramets of *S. pungens* and 20 ramets of *C. mariscoides*).

For both systems, ramets were assumed to be unconnected at the beginning of the simulations, and an identical spatial arrangement was used in all simulations.

Each parameter combination was run in 20 replicate simulations. At the end of each simulation, we recorded the numbers of ramets of each species to calculate Simpson's diversity index as $D = 1 / \sum_i \left(\frac{n_i}{\sum_j n_j} \right)^2$, where n_i is a total number of ramets of the *i*-th species. Values of the diversity index were averaged over replicate runs of individual parameter combinations. We then fit a type II ANOVA model with trait mean, trait standard deviation and their interaction as random factors using restricted maximum likelihood approach (see e.g. Venables & Ripley 1999) to identify relative contributions of these three factors to the variance in Simpson's diversity across simulation runs. The calculation was done using the function VARCOMP (S-PLUS, 2000)

Results

Manipulation of trait standard deviation had strong effects on diversity in some traits in both the mountain grassland and the fen systems (Fig. 2). However, results differed considerably among traits, with increasing dispersion leading to both increases and decreases in community diversity. Increasing dispersion of traits directly affecting acquisition and use of resources by individual ramets and therefore ramet-level productivity (ramet initial size, maximum ramet growth rate in the fen system, ramet life span and internode cost in the mountain grassland system) typically led to a decrease in diversity of the resulting community (Fig. 2). Internode cost in the mountain grassland system showed a unimodal response indicating that diversity was highest around the observed (baseline) dispersion and decreased with either lower or higher dispersion. A tendency towards a unimodal response was also shown by terminal branching probability in the mountain grassland system, although not peaking at the observed dispersion.

In most cases, species with traits leading to higher ramet-level productivity (larger initial ramet size, faster maximum ramet growth rate, longer-lived ramets and lower internode costs) became increasingly dominant with greater dispersion of that trait (not shown), leading to lower diversity of the system. However, increasing dispersion of architectural traits, with less direct effects on ramet-level productivity, mostly showed increases (e.g. dormant bud activation in the fen) or no change in diversity (e.g. branching angle in the mountain grassland) (Fig. 2). Only one architectural trait, terminal branching probability in the mountain grassland, showed a pattern of lower diversity with increasing dispersion similar to that shown by traits leading to higher ramet-level productivity (Fig. 2).

When the mean trait value in the community was manipulated around the baseline observed value, as well as the standard deviation, it also had a discernible effect for most traits (Figs 3, 4), especially as it interacted with the degree of trait dispersion. Analysis of variance components showed that in half of the cases (6 out of total 12 manipulated trait-community combinations), the interaction between trait mean and trait SD accounted for more variance than did the trait SD (Fig. 5). Interactions between trait SD and mean were particularly strong for internode cost (both systems), branching probability and ramet life span (grassland system), and internode length (fen system). While these interactions were strong, in most cases, they did not result in changing the signs of the relationships between dispersion and diversity from those observed at the observed, baseline mean trait value (Figs 3,4).

The effects of change in trait spacing (i.e. regular instead of the baseline, observed spacing) were small in most traits, with substantial effects only in a few of the traits that had clustered spacing in the field systems; not surprisingly manipulation of traits with more regular spacing in the field had little effect (Fig. S2).

Discussion

LIMITING SIMILARITY OR COMPETITIVE HIERARCHY?

Our simulation results show that while increasing dispersion in some traits (given the field-observed values of the trait means) can yield higher diversity of the resulting community as is generally assumed in the literature on trait structure of communities, it is not a general pattern. First, manipulation of some traits had little if any effect on diversity. Secondly, and more interestingly, in a number of other traits, an increase in trait dispersion led to a pronounced decrease in diversity, indicating that communities composed of species that differ substantially in that trait are unlikely to occur.

This result strongly suggests that the assumption of limiting similarity does not hold for all the traits examined and alternative mechanisms operate. We suggest that traits in which divergence leads to declining diversity are those that confer advantage in competition (Mayfield & Levine 2010). Therefore, species-rich communities will be those with little variation in trait values associated with position in competitive
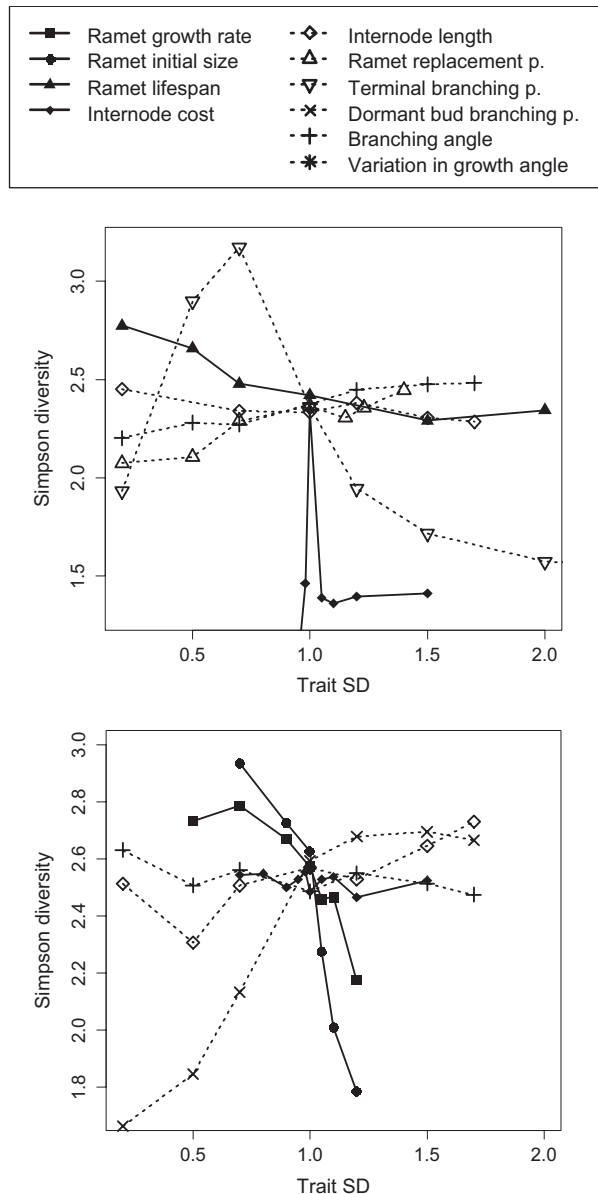
Fig. 2. Effect of changing trait standard deviation of individual traits on community diversity, while keeping the mean trait value for the community at its baseline value. Values of standard deviation are expressed relative to baseline values (SD = 1). Upper panel – fen, lower panel – mountain grassland. Solid lines are growth traits, and dashed lines are architectural traits.

all but one of these traits, increasing dispersion either had no effect on diversity or led to higher diversity as expected from a limiting similarity type argument. One possible reason for enhanced coexistence with increasing dispersion of most of the architectural traits is that greater differences in patterns of horizontal expansion among species increase the potential for spatial segregation and hence magnitude of intraspecific relative to interspecific interactions. On the other hand, Wildová, Goldberg & Herben (2012) did not find any evidence of spatial segregation using a similar model.

One possible caveat to these results on trait dispersion is that we used standard deviation to quantify the degree of trait dispersion and therefore increased the range as well as the spacing of traits. This was necessary because of the relatively few species in the communities we studied. For example, with only four species, changing from baseline to regular spacing would mean changing only the 'inner' two species, and, not surprisingly, such changes had minimal effects in preliminary simulations (Fig. S2).

Thus, the results support our hypothesis that statements on trait overdispersion/underdispersion in communities have little meaning without further information about the functional role of that trait. In particular, it is critical to understand whether the trait is one that affects niche differentiation or affects competitive ability for shared resources and therefore position in a competitive hierarchy. Ackerly & Cornwell (2007); (see also De Bello 2012) suggested that traits can be described as related to environmental filtering (β traits, likely to converge within communities) or related to coexistence within communities (α traits, likely to diverge within communities). Our results suggest that α diversity traits relevant to community assembly at a given location actually constitute two different kinds of traits that can have very different consequences for community assembly: competitive hierarchy traits and niche differentiation traits (Mayfield & Levine 2010).

Based on the relatively small subset of traits we analysed here, we suggest the hypothesis that traits directly related to rates of resource accumulation and growth rate will often be competitive hierarchy traits rather than niche differentiation traits and thus not be relevant to processes of limiting similarity. On one hand, this implies that large differences among species in the most widely measured traits such as specific leaf area (SLA) or wood density, which are used as proxies for plant function precisely because they are so highly correlated with growth rate (or at least maximum potential growth rate), may actually more often result in competitive exclusion than in coexistence. This suggests that observations of overdispersion of such traits in communities are unlikely to be related to why such species coexist. On the other hand, in heterogeneous environments with variation in degree of resource limitation and trade-offs among species along the leaf or wood economic spectrum (Wright *et al.* 2004, 2010), variation in growth rate may lead to coexistence through life-history trade-offs (Mouquet, Moore & Loreau 2002). These alternative hypotheses could be tested with mechanistic, trait-based demographic models of the type we used here that include more physiological and morphological traits related
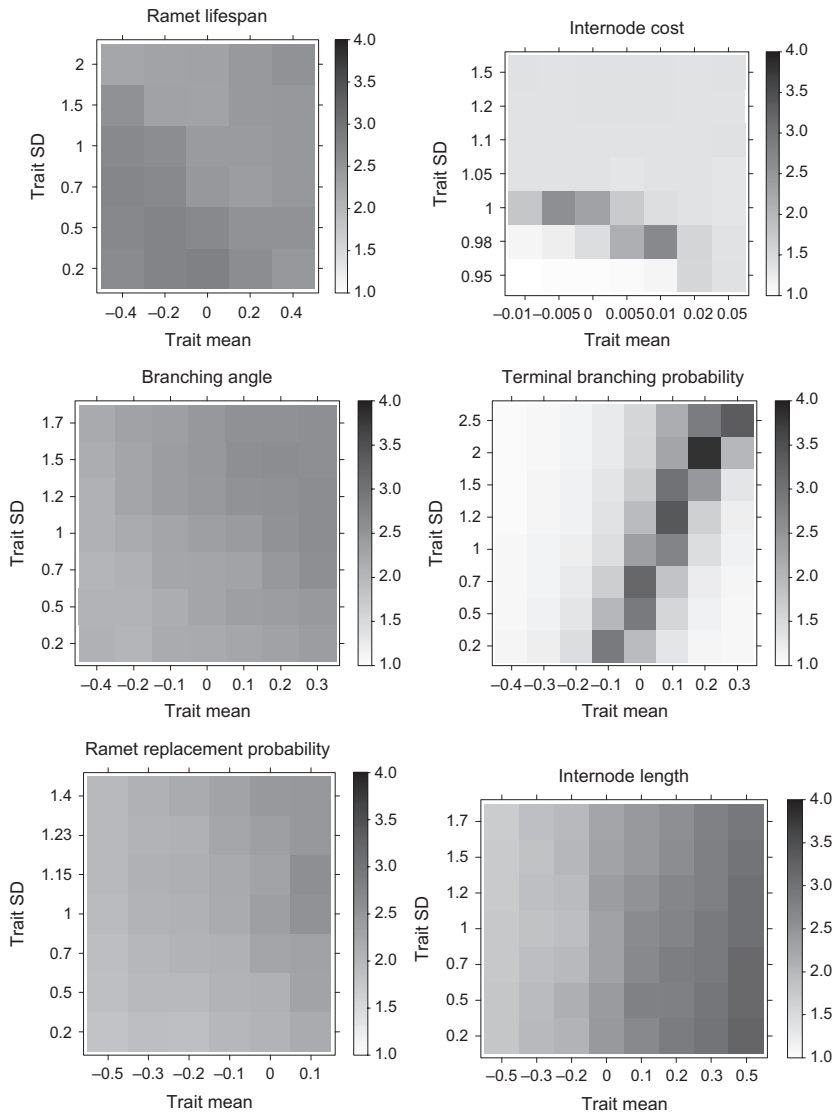
hierarchies and consequently slow rates of competitive exclusion (Aarssen 1983; Ågren & Fagerström 1984; Chesson 2000; Adler, HilleRisLambers & Levine 2007). This interpretation is consistent with the fact that the traits for which high dispersion is associated with low diversity in our study are typically traits such as ramet growth rate or ramet size, and such traits are often correlated with position in competitive hierarchies (Keddy 2001; Schamp, Chau & Aarssen 2008; Violle *et al.* 2009). The remaining traits we investigated are all related to spatial arrangements of biomass rather than directly to rate of biomass accumulation (branching probabilities and angles, internode length, ramet replacement probability). For

Fig. 3. Combined effects of manipulating trait mean (*x*-axis) and trait standard deviation (*y*-axis) on Simpson diversity in the mountain grassland system. Shading represents values of Simpson diversity. Upper row: growth traits; lower two rows: architectural traits. Note that diversity is scaled identically for all traits. Values of standard deviation and mean for each trait are expressed relative to their baseline values (i.e. the baseline value of SD for each trait is 1 and of the mean for each trait is 0). The shapes of plots are different because of different numbers of values used.

directly to resource acquisition, as well as incorporate environmental heterogeneity. Similarly, observations of underdispersion of traits that are often interpreted as related to environmental filtering and therefore to β diversity, may actually be related to coexistence in that community, that is, be α diversity traits, through equalizing mechanisms *sensu* Chesson (2000).

CONTEXT DEPENDENCE OF THE EFFECTS OF TRAIT DISPERSION

Another important finding of our simulations is the often strong interactions between trait dispersion with the trait mean on community diversity, that is, effects of trait dispersion and trait mean are non-additive, although it is important to note that in most cases, the sign of the relationship between dispersion and diversity does not change with the trait main. Nevertheless, because the magnitude of the effect of dispersion on diversity depends on trait means, predictions on trait overdispersion/underdispersion in plant communities are not fully independent of the absolute values of the trait

in the community in question. While in our specific parameterizations we may assume that trait means are known with reasonable certainty and hence dispersion can be analysed *per se*, this finding could have important consequences for general statements regarding effects of trait dispersion on diversity. Existence of the interaction of the degree of dispersion of a trait and its mean value is a likely explanation for inconsistent results on overdispersion of a given trait in different habitat and community types (Schamp, Chau & Aarssen 2008; Cornwell & Ackerly 2009; Pakeman, Lennon & Brooker 2011). Strong interactions also support earlier proposals that trait overdispersion could be confined to some environmental conditions (and hence trait means), although there is little agreement in the literature on the nature of this relationship (Weiher & Keddy 1995; Grime 2006; Schamp, Chau & Aarssen 2008).

The effect of degree of dispersion of individual traits on diversity was not even always consistent between the two systems examined in this study. This may be due either to differences in trait mean values between the two systems or, as we have shown using similar approaches, because the
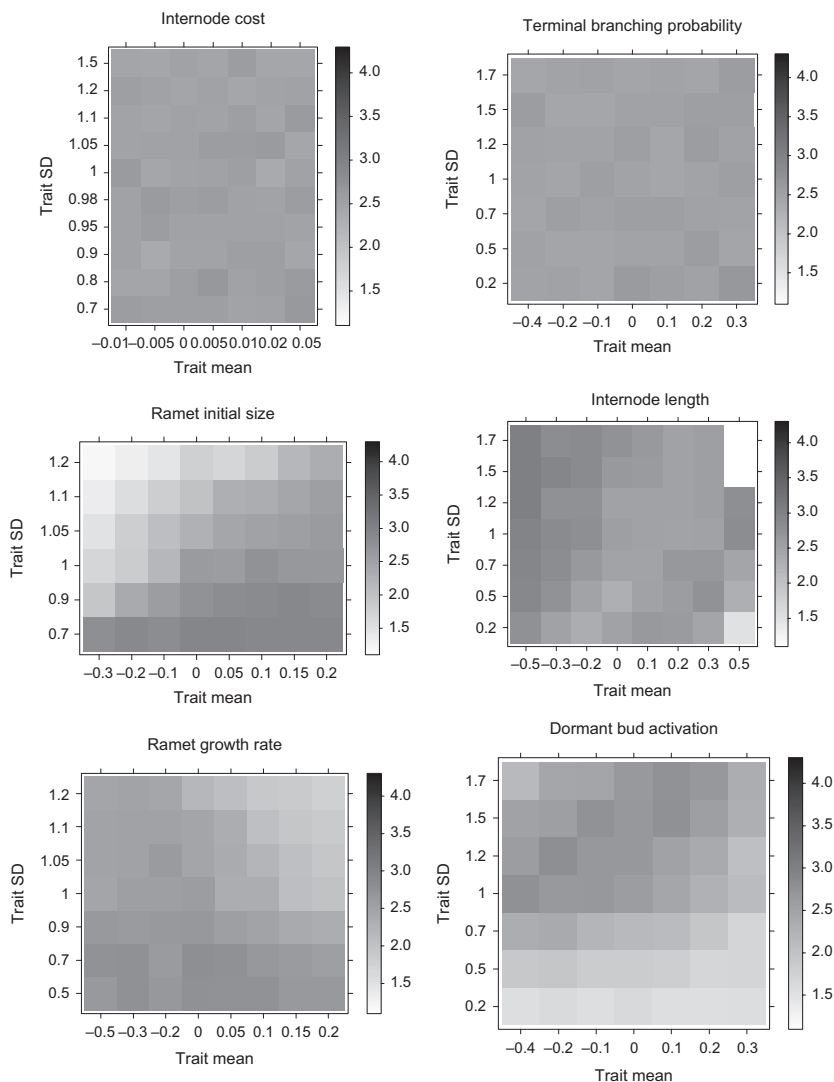
Fig. 4. Combined effects of manipulating trait mean (*x*-axis) and trait standard deviation (*y*-axis) on Simpson diversity in the fen system. Shading represents values of Simpson diversity. Left pane: growth traits; right pane: architectural traits. Note that diversity is scaled identically for all traits. Values of standard deviation and mean for each trait are expressed relative to their baseline values (i.e. the baseline value of SD for each trait is 1 and of the mean for each trait is 0). In internode length, not all combinations of trait mean and SD were tested, as combination of high standard deviation and high mean produced internodes too long relative to the simulation frame.

effect of changes in value of a given trait depends on the values of other traits, both within the same individual (e.g. Wildová *et al.* 2007; Goldberg, Herben & Wildová 2008) and of the other species in the community (Yu *et al.*, unpubl. data). While perhaps not surprising, such context dependency is usually not taken into account in interpretations of trait dispersion in the literature, even though it could change interpretations of patterns of trait dispersion across species.

SINGLE VS. MULTITRAIT ANALYSES

Both a strength and a limitation of this study were that we manipulated one trait at a time to examine the consequences for community diversity. This enabled us to detect distinct functional consequences for different traits and infer how different traits contribute to community assembly. At the same time, manipulation of single traits ignores the fact that traits are often part of more complex syndromes involving trade-offs such that both positive and negative correlations among certain traits are likely (Grime *et al.* 1997; Wright *et al.* 2004; Bruun & ten Brink 2008; Herben *et al.* 2012). Such trait correlations effectively reduce the dimensionality of the

system and hence the number of free parameters that can be independently varied. Nevertheless, such trait correlations tend to be noisy so it is unlikely that they would be strong enough within a single community to result in a single major trade-off axis that would reduce variation in all traits to a single dimension. Consequently, we expect traits will be at least partly independent such that we can analyse consequences of each trait for assembly separately. Consistent with this argument, several recent studies have shown clearer patterns of trait structure along environmental gradients using analyses of single functional traits than multitrait indices (Spasojevic & Suding 2012; Butterfield & Suding 2013). On the other hand, Angert *et al.* (2009) found that, in a community consisting only of small-statured annual plants, use of a multivariate trait space that accounted for strong trade-offs among a suite of traits provided stronger correlations with differences in population dynamics among species than did use of simple correlations between pairs of traits. Under what circumstances and for what questions individual traits or multivariate trait indices are more likely to be appropriate is thus still an open question but will clearly depend in part on the strength of correlations among the traits in questions.
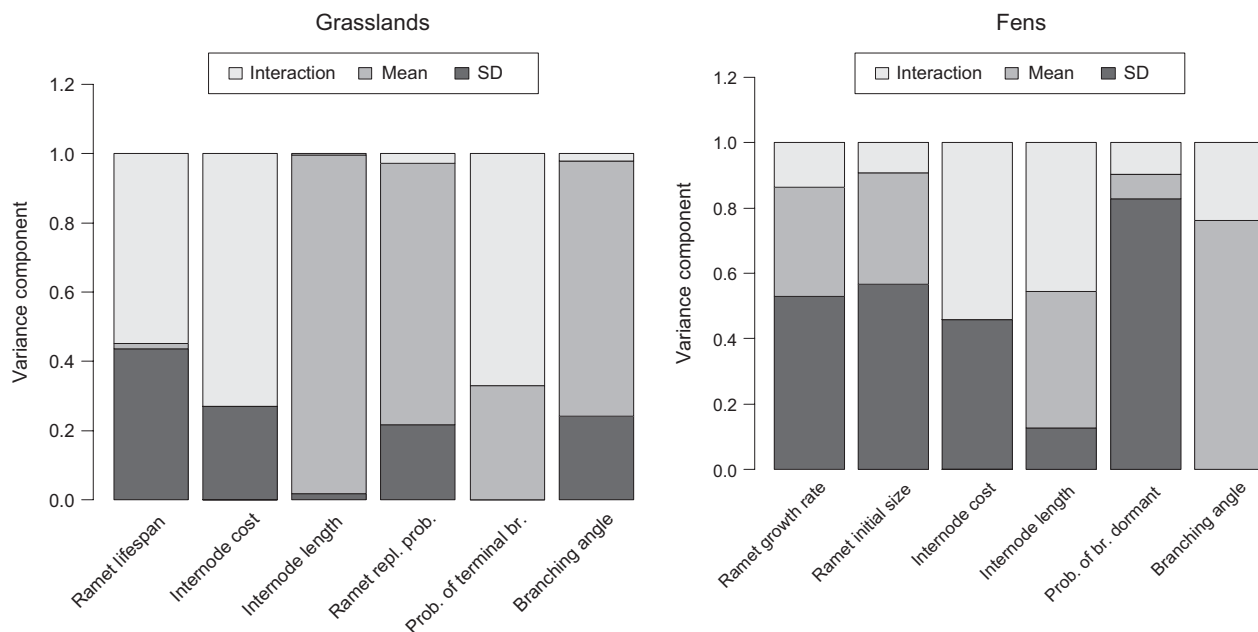
Grasslands

Fens

Fig. 5. Variance components in Simpson diversity due to the trait dispersion (SD), mean trait value, and their interaction. The values are standardized to sum to unity.

Conclusions

While our approach cannot provide an answer to whether a particular community structure is overdispersed or underdispersed, it does explore the mechanistic effect of dispersion of trait values on community dynamics independently of the species pool definition and therefore has important implications for the interpretation of patterns of over- or underdispersion. With this proviso, the results suggest that statements on trait overdispersion/underdispersion in communities have little meaning without further information about whether the trait is one that affects niche differentiation or affects competitive ability for shared resources. They also show that effects of some traits cannot be assessed independently of the trait means and of values of other traits possessed by that species. We contend that no real progress in trait ecology can be attained if these two limitations are not properly addressed. First, we should use functional approaches (experiments, models with the same physiological and morphological traits as used in empirical studies) to develop reasonable knowledge on which traits tend to be associated with coexistence and which with competitive hierarchy within environments, as well as with the habitat filtering associated with beta diversity across environments. In addition, understanding the extent to which the same traits could contribute to different processes is a critical area for future research.

Secondly, we should develop generalizations about which traits are more consistent in their consequences (and for which kinds of consequences) and which tend to be very context dependent. In this paper, we use context dependence to indicate dependence of effects of one trait on values of other traits, but its broader understanding may include also environmental contingency of trait effects. Context-dependent traits offer an exciting research field in itself, but clearly are not suited for large-scale generalizations, at least not in the current state of knowledge.

A better understanding of the mechanistic linkages between traits and community/ecosystem function is central to developing a predictive, trait-based ecology. We suggest that *in silico* experiments with 'tamed field systems', that is, mechanistic models with detailed parameterizations that approximate the key dynamics of field systems, is one very useful tool to move this field forward.

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Supporting Information

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

Appendix S1. Main structural assumptions and formulae used in the model.

Table S1. Constants used to manipulate means and standard deviations of individual traits in the simulations. Values under 'Mean' refer to amounts added or subtracted from the observed baseline value for each trait in each translational change of all trait values (on the scale of decadic logarithms); 0 hence indicates no change of the mean trait value. Values under 'SD' refer to the multiplicative constants applied to the baseline trait values to decrease (if smaller than 1) or increase (if larger than 1) trait values on the log scale.

Figure S1. Baseline spacing of individual traits in the field-parameterized systems.

Figure S2. Effect of manipulating spacing while keeping the range and mean constant.