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Dispersion of traits related to competitive ability in an old-field plant community

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Summary

1. We investigated patterns in the dispersion (i.e. spread and spacing) of plant species traits that are frequently associated with competitive ability, in an old-field plant community. In contrast with previous studies, we found no evidence for significant over- or under-dispersion of maximum plant height, maximum plant biomass, or seed mass.

2. These findings hold across three plot sizes (10 × 10 cm, 30 × 30 cm, 50 × 50 cm), and when plot size is measured in terms of number of ramets (50 ramets, 250 ramets or 500 ramets) rather than per unit area. Plot size, however, significantly affected the direction of dispersion observed across test statistics, supporting previous studies that have observed that trait dispersion patterns are sensitive to plot size.

3. While no significant dispersion was detected, dispersion direction, measured as the tendency for a two-tailed test to indicate trends for a given trait, was more frequently observed when analyses were weighted by abundance. Abundance weighted analyses had significantly different dispersion directions compared with presence/absence analyses for one of three traits considered. These findings suggest that abundance weighted analyses may yield more consistent trait dispersion patterns.

4. *Synthesis.* Our results may be interpreted as evidence for limited, if any, functional niche partitioning between co-occurring species via size-mediated differences in rooting depth or physical space niches (i.e. limiting similarity). Alternatively, some species with large differences in competitive traits may avoid competition through niche separation, while others may simply compete asymmetrically, leading to overall patterns of dispersion that cannot be distinguished from random. This interpretation supports recent perspectives that niche and neutral theoretical concepts are not mutually exclusive; both, working together, can be applied to the interpretation of plant community assembly and structure.

Key-words: coexistence, competitive asymmetry, competition, convergence, divergence, limiting similarity, niche separation, over-dispersion, physical space niche, under-dispersion

Introduction

A central goal in community ecology is to understand how species are filtered from the species pool, and organized within communities (Diamond 1975; Taylor *et al.* 1990; Keddy 1992; Weiher & Keddy 1995; Zobel 1997). One group of these 'assembly rules' that has received a great deal of attention is the organization of traits within and among communities. These analyses are increasingly relevant as ecologists explore the influence of several target traits in driving important ecological patterns and processes (Díaz *et al.* 1998; Westoby *et al.* 2002; McGill *et al.* 2006; Westoby & Wright 2006). Trait patterns or 'rules' have been referred to using a variety of terms, including trait convergence/divergence (MacArthur & Levins 1967; Grime 2006), trait over- and under-dispersion (Weiher & Keddy 1995; Weiher *et al.* 1998; Franzen 2004), limiting similarity vs. 'clumping' (Stubbs & Wilson 2004), and trait filtering (Díaz *et al.* 1998; Cornwell *et al.* 2006; Ackerly & Cornwell 2007). These different names arise from subtle differences in what trait pattern is being explored. For example, trait dispersion may refer to some measure of the overall spread of a trait within a given unit of space (i.e. measures of overall spread such as trait range, or variance), or to the 'evenness' of trait spacing among co-occurring species (e.g. variance in nearest trait distance among co-occurring species, mean nearest trait distance, or minimum

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nearest trait distance). For convenience, we will refer to these patterns in general as trait dispersion, although we will discuss the implications of each pattern specifically.

Weiher & Keddy (1995) have generated a series of important theoretical predictions concerning trait dispersion in natural communities, the majority of which have received only limited attention. Weiher & Keddy (1995) predict that the degree to which traits will be over- or under-dispersed will vary along a gradient extending from extremely stressful conditions (caused by environmental adversity) to extremely productive habitats in which species primarily face adversity from competition. Traits related to success under stressful conditions such as drought, disturbance or predation are predicted to be under-dispersed (e.g. similar traits co-occurring more often than expected by chance), while at the other extreme, in communities characterized by 'competitive adversity', Weiher & Keddy (1995) predict that traits associated with competition will be over-dispersed (e.g. greater range of traits or trait spacing than expected by chance), due to increased selection for niche differentiation. In contrast, Grime (2006) predicts that traits associated with competition will be under-dispersed (convergence) within relatively undisturbed, productive communities. Grime (2006) contends that traits related to competition should be under-dispersed, as species with traits conferring relatively poor competitive ability will be competitively excluded in fertile/productive habitats (Buckland & Grime 1996). This is further supported by Freckleton and Watkinson's (2001) findings that interspecific competitive effects are more asymmetric between two species of increasingly different size. Thus, there are two contrasting theoretical bases for predicting the dispersion of traits commonly associated with response to competition, one predicting over-dispersion, perhaps due to limiting similarity/functional niche separation, the other predicting under-dispersion of these traits because only those species with relatively similar competitive ability avoid competitive exclusion.

Empirical evidence thus far has been inconsistent. Weiher *et al.* (1998) present evidence for over-dispersion of species height and shoot biomass, two traits commonly associated with competitive ability, in wetland communities. Stubbs & Wilson (2004), however, reported significant *under-dispersion* of plant height in a New Zealand sand dune community (albeit only at one scale; it was not significantly dispersed at any other scales, and not at all when analyses were weighted by abundance). Franzen (2004) observed that seed size and seed number (per species/per season) were under-dispersed in a Swedish grassland. Predictions by Weiher & Keddy (1995) concerning decreased dispersion with increased scale require further investigation, although work by Stubbs & Wilson (2004) has demonstrated that trait dispersion patterns do vary with the scale of investigation.

Plant species size has been repeatedly implicated as an important determinant of competitive ability (Goldberg 1987; Gaudet & Keddy 1988; Keddy & Shipley 1989; Goldberg & Landa 1991; Rosch *et al.* 1997; Freckleton & Watkinson 2001; Howard & Goldberg 2001; Keddy *et al.* 2002; Warren *et al.* 2002; Fraser & Keddy 2005; Jumpponen *et al.* 2005; Lamb *et al.* 2006). However, it has been pointed out that, in general, relatively small plant species predominate in nature (Aarssen & Schamp 2002; Aarssen *et al.* 2006), and that studies implicating species size have seldom measured the reproductive component of fitness in the context of competition (Aarssen & Keogh 2002). In spite of such objections, thus far, experimental evidence suggests that large species enjoy a competitive advantage over small species and that competitive relationships among coexisting species are predominantly hierarchical (Shipley 1993) and asymmetrical (Weiner 1990). Additionally, seed size has been implicated as an important determinant of seedling competition (Eriksson 1997; Turnbull *et al.* 1999; Leishman 2001). Evidence suggests that large seeded species may be increasingly likely to survive shading or herbivory (Moles & Westoby 2004) and thus may play an important role in competitive response at the seedling stage.

Theoretical and empirical evidence suggests that body size for animals may indeed be responsible for niche differentiation (Hutchinson 1957; Wilson 1975; Bowers & Brown 1982). Similarly, it has been proposed that plant species size may contribute to functional niche differentiation if large and small species have different rooting depths (Berendse 1979, 1981). Although there is some evidence of this (Fargione & Tilman 2005), the predominance of this form of niche separation within communities has not been explored. Recently, Aarssen *et al.* (2006) discussed an alternative theoretical pathway for functional niche separation on the basis of plant species size differences. The tendency for traits related to species size to be over-dispersed may also result from the inability of relatively large species to effectively capture all resources, such that small patches of resources between large species are filled by relatively smaller plant species with lower resource requirements (Aarssen *et al.* 2006). Mechanistically, large species, through the self-thinning process, leave 'physical space niches' available to relatively small species, increasing the likelihood that a small and large species will be found growing together (i.e. over-dispersion). For these reasons we believe that evidence for over-dispersion of size-related traits may be more likely in communities where size plays a strong role in functional niche separation or perhaps under conditions where large plants may ameliorate environmental conditions, enabling small species to colonize nearby (e.g. facilitation in sand dunes, Shumway 2000).

We explore these issues by examining the dispersion of maximum plant biomass, maximum plant height and seed mass in an old-field plant community. We predict that the dispersion of traits related to competitive ability will be suggestive of the degree to which these traits represent functional niche separation (i.e. over-dispersion), or contribute to competitive exclusion and a contraction of trait variation (i.e. under-dispersion). We further investigate the prediction of Weiher & Keddy (1995) that significant patterns of dispersion are scale dependent, by exploring the impact of plot size (Franzen 2004; Stubbs & Wilson 2004). Lastly, we consider the importance of plant size-density relationships on trait dispersion by measuring traits per unit area vs. per unit ramet number (Zobel & Liira 1997).

Methods

STUDY SITE

This research was conducted from June to September 2003 at the Queen's University Biology Station, Chaffey's Locks, Ontario, Canada (44°34′ N, 76°20′ W), in the Lane Sargeant Experimental Field. This field is on abandoned farmland and has been managed under a strict disturbance regime with some sections hayed each year, while others are tilled and/or ploughed on different yearly programs. The portion of the field used in this research had previously been undisturbed for a period of 31 years (neither hayed nor tilled nor ploughed) and is 100 × 27 m in size. The plant species living in the field are largely perennial in habit and are typical of what would be found in old-field vegetation in this region. The five most common species within this plant community (measured in terms of ramet number) were *Poa compressa*, *Carex cryptolepis*, *Phleum pratense*, *Elymus repens* and *Daucus carota*.

DATA COLLECTION

Vegetation plots were located within the field using a random number table and each was assigned to one of the three plot sizes: 10 × 10 cm, 30 × 30 cm, and 50 × 50 cm. Within plots, each ramet was enumerated and identified to species for fixed increments of 10 × 10 cm until the desired plot size was reached. At that point, individual ramets were enumerated and identified as advocated by Zobel & Liira (1997) until a fixed ramet number was reached. For example, fixed plots of 10 × 10 cm were extended to 40 ramets (if that number had not already been reached), 30 × 30 cm to 250 ramets, and 50 × 50 cm plots to 500 ramets. Because the number of ramets per plot for flexible plots (i.e. flexible in terms of area, but fixed in terms of ramet number) was adjusted after collection to match more closely the average number of ramets for the fixed sized plots used, the number of plots defined by area and those defined by ramet number is not equal. The number of plots in each size class was determined such that overall area sampled per plot size was relatively equal, and overall species richness was similar across plot sizes. Species richness per plot varied both within and among the different plot sizes (Fig. 1).

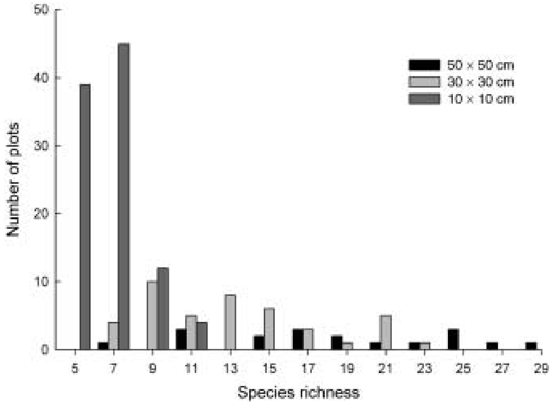

Fig. 1. A frequency distribution of the number of observed plots in each of the three fixed-plot size categories (50 × 50 cm, 30 × 30 cm, 10 × 10 cm) with different species richness values. Each bar represents a range of two species richness values. For example, the first three bars from the left (although only one is visible) represent plots with species richness values of four to five.

After plot data were collected, trait data were collected from specimens in the field. Because biomass, height and seed mass have been identified as being strong predictors of a species' ability to competitively affect other species (i.e. biomass, height), or to respond to competition from surrounding vegetation (i.e. seed mass), species values for these were desired. Because variation in these traits exists in the field, both within and among species, the source of which can not fully be accounted for, the potential height and biomass were assessed as the maximum of each from 10 specimens collected in the field when individuals of each species had reached flowering. This maximum value was used to approximate the trait value that could be obtained in the absence of competition. The traits of interest were those representing the *potential* competitive ability of that species; hence, size data were not collected for all species in each plot. Biomass was measured as dry mass (g) after 10 days at 80 °C in a drying oven. Maximum height was measured as length along the main stem of the sample from the base to the highest point on the plant (including reproductive parts). We included reproductive tissue in this measure of height because reproductive tissue will most certainly deny light to competitors as much as photosynthetic tissue. This is particularly important given that size is generally considered to be important largely in terms of asymmetric competition for light. Seed mass data were collected from the field and from published trait data. Seeds were weighed to 1000th of a gram and were determined as the average of 50 seeds. Within-community variation in the three target traits is highlighted in Fig. 2. Variation in species maximum height and maximum biomass spans two orders of magnitude, while variation in seed mass spans four orders of magnitude (Fig. 2).

DATA ANALYSES

A null modelling approach was employed to test our predictions, as advocated by several authors (Weiher *et al.* 1998; Stubbs & Wilson 2004; Cornwell *et al.* 2006). In this model, we randomized trait data with respect to the site by species matrices (presence/absence and then abundance). This technique, employed by Stubbs & Wilson (2004), conserves community structure entirely, both for presence/absence, and abundance-weighted analyses, while only randomizing the element of interest (i.e. trait values), and is therefore superior to techniques in which the community matrix is randomized (e.g. Weiher *et al.* 1998; Franzen 2004). Our null model examines the probability that plot-level trait relationships across the community significantly differ from what would be expected by chance were those species occupying plots to be randomly assigned traits from all species represented in the community (randomization occurs without replacement). We generated distributions of each test statistic from 3000 randomizations of the trait matrix. Results were checked against tests using 5000 randomizations with no change in results. Because the traits analysed could be either over- or under-dispersed, all tests are presented using two-tailed *P*-values, which favours one direction of dispersion independent of whether results are significant. All *P*-values were calculated as:

$$P = \text{MIN}\,[2S/(3001),\ 2\,L/(3001)]$$

where S and L refer to the number of randomized test statistics greater than or equal to, or less than or equal to, the measured test statistic (cf. Bersier & Sugihara 1997). All tests were performed using Matlab code developed by the authors.

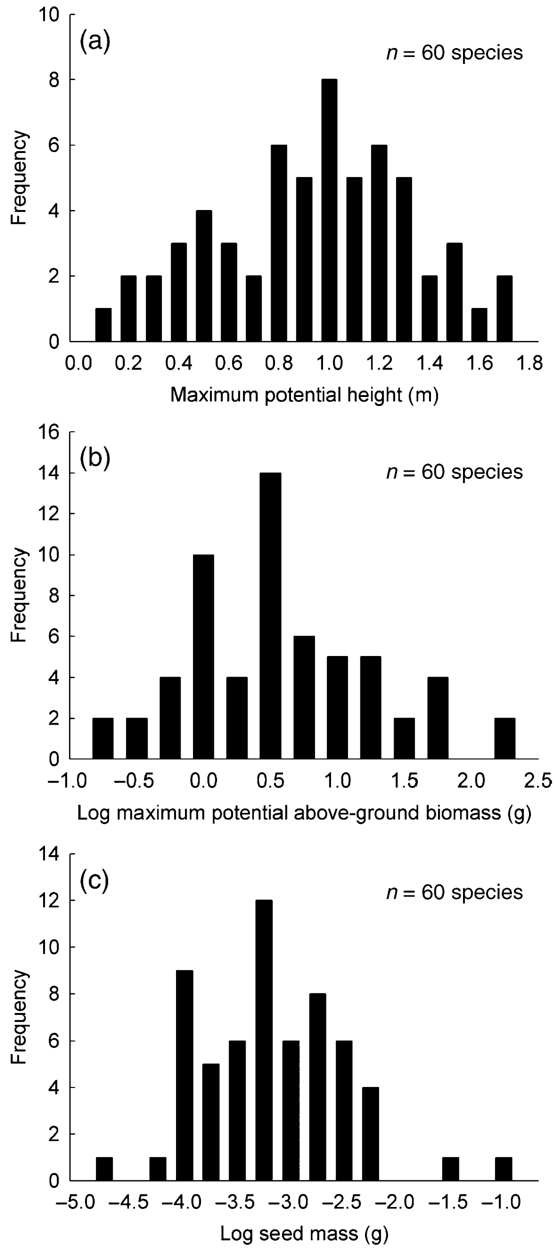

Fig. 2. Three frequency histograms highlighting the within-community variation in species traits within the target old-field plant community. Panel (a) depicts variation in maximum potential species height (m), panel (b) depicts variation in maximum potential above-ground biomass (dry weight in g), and panel (c) depicts variation in species seed mass (g). Both maximum potential biomass and seed mass have extremely right skewed distributions in this community, and thus distributions are $\log_{10}$ transformed for greater clarity.

As suggested by Stubbs & Wilson (2004), a collection of test statistics was used to analyse the dispersion of traits in the target plant community. Our interest is predominantly in testing whether traits commonly attributed to competitive ability are likely to be over- or under-dispersed in the community. To this end, we used the following test statistics, many of which have been previously employed in similar tests (see Weiher *et al.* 1998; Stubbs & Wilson 2004; Cornwell *et al.* 2006). (i) *Range*. We measured the range in target traits within plots, and then used the mean range among plots as a community measure of how variable a trait is, on average, within plots. (ii) *Variance (var)*. We measured the variance in target traits within plots and again used the mean of this value across plots as a community measure of plot level variance in analysed traits. We standardized variance to the range, as advocated by Stubbs & Wilson (2004). (iii) *Mean nearest trait distance (meanNTD)*. This was calculated as the mean nearest Euclidean trait distance between each species (or ramet in abundance weighted analyses) within plots. The mean of plot level meanNTD among all plots was used as the community measure of how spaced traits are within plots. (iv) *Variance in nearest trait distance (varNTD)*. This was simply a measure of the variance in mean Euclidean distances between each species (or ramet) and its nearest species in trait space within plots. As with other test statistics, a mean value was calculated among plot level variances to derive a community level measure of how evenly traits are spaced within plots. (v) *Minimum nearest trait distance (minNTD)*. This was the smallest NTD within plots (Weiher *et al.* 1998). This test statistic was excluded from analyses using abundance data as repeated occurrences of species in plots result in minNTD values of zero in virtually all cases. (vi) *Convex hull volume (CHV)*. As trait relationships may vary in more than one dimension, we use the convex hull volume per plot for all three traits considered, as a measure of n-dimensional trait variation. The mean of all plot-level convex hull volumes in the community was considered as a community level measure of three-dimensional trait variation (Cornwell *et al.* 2006). Trait data were standardized to a mean of zero with unit variance, as advocated by Cornwell *et al.* (2006).

All tests were performed for all three plot scales and for both fixed and flexible plot types for comparative purposes. Significant *P*-values were corrected using the Dunn-Sidak method due to the volume of tests. Such corrections were based on the number of traits considered in the analysis.

Results

GENERAL TRAIT PATTERNS

We found no support for significant dispersion of those traits explored in this study (Table 1). Maximum height, maximum biomass and seed size are no more evenly distributed, nor more aggregated, than would be predicted by chance (minNTD, meanNTD, varNTD; Table 1). Furthermore, trait spread was no greater, and no less, than would be predicted by chance (range, var; Table 1).

PLOT SIZE EFFECTS

Because none of the traits examined were significantly over- or under-dispersed in the target community, it was more difficult to assess the impact of using different plot sizes. However, the two-tailed nature of our test allowed us to assess the consistency of *direction* of dispersion across plot sizes, and across plot types, using chi-squared tests. We tested whether dispersion direction changed more frequently than expected across plot sizes (null expectation of zero difference). This test was conducted across all traits to improve statistical power, but changes were assessed as paired changes per test statistic, per trait. In using this test, we assume that variation in the direction of dispersion is equally likely among test statistics used. We excluded CHV results from these tests, as they are not independent of the individual trait tests. We found no

Table 1. The results of trait dispersion analyses comparing three different fixed plot sizes (10 cm, 30 cm, 50 cm plot sides), and three different flexible plot sizes (40, 250, 500 ramets)

		Fixed			Flexible		
Trait	Test statistic	10 cm	30 cm	50 cm	40 ramet	250 ramet	500 ramet
Max height	Range	0.512*	0.315*	0.565†	0.394†	0.938†	0.538†
	var	0.485*	0.345*	0.774†	0.620†	0.866*	0.651†
	minNTD	0.956†	0.342†	0.510*	0.139†	0.505†	0.183†
	meanNTD	0.683*	0.917*	0.353†	0.250†	0.627†	0.565†
	varNTD	0.112*	0.433†	0.797†	0.545†	0.846*	0.863*
Max biomass	Range	0.607*	0.739*	0.323*	0.896†	0.821*	0.739†
	var	0.978†	0.965†	0.405*	0.731†	0.884†	0.638†
	minNTD	0.307*	0.513*	0.585*	0.379*	0.229*	0.323*
	meanNTD	0.679*	0.857*	0.567*	0.879†	0.956*	0.669†
	varNTD	0.708†	0.738†	0.350*	0.572†	0.750†	0.669†
Seed mass	Range	0.452†	0.440†	0.364†	0.640†	0.358†	0.436†
	var	0.412†	0.516†	0.305†	0.659†	0.479†	0.461†
	minNTD	0.942*	0.219†	0.216†	0.806*	0.377†	0.358†
	meanNTD	0.477†	0.363†	0.235†	0.669†	0.354†	0.361†
	varNTD	0.491†	0.686†	0.319†	0.627†	0.655†	0.652†
All traits	CHV	0.506†	0.927†	0.979†	0.273†	0.659†	0.342†

* and † refer to a tendency towards under- or over-dispersion, respectively, in two-tailed analyses.

significant plot size effect on changes in dispersion direction between 10 × 10 cm and 30 × 30 cm plots ($\chi^2 = 0.26$, d.f. = 1, $P = 0.610$), between 30 × 30 cm and 50 × 50 cm plots ($\chi^2 = 2.4$, d.f. = 1, $P = 0.1213$), but found that dispersion direction changed significantly between 10 × 10 cm and 50 × 50 cm plots ($\chi^2 = 4.26$, d.f. = 1, $P = 0.0389$). We used the same tests among flexible plot sizes and found that dispersion direction did not significantly change across plot size when flexible plots were used (40 vs. 250 ramet, $\chi^2 = 1.67$, d.f. = 1, $P = 0.\ 1976$; 250 vs. 500 ramet, $\chi^2 = 0.6$, d.f. = 1, $P = 0.4386$; 40 vs. 500 ramet, $\chi^2 = 0.066$, d.f. = 1, $P = 0.7973$). Thus there is no significant effect of plot size on the direction of trait dispersion when plots are measured per fixed number of ramets.

FLEXIBLE VS. FIXED PLOT SIZE

We further examined the impact of using plots measured per unit area compared with those measured per fixed number of ramets, using a similar set of within-trait chi-squared tests comparing the number of changes in dispersion direction between comparably sized fixed and flexible plots. For example, we classified a change in dispersion direction between 10 cm and 40 ramet plots, for a given test statistic, as one of four possible changes in dispersion direction for maximum height. We considered such changes between all three plot 'sizes' and for maximum plant height found that dispersion direction changed significantly more often than expected if there was no difference between using the two plot types ($\chi^2 = 5.4$, d.f. = 1, $P = 0.039$), but found no significant effect of fixed vs. flexible plots on the direction of dispersion for maximum biomass, or seed mass ($\chi^2 = 2.4$, d.f. = 1, $P = 0.1213$; $\chi^2 = 0$, d.f. = 1, $P = 1$, respectively). Hence, the importance of using fixed vs. flexible plots to examine trait dispersion appears to be trait dependent.

Table 2. The results of trait dispersion analyses for flexible plot sizes (40, 250, 500 ramets) when analyses are weighted by abundance

Trait	Test statistic	40 ramet	250 ramet	500 ramet
Max height	Range	0.277*	0.223*	0.229*
	var	0.326*	0.347*	0.230*
	meanNTD	0.323*	0.271*	0.517*
	varNTD	0.432*	0.585*	0.938*
Max biomass	Range	0.944†	0.929*	0.852*
	var	0.950*	0.460*	0.363*
	meanNTD	0.777†	0.380†	0.757†
	varNTD	0.741†	0.425†	0.565†
Seed mass	Range	0.350†	0.210†	0.191†
	var	0.761†	0.852†	0.786†
	meanNTD	0.341†	0.190†	0.192†
	varNTD	0.558†	0.222†	0.321†

* and † refer to a tendency towards under- or over-dispersion, respectively, in two-tailed analyses.

ABUNDANCE WEIGHTED ANALYSES

For comparison, we analysed flexible plots both as only presence/absence data, and weighted by species abundance. We found no significant trait dispersion when analyses were weighted by species abundance (Table 2). Differences in dispersion direction among test statistics were generally reduced when analyses take species abundance into account, and chi-squared tests across flexible plot sizes revealed no significant effect of plot size, indirectly demonstrating the impact of abundance on trait dispersion analyses. This was confirmed by examining changes in dispersion direction between flexible plots based on presence/absence data and corresponding plots where abundance was taken into account. We found that analysing maximum height data using abundance changed dispersion direction significantly more often than expected if incorporating abundance data had no effect on dispersion direction ($\chi^2 = 8.33$, d.f. = 1, $P = 0.0039$). Analyses using abundance data did not lead to significant changes in dispersion direction for maximum biomass ($\chi^2 = 2.083$, d.f. = 1, $P = 0.1489$), or for seed mass (zero changes: $\chi^2 = 0$, d.f. = 1, $P = 1$).

TRAIT-BASED TRENDS IN DISPERSION DIRECTION

We further tested for overall trends in the direction of dispersion for each trait, as a way of assessing the tendency for a trait to contribute to niche differentiation in the target plant community. We used chi-squared tests to determine whether traits were more consistently dispersed than would be expected if dispersion direction were assigned randomly. Tests were conducted across plot sizes for each trait, and were assessed for fixed and flexible plots independently (i.e. two tests per trait). We found that maximum biomass showed a significant tendency towards over-dispersion in flexible plots ($\chi^2 = 7.5$, d.f. = 1, $P = 0.0062$), and that seed mass showed a significant tendency towards over-dispersion in both fixed and flexible plots ($\chi^2 = 4.03$, d.f. = 1, $P = 0.0447$; $\chi^2 = 5.633$, d.f. = 1, $P = 0.0176$, respectively). Maximum height showed no significant tendency in dispersion direction for either fixed or flexible plots.

When abundance data were incorporated, maximum height showed a significant tendency towards under-dispersion ($\chi^2 = 6.0$, d.f. = 1, $P = 0.0143$), while seed mass again showed a significant tendency towards over-dispersion ($\chi^2 = 1$, d.f. = 1, $P < 0.0001$). Overall, consistency of dispersion direction was trait-specific and generally more consistent when abundance data were incorporated.

Discussion

GENERAL TRAIT PATTERNS

Our investigation produced no evidence of trait-based organization of species in our target community. The target community was randomly assembled with respect to all three traits considered. This is contrary to the predictions outlined by Weiher & Keddy (1995), suggesting that in plant communities with relatively intense competition (i.e. undisturbed, and lacking in significant environmental stress), traits related to competitive ability should be over-dispersed. Our results are also in contrast to the predictions of Grime (2006) that competitive traits should be under-dispersed due to the exclusion of less competitive species. These findings also contrast those of other studies, which have revealed significant patterns of over- or under-dispersion of multiple traits, including those examined in this study (Weiher *et al.* 1998; Franzen 2004; Stubbs & Wilson 2004). We suggest that these inconsistencies result because traits such as plant height, mass and seed mass contribute to functional niche separation for some species combinations, but may also contribute to competitive asymmetry for other species combinations. Both effects, acting simultaneously therefore, may generate an overall pattern of dispersion that is indistinguishable from what can be expected by chance, depending on which effect predominates. This idea is consistent with the work of Scheffer & van Nes (2006), who demonstrate that co-evolution under competitive conditions can result in species that are sufficiently divergent to coexist through niche differentiation, but can also result in clusters of very similar species that coexist by competing relatively equally. If neither of these two evolutionary possibilities predominates in a particular plant community, we can expect the combination of the two to lead to relatively neutral or random patterns of trait dispersion.

While none of our tests demonstrated significant trait dispersion in either direction, the nature of our two-tailed tests can reveal trends in the direction of dispersion for the traits of interest. Seed mass showed a significant tendency towards over-dispersion, independent of whether fixed or flexible plots were considered. Maximum biomass showed a significant tendency towards over-dispersion, but only when flexible plots were considered, and this effect disappeared when abundance was incorporated into the analysis. Maximum height showed no significant tendency in directional dispersion for either fixed or flexible plots. These results demonstrate that dispersion patterns are sensitive to particular traits and to the use of plots based on a fixed area or fixed number of ramets. It is therefore difficult to conclude anything about the tendency for maximum height and maximum biomass to be dispersed in a particular direction in terms of trait spread (range, variance), the evenness of plot level trait distribution (meanNTD, varNTD), or minimal differentiation in trait value among co-occurring plant species (minNTD).

When we considered abundance-weighted analyses, maximum height tended towards under-dispersion, and seed mass tended towards over-dispersion (i.e. larger range of seed sizes, and more evenly spaced seed sizes tending to co-occur more than expected by chance). This analysis, of course, needs to be tempered with the understanding that all traits were no more under- or over-dispersed than expected by chance, and we bring attention to it only as a way of suggesting that seed mass, the most consistent trait in terms of dispersion direction, may contribute relatively more to functional niche separation than to competitive asymmetry. A theoretical basis for over-dispersion in seed mass has been observed from game theoretical models (Geritz 1995; Fagerström & Westoby 1997; Rees & Westoby 1997; Geritz *et al.* 1999) and the competition-colonization trade-off (Turnbull *et al.* 1999, 2004, 2005). Large seeded species may enjoy an advantage in competing for germination sites against smaller seeded species (e.g. Moles & Westoby 2002; Turnbull *et al.* 2005), while smaller seeded species may have an increased probability of reaching potential sites as a result of a seed size-number trade-off (but see Leishman 2001). Our results stand in contrast to those observed by Franzen (2004), who observed that seed traits were significantly under-dispersed and also do not support a predominant competition-colonization trade-off based on seed size for our old-field community. The inconsistency of results across study sites suggests that different communities may be structured according to different assembly rules. Or perhaps the somewhat idiosyncratic nature of seed dispersal within communities via wind and/or animal vectors may preclude any coherent expectation concerning the dispersion of species according to seed mass within communities.

The incorporation of abundance data in our analyses significantly influenced the observed patterns of trait dispersion for one of the three traits considered. This is most likely to be due to the effect of species intraspecific aggregation patterns, as abundance patterns tended to contribute to an overall tendency towards under-dispersion (except in the case of seed mass). The degree to which intraspecific aggregation affects dispersion patterns is limited by the maintenance of plot-level relative abundance distributions within our null model. Were abundances randomized, rather than species traits, the impact of intraspecific aggregation on trait dispersion would be much stronger as randomized abundances would tend towards greater evenness. In such an analysis, species traits in actual vegetation would generally be significantly under-dispersed, as the test would approximate a significance test for intraspecific aggregation. This is particularly important given that a central goal in some trait dispersion analyses is to test whether similar or different traits are more or less often found co-occurring. Intraspecific aggregation, which is extremely common, especially among clonal plant species, is a form of trait under-dispersion among co-occurring ramets. Intraspecific aggregation has been proposed as a way for competitively inferior species to avoid costly interspecific competitive interactions (Monzeglio & Stoll 2005). If intraspecific aggregation is beneficial to competitively inferior species, but costly to competitively superior species (for which intraspecific competitive effects will be strongest under hierarchical competition), it is again not surprising that overall dispersion of traits related to competition is neutral.

Further, we found that community level, within-plot variation in n-dimensional trait space was not significantly dispersed in a given direction, suggesting that trait space within plots in this plant community is no more contracted or expanded than would be expected by chance. This is perhaps expected, given that the three traits considered in this study are less likely to be negatively traded off than other traits might be (no significant positive or negative correlations among traits; results not shown).

FIXED VS. FLEXIBLE PLOTS

It is intuitive that fewer plants will occupy a plot of fixed size when one or more of the constituent species are large (Oksanen 1996). Given that density is related to size among plant species (White 1980; Enquist *et al.* 1998), and that diversity in fixed plots can be a function of both plant size and density (Oksanen 1996), dispersion patterns measured per unit area will be driven by the contribution of large species to a given plot of fixed area. Further evidence of this effect can be found in work by Weiher *et al.* (1998) and Franzen (2004) showing that the mean NTD was negatively correlated with plot species richness. Therefore, it is not surprising that different trait dispersion findings can be found when flexible plots, defined per fixed ramet number, are used (Zobel & Liira 1997). Our findings suggest that trait dispersion can be measured both as a function of fixed area and as a function of fixed ramet number, and that the use of each, while producing the same result overall in this study, has the potential to alter the observed pattern of dispersion.

PLOT SIZE EFFECTS

Intraspecific aggregation is common within plant communities (e.g. Mahdi & Law 1987; Rees *et al.* 1996), with the potential for species-specific patterns of aggregation driven by factors including environmental patchiness, variation in seed shadow (Willson 1993; Nathan & Muller-Landau 2000), and clonal strategy (Lovett Doust 1981; Pauliukonis & Gough 2004), strong interspecific competition (Turnbull *et al.* 2004) or combinations of these elements (e.g. Humphrey & Pyke 1997; Turnbull *et al.* 2004; Seabloom *et al.* 2005). Patterns of intraspecific aggregation, and the potential for aggregation to scale with plant size, may significantly influence patterns of dispersion such that realized patterns across species may result from a large variety of processes. The degree to which studies of trait dispersion observe consistent trends may be a reflection of how variably these influences act upon communities.

Conclusions

We found no evidence for significant dispersion of traits commonly related to plant species competitive ability across three different plot sizes. Our results add to evidence suggesting that many species traits are neutrally assembled within communities (Weiher *et al.* 1998; Stubbs & Wilson 2004). These results were consistent when analyses were performed on abundance-weighted data, or on plots defined by a fixed ramet number. These findings are contrary to a wide array of predictions in the literature and lend no support to a predominant effect of competition on contracting the average spread of competitive traits in vegetation plots *within* a plant community (Grime 2006), nor the prevalence of co-occurring species possessing either a wider spread of traits, or a more evenly distributed spread of traits (Weiher & Keddy 1995; Stubbs & Wilson 2004), as might be expected if either the competition-colonization trade-off were important in determining community patterns, or if differences in traits related to competition resulted in some form of functional niche separation. These results may signal a combined and competing influence of these two processes, or that variation in these traits neither contributes strongly to competitive success, nor niche segregation in this community, and simply represents some form of ecological equivalence whereby trait variation may result in overall similarity in the fitness of co-occurring species (Aarssen 1983, 1989, 1992; Hubbell 2001, 2005; Marks & Lechowicz 2006).

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