



The assembly of forest communities according to maximum species height along resource and disturbance gradients

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An ongoing debate in ecology concerns the relative importance of competition in driving community patterns, especially along gradients of disturbance and productivity. We used a null model to address this question by testing for non-random organization of forest species according to maximum height, a trait associated with competitive ability for light. Specifically, we compared the species present in 409 different temperate forest plots with the pool of potentially present species ($n = 639$ species), spanning a $50\,000\text{ km}^2$ area of southern Ontario, Canada. In contrast to current theory, coexisting forest species were neither more similar (i.e. convergent), nor more different (i.e. limiting similarity) in maximum height than expected by chance. However, coexisting forest species had larger maximum heights on average, and their maximum heights were more symmetrically distributed than expected by chance, suggesting that competition has reduced the representation of smaller plant species within plots (i.e. higher turn-over of species with smaller maximum heights among forest plots). We explored the possibility that our findings resulted from smaller species having relatively narrower niches; however, a conclusive test of this explanation will require knowledge of fundamental, rather than realized niche breadth. We also tested the prediction that the influence of competition changes along gradients of productivity and disturbance by examining how the effect size of our null model tests changed along these gradients. We observed that species with smaller maximum heights were increasingly under-represented in more productive forest communities, suggesting an increased role for competition in determining species membership in more productive communities. In contrast to theory, however, the effect size of our tests did not significantly change along a gradient of forest disturbance. In summary, we found evidence that maximum species height plays a significant role in driving the non-random organization of plant species among hundreds of mature forest plots, and that this role is more pronounced in more productive forest plots.

How important is competition in the assembly and organization of communities? This question is of central interest to ecologists, and has been the focus of much debate (Diamond 1975, Connor and Simberloff 1979, Zobel 1992). In general, it is accepted that competition plays a role in community dynamics (Schoener 1983, Aarssen and Epp 1990, Goldberg and Barton 1992, Gurevitch et al. 1992, Gotelli and McCabe 2002); however, debate continues over whether, and how, competition's influence should vary across important ecological gradients. This debate is related to predictions arising from plant strategy theories. While current theories differ in details, they generally agree that gradients of resource availability, whether controlled by disturbance and productivity (Grime 1979), or only by disturbance (Taylor et al. 1990) can influence the degree to which competition impacts on

community structure (but see Tilman 1982, 1987, 1988 for disagreement concerning resource/productivity gradients).

Grime's prediction (1979) that competition importance should increase with increasing resource availability, has fueled a great deal of debate (Tilman 1987, Thompson and Grime 1988), and research has yielded mixed results (DiTomasso and Aarssen 1991, Reader et al. 1994, Bonser and Reader 1995, Gaudet and Keddy 1995, Keddy et al. 1997, Pugnaire and Luque 2001, Brooker et al. 2005). Thus, the notion that the importance of competition increases with resource availability, and consequently is of relatively little importance in resource impoverished circumstances, is still very much a matter of debate (Craine 2005, Grime 2007). The prediction that the intensity or importance of competition should increase with a decreasing frequency or intensity of disturbance is more generally accepted, although it has been demonstrated that competition can play a role in communities of annual plant species that endure frequent disturbance (Rees et al. 1996). In general, disturbance will decrease plant density or biomass and increase the ratio of resource supply relative to demand

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resulting in reduced competition among plants (Grime 1979, Taylor et al. 1990).

Exploring the influence of competition along gradients of disturbance and productivity has typically relied on the use of short-term manipulative experiments, which control for other important effects such as herbivory, dispersal and realistic soil conditions (Bonser and Reader 1995). While this approach can reveal the potential for competition intensity to change along gradients, it cannot inform us of whether it does so in natural communities and over extended time periods (Keddy 2007). An emerging, but thus far under-utilized, method for exploring the influence of competition in mature, natural communities is to examine how traits related to competitive ability are organized along important gradients (Weiher and Keddy 1995). These tests generally employ a null model analysis of natural community data to determine whether species are filtered non-randomly from a larger to a smaller scale according to specific traits of interest (Weiher et al. 1998, Stubbs and Wilson 2004, Schamp et al. 2008). For example, null models may address how species traits are organized among plots within a community, or among communities within a region.

There are two predictions about how traits related to competition should be organized along gradients of resource availability. First, Grime (2006) predicts that increasing resource availability will act as a convergence filter such that coexisting species in productive habitats will have more similar traits than expected by chance (i.e. a smaller range or variance in traits). Therefore, under resource rich conditions, less competitive species are competitively excluded, leaving only species with relatively similar competitive traits. Contrastingly, Weiher and Keddy (1995) predict that in productive conditions, competitive traits will be divergent (i.e. larger trait range, larger minimum and mean trait distance, and smaller variance in trait distance). This prediction corresponds with limiting similarity theory, which hypothesizes that past competition has led to niche differentiation and that coexisting species will be sufficiently different as to avoid competition (Stubbs and Wilson 2004). The only direct test of these predictions along an environmental gradient using a null modeling approach found that multivariate trait volume in wetland communities was greater than expected by chance, providing evidence of limiting similarity, and observed that this effect was more pronounced in more fertile conditions (Weiher et al. 1998). Contrastingly, Grime (2006) cites several examples from the literature in support of the convergence of many traits related to highly fertile conditions, although methodological differences make it difficult to compare these examples with the findings of Weiher et al. (1998). One possible reconciliation for the opposing predictions of Grime (2006) and Weiher and Keddy (1995) is that some traits will contribute more to niche differentiation (i.e. limiting similarity), while others may contribute more to competitive ability resulting in different expectations for different traits (Schamp et al. 2008). Evidence thus far suggests that patterns in trait convergence and divergence can vary with trait, scale, and habitat (Stubbs and Wilson 2004, Schamp et al. 2008). It is also possible that some traits will contribute to competitive interactions for some combinations of species, while contributing to niche differentiation for others

within the same community. Under such conditions, patterns for some traits may be indistinguishable from what is expected by chance (Schamp et al. 2008).

In this paper, we test for evidence that competition plays a role in organizing species among 409 natural forest plots in Ontario. Specifically, we investigate whether plant species are organized non-randomly into forest communities with respect to one particular trait, maximum species height, and whether this process changes across natural gradients of disturbance and productivity. Maximum species height was chosen for this analysis for three reasons. First, maximum species height is an important functional trait (Westoby 1997, Westoby et al. 2002) that is frequently associated with competitive ability for light (Gaudet and Keddy 1988, Goldberg and Landa 1991, Rosch et al. 1997, Howard and Goldberg 2001, Warren et al. 2002, Fraser and Keddy 2005), and is therefore an excellent candidate for testing the predictions of Grime (2006), and Weiher and Keddy (1995). Second, maximum species height varies considerably both within and among plant communities, making it an appealing candidate for such analyses. Lastly, maximum species height data is widely available for many species in published floras and can therefore be used in the analysis of large regional datasets. This analysis extends earlier null model investigations of trait organization to forest communities, in which competition for light should play a large role, and is the first to test whether independent disturbance and productivity gradients influence patterns of trait organization across hundreds of naturally occurring plant communities. For convenience, we frequently refer to species with large or small maximum heights as tall and small species respectively.

Methods and material

Forest data

Data were collected as part of the Ecological Land Classification (ELC) project for southern Ontario forests undertaken by the Ontario Ministry of Natural Resources (Lee et al. 1998, Schamp et al. 2003). Data were collected from mature natural forests (> 50 years old) spanning the range of landforms, soils and topographies in the region and therefore capture the full extent of gradients of both productivity and disturbance ($n = 409$). The study spans a 50 000 km² region of deciduous and mixed coniferous–deciduous forests in southern Ontario. The most common tree species are *Acer saccharum*, *Fraxinus americana*, *Acer rubrum*, *Prunus serotina*, *Ostrya virginiana*, *Tilia americana* and *Quercus rubra*. The most common herbaceous species include *Maianthemum canadense*, *Epipactis helleborine*, *Arisaema triphyllum*, *Polygonum pubescens* and *Maianthemum racemosum*.

In each forest plot, all vascular plant species within a 10 × 10 m square were identified; all forests were sampled between 1996 and 2003. This plot size was chosen to be large enough to represent the forest community, but small enough to reduce the influence of habitat heterogeneity (Lee et al. 1998). To remove the potential for bias that results from taller species occurring in a plot but only as small plants, we only listed tree species as present in a plot if

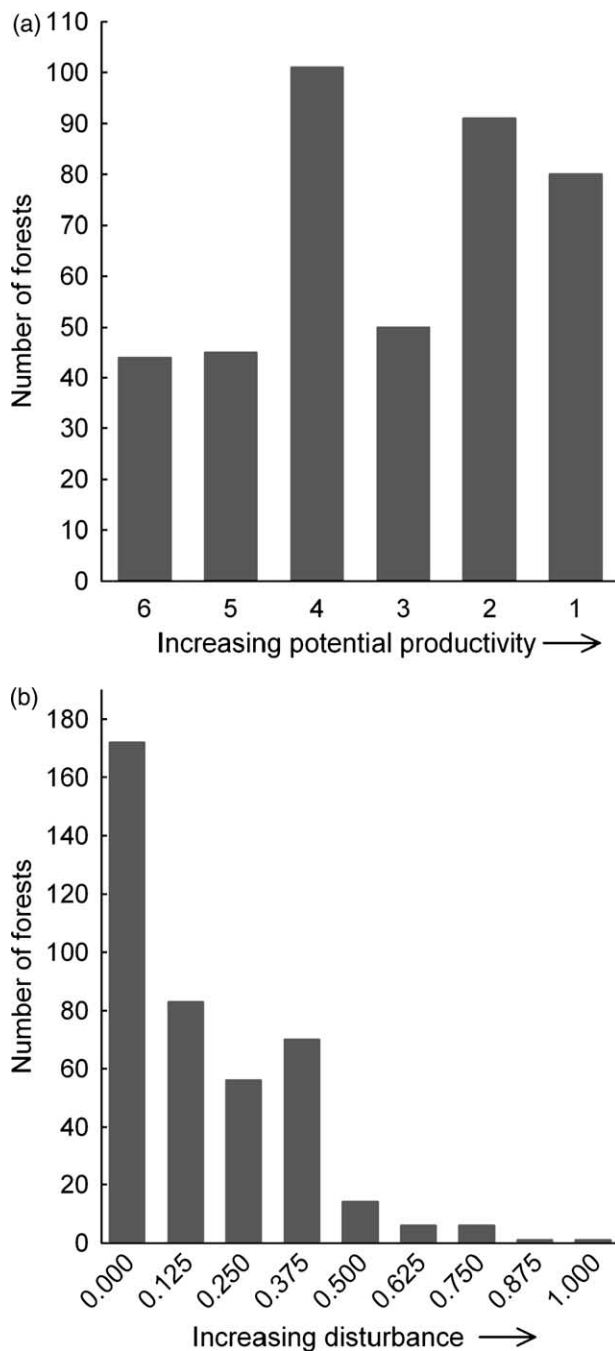


Figure 1. Frequency histograms showing the distribution of forest plots along gradients of potential productivity (a) and disturbance (b). The potential productivity gradient is represented by ordinal classes extending left to right from class 6, which is least productive, to class 1, which is most productive. Disturbance, while calculated as a continuous index, was limited in variation such that all nine different values calculated for forest plots could be used as discrete ordinal bins for this histogram (b).

they had reached the sub-canopy or canopy layer. In some cases, the ELC dataset consisted of multiple plots in the same forest; only one plot per forest was included in the analysis to set a baseline for statistical independence. Also, because forests varied greatly in size and connectivity, the criteria of plots being in separate forests was sometimes

unclear. Therefore, plots used in analyses were limited to those that were greater than one kilometer apart.

To obtain species-specific trait data, we collected data on maximum species height for each of the 639 species observed in our forests data from published floras (Gleason and Cronquist 1991). For tree species, we used maximum height data collected from our study region as part of the ELC project. The maximum potential height for tree species was the maximum height per species observed from 5900 field measurements of 67 tree species.

Forest productivity

Forest plots were classified according to their production potential for forestry using a system of classification based on annual projected yield (Schamp et al. 2003). This classification system is based on a habitat's potential for the growth of native tree species measured as wood volume per land area, and is based on forests throughout Canada (Environment Canada 1965). The required soil data for CLI productivity classification includes: effective texture, moisture, drainage, and depth to bedrock. As part of the ELC project, these data were collected for each forest from a soil pit dug near the centre of each plot (Lee et al. 1998, Schamp et al. 2003). Soil characteristics were then used in conjunction with CLI criteria to place each forest plot into a potential productivity class ranging from the most productive class, class 1 ($>7.8 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) to the least productive class, class 6 ($0.8\text{--}2.1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$; Dept of Regional Economic Expansion 1970). Potential productivity varied substantially across forests in Ontario, with intermediate-to-productive forests being most common (Schamp et al. 2003) (Fig. 1a).

Forest disturbance

Disturbance data were also collected for each forest plot. These are predominantly presence/absence data for 12 classes of disturbance that have the potential to affect vegetation (Table 1). For some disturbance classes, companion data were available identifying how recently the disturbance took place (Table 1). For each forest, and for each of the 12 disturbance classes, a rank of one, two or

Table 1. A list of disturbance sources recorded for forests in the Ecological Land Classification for southern Ontario forests. Asterisks indicate disturbances for which temporal data (i.e. time since disturbance), was also recorded.

Disturbance
1. Wood harvest*
2. Agriculture*
3. Seasonal flooding
4. Disease
5. Pests*
6. Wind damage*
7. Insect outbreak*
8. Trails
9. Fire*
10. Plantation species
11. Maple syrup operation
12. Misc. human disturbance

three, was assigned according to how severe, or how recent the disturbance was (i.e. 12 scores of 1–3 for each forest). A value of one represents either a less severe or a less recent disturbance while a value of three represents a very recent disturbance, and a value of two is intermediate. For those disturbance classes without data on when the disturbance occurred, we assigned a value of one, unless, as in the case of seasonal flooding, it is implied that disturbance is recent; in this case, the disturbance was assigned a value of three. For those disturbances that included information on how recent the disturbance was, a one was assigned if the disturbance occurred prior to the year 1940, a two was assigned if disturbance occurred between 1940 and 1980, and a three was assigned if the disturbance was more recent than 1980. While some of these disturbances will most certainly have greater impacts on vegetation than others, because their impact was not directly measured (i.e. in terms of plant damage or mortality), we weighted each disturbance class equally. Consequently, our disturbance index was calculated as the sum of all disturbance values per forest plot, divided by the maximum disturbance value recorded among forest plots, such that the index ranged between zero (completely undisturbed) and one (the observed maximum of disturbance). While variable across forests in this region, disturbance tended to be relatively low (Fig. 1b).

Data analyses

We used a null model to test our predictions (Schamp et al. 2008). In this model, we randomized trait data (maximum species height) with respect to the site by species presence/absence matrix. This method of randomization conserves community structure (i.e. species richness per forest) while randomizing only the trait values among all observed forest species. This model tests the probability that plot level trait distributions differ significantly from what is expected if traits were assigned to species at random (without replacement). We generated distributions of each test statistic from 3000 randomizations of the trait matrix. Because the test statistics employed could be either greater or less than expected by chance, our procedure was analyzed as a two tailed test with *p*-values calculated as:

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

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 (Bersier and Sugihara 1997). All null model tests were performed in Matlab using code developed by the authors.

Table 2. A summary of predictions demonstrating how each test statistic provides evidence in support of a specific theoretical prediction. Where no theoretical prediction is listed, no mechanism has been proposed to drive such a result.

Test statistic	Observed > expected	Observed < expected
Mean	size-advantage	size-disadvantage
Skew	size-advantage	size-disadvantage
Range	limiting similarity	convergence
MeanNTD	limiting similarity	convergence
VarNTD		limiting similarity

A collection of test statistics was used to analyze trait organization among forest plots and address specific predictions concerning how competition may be shaping forest composition (Table 2): (1) Mean – this tested whether species that were present in forest plots tended to be taller than expected by chance. This test statistic has not previously been employed, but is useful for testing whether smaller or larger trait values are favoured. (2) Skew – this is a measure of distribution symmetry and inequality. Species size distributions are consistently right-skewed (positively skewed) across habitats and across scales, although the degree of skew varies (Aarssen and Schamp 2002, Aarssen et al. 2006). Changes in skew can therefore provide further detail concerning whether taller or smaller species are more or less favoured in forest plots than expected by chance. (3) Range – this was calculated as the maximum height recorded per plot minus the minimum height recorded for the same plot. Range of maximum height was used as a measure of trait variation. If the range of a trait is larger than expected by chance, this indicates evidence supporting limiting similarity while a smaller range than expected suggests trait convergence (Grime 2006; Table 2). (4) Mean nearest trait distance (meanNTD) – this was calculated as the mean nearest Euclidean trait distance between each species within forest plots. The mean of plot level meanNTD among all plots was used as the measure of how spaced traits are within forest plots. Higher NTD values than expected support limiting similarity theory (Weiher and Keddy 1995), and smaller meanNTD values suggest trait convergence (Grime 2006; Table 2). (5) Variance in nearest trait distance (varNTD) – this is a measure of the variance in Euclidean distances between each species and its nearest species in trait space within forest plots and indicates how evenly species are spaced in terms of maximum species height. Values of varNTD that are lower than expected have been cited as evidence for limiting similarity (Stubbs and Wilson 2004; Table 2).

We also tested whether species organization according to maximum species height changed along gradients of forest productivity and disturbance. We introduce a new method for testing how trait organization changes along environmental gradients. We used rank correlations to compare effect sizes (*z*-scores) of our tests among forests spanning our disturbance and productivity gradients (both ordinal variables). *z*-scores for each forest plot and each test statistic were calculated as (O-M)/S, where O is the observed value for each test statistic and forest plot, and M and S are the mean and standard deviation respectively for each test statistic across 3000 randomizations of the trait distribution for that plot. The independence of disturbance and potential productivity was assessed using a contingency table analysis.

Results

Trait organization among forest plots

Species within plots were significantly taller than expected by chance (i.e. higher mean species size than expected; *p* < 0.0001, Table 3). Further, species maximum height

Table 3. The results of null model tests exploring significant differences in forest size distributions (observed) relative to what is expected if species were organized within forests randomly with respect to maximum species height (expected). Results were calculated as an average across $n=409$ forest plots. Bold values indicate significance at $\alpha=0.05$. *indicates a finding that has traditionally been associated with support for limiting similarity, but because of its relationship with skew, is also consistent with a size-advantage.

Test statistic	p-value	Obs > Exp	Obs < Exp	Theory support
Mean	<0.0001	obs > exp		size-advantage
Skew	<0.0001		obs < exp	size-advantage
Range	0.094	obs > exp		
MeanNTD	0.904	obs < exp		
VarNTD	0.0153		obs < exp	limiting similarity*

distributions were significantly less skewed than expected by chance, ($p < 0.0001$, Table 3). These findings indicate that taller species are over-represented, and smaller species are under-represented within forest plots in the study region and support a size-advantage in competition among forest species.

The range of maximum species height within forest plots was no larger or smaller than expected by chance ($p = 0.094$, Table 3), which does not support predictions related to convergence (Grime 2006) or limiting similarity (Weiher et al. 1998). However, coexisting species were more evenly spaced in terms of maximum height than was expected by chance (i.e. varNTD was smaller than expected; $p < 0.0001$, Table 3), consistent with predictions from limiting similarity theory. On the other hand, coexisting forest species were no more different than one another in maximum height, on average, than expected by chance (i.e. meanNTD was no larger or smaller than expected by chance, $p = 0.904$, Table 3), which is contrary to the predictions of limiting similarity theory.

Trait organization and gradients of productivity and disturbance

The influence of productivity and disturbance gradients on species organization was assessed separately because a contingency table analysis demonstrated that these gradients are independent for our forest plots ($\chi^2 = 35.9$, $DF = 40$, $p = 0.656$).

The effect size of our null model tests changed significantly across forest productivity classes. In particular, the observation that species coexisting in a given plot had larger maximum heights than expected by chance was significantly greater in more productive forests ($\rho = 0.188$, $p < 0.0001$; Fig. 2a). Likewise, the finding that forest species size distributions are less skewed than expected by chance was also significantly greater in more productive forests ($\rho = -0.146$, $p = 0.003$; $\rho = -0.188$, $p < 0.0002$ respectively, Fig. 2b). Thus, tall species were increasingly over-represented, and smaller species were increasingly under-represented as productivity increased. Effect sizes for other test statistics did not vary significantly with forest productivity suggesting that any role for limiting similarity in forest communities is not influenced by forest productivity. Effect sizes for our tests did not change along a gradient of disturbance, independent of the test statistic used (Table 4).

Discussion

Organization of species according to maximum height

We found evidence for assembly rules governing the composition of forests in the southwestern region of

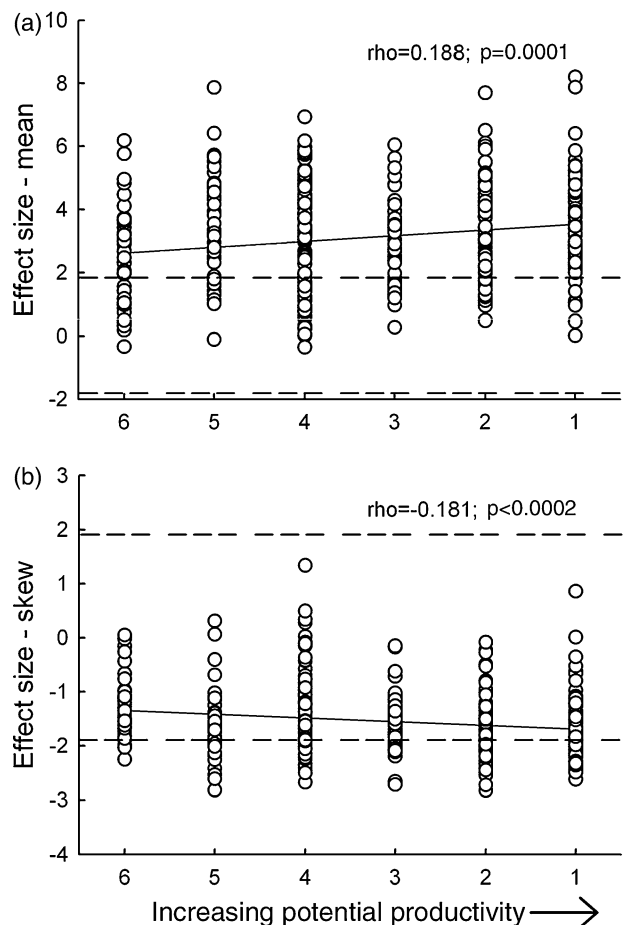


Figure 2. Rank correlations between potential forest productivity and effect sizes for two test statistics: mean (a), and skew (b) respectively. Due to the high level of variation in these correlations, we have included trend-lines to identify significant correlation trajectories. y-axes represent z-scores, which are a standardized measure of the degree to which the test statistic differed from what was expected by chance. As such, statistically significant effect sizes ($\alpha=0.05$) are indicated when plots (each data point is a forest plot) are less than -1.96 (observed < expected), or greater than 1.96 (observed > expected). Significance boundaries are indicated by dashed horizontal lines at these values.

Table 4. Results of rank correlation analyses between disturbance, and all seven test statistics used to measure how species were filtered into forest plots with respect to maximum species height per plot ($n = 409$ for each correlation).

Test statistic	rho	p-value
Mean	0.0367	0.459
Skew	-0.0188	0.705
Range	0.0780	0.115
MeanNTD	0.0518	0.296
VarNTD	0.0204	0.680

Ontario, Canada (Weiher and Keddy 1995). Communities of forest plant species in this region are organized non-randomly with respect to maximum species height. This finding stands in contrast to findings that herbaceous plant species are organized randomly with respect to maximum height among plots within an old-field plant community (Schamp et al. 2008). Specifically, species in forest plots were significantly taller than expected by chance, and forest size distributions were less skewed (i.e. more symmetrical) than expected by chance (Table 3). These results are consistent with the traditional prediction that competition for light will be important in structuring forest communities, and that a larger maximum height will confer a competitive advantage (Table 3). These results are also consistent with the predictions of Grime (1979) and Taylor et al. (1990) that competition will be intense and important in later-successional communities (i.e. forests) that are more distantly removed from large-scale disturbance, and with studies supporting a size-advantage in competition (Goldberg and Landa 1991). Importantly, the finding that the range of maximum species height in forest plots is no smaller than expected by chance seems contrary to the notion of a size-advantage because it means that the presence of tall species does not lead to the exclusion of all small species (Aarssen and Schamp 2002, Aarssen et al. 2006). In fact, in every study site, the vast majority of resident species are relatively small, i.e. species size distributions are strongly right-skewed. Thus, if our results are to be interpreted as evidence of a size-advantage, it must necessarily be only a partial and very limited advantage, with other traits (related to survival and reproduction) also probably contributing to competitive ability (Aarssen and Keogh 2002).

We also found evidence that coexisting forest species were more evenly spaced in terms of maximum height than was expected by chance (i.e. observed varNTD < expected; Table 3), a finding that suggests support for limiting similarity theory (Stubbs and Wilson 2004). However, changes in varNTD, or how evenly distributed species are with respect to maximum height, are related to how skewed species size distributions are within forest plots. Thus, varNTD may not be useful for testing predictions related to limiting similarity theory (Stubbs and Wilson 2004, Schamp et al. 2008). In support of this notion, we observed that coexisting species are no more different in maximum species height than expected by chance (i.e. range, meanNTD, Table 3) offering no support for the predictions of limiting similarity theory. Thus, our results are all consistent with a relative under-representation of small species and over-representation of tall species in forest plots. Given that small species are far more common than tall

species (Aarssen and Schamp 2002) this necessarily means that there is significantly greater turnover of small species among forest plots within this region (i.e. higher beta diversity for small plant species), which is confirmed by a positive correlation between maximum species height and the number of forest plots in which species are found ($r = 0.299$, $p < 0.0001$).

To clearly illustrate these results, Fig. 3 shows how species filtering alters the distribution of maximum species height in forest plots (Fig. 3c), relative to what would be expected if species were filtered randomly with respect to this trait (Fig. 3b). The regional- and plot-scale distributions of maximum species size depicted in Fig. 3 are less positively skewed than actual distributions to more clearly visualize distribution changes across scales.

While our data are consistent with the interpretation that competition is important in organizing species among

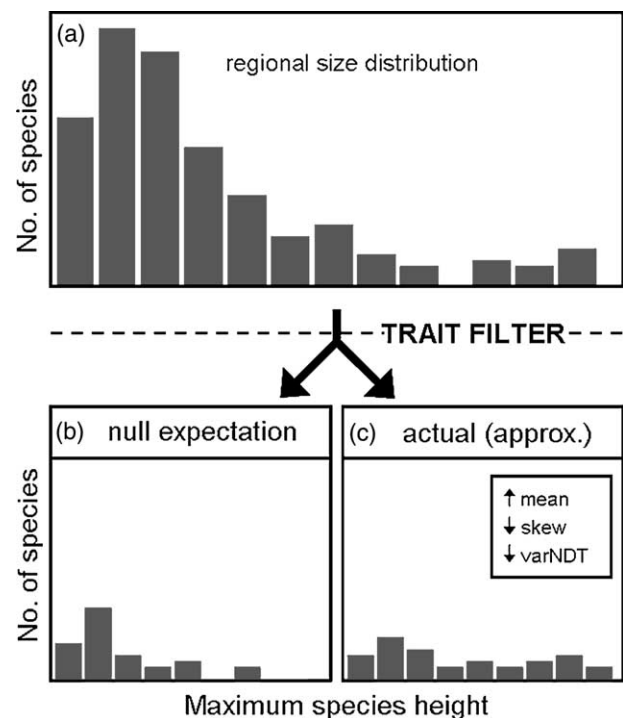


Figure 3. A diagram depicting how plant species are filtered into forests from the regional pool, according to maximum height (a). With respect to maximum height, species may be filtered neutrally, or randomly (b), or non-randomly, and directionally, as was observed for our actual forest data (c). Panel (a) is an approximation of the species size distribution for our study. In reality, the distribution is even more skewed and biased towards small plant species than is depicted. We used this approximation to visualize changes better. Panel (b) is an estimation of what size distributions, on average, would look like if size were assigned to species in forests randomly from the regional pool (our null hypothesis); consequently, it more closely approximates the trends in the regional pool size distribution (a). Panel (c) is an approximation of the average species size distribution for actual forest plots in our study. This distribution is much more symmetric than the null expectations due to the over-representation of tall species (i.e. trees), and under-representation of small species. Panel (c) visualizes how actual forests had a larger mean, and lower skew, variance/range and varNTD than expected if height were filtered randomly (b).

forest plots and that larger maximum height confers a competitive advantage in these light-limited communities, two alternative explanations are worth considering. First, it is important to recognize that all of the small species in this study successfully coexist with tall species in at least one forest plot. Hence, the greater-than-expected rate of small species turn-over observed among forest plots may be due to intense competition between the vastly more numerous small species for limited resources (i.e. space). Small species are likely differentiated from larger species in terms of their 'physical space niches' (Aarssen et al. 2006) – i.e. the amount of physical space necessary to contain/provide enough resources for a plant to reach the size necessary to produce offspring. Obviously, trees require much larger physical space niches compared with understory herbs. It follows that small species will overlap widely with respect to physical space niche, and therefore may compete more intensely with other small species than with taller species. In addition, competitive inter-relationships between small species may differ in nature among different forest habitats – i.e. competitive ability may be a product of genotype (or species) $\times$ environment interaction, involving different roles for different traits in different habitat types (Aarssen 1983), resulting in different combinations of small species in different forests (i.e. higher β -diversity).

To explore the possibility that competition among small species is more intense, we tested whether small species are more subject to competitive sorting with a post-hoc null model analysis of co-occurrence (sensu Gotelli and McCabe 2002). We tested whether smaller herbaceous species, or taller woody species in our forest plots had higher C-scores (Stone and Roberts 1990) than expected if forest plots are assembled randomly (3000 randomizations, each using 30 000 sequential swaps). A higher C-score than expected by chance signifies lower co-occurrence and therefore increased structuring by interactions (Gotelli and McCabe 2002). Our study forest plots had significantly higher C-scores than expected by chance (herbaceous: $p = 0.003$; woody: $p = 0.003$). We compared effect sizes of these tests and found that interactions appear to play a greater role in the organization of woody species among forest plots (herbaceous: z -score = 15.48; woody: z -score = 22.33). Thus, we found no support for an increased influence of competition among smaller, herbaceous species compared to taller woody species.

Another explanation for our results is that species with smaller maximum heights have narrower fundamental niches than those with larger maximum heights, and thus the presence of a given small species in a forest may depend more on niche structure than on competition with tall species (Aarssen et al. 2006). To explore this possibility, we tested for a relationship between niche breadth and species size among forest plants. Because many estimates of niche breadth are based on presence/absence data, and it has been argued that determining specialization requires a null model (Pither and Aarssen 2005), we estimated niche breadth only for those species that could be distinguished as having significantly narrower, or significantly wider niche breadths than expected by chance under this null model. We calculated niche breadth for these forest species along gradients of moisture and drainage as the range of the environmental gradient that each species spans. We found

that relative specialization along gradients of moisture and drainage were unrelated to species size ($r = -0.024$, $p = 0.845$; $r = 0.073$, $p = 0.55$, respectively). These results then do not support the explanation that increased turn-over of smaller species among forest plots is due to small species having narrower niches. Another study of forest species in Germany found no relationship between niche breadth for pH and species size ($r = 0.005$, $p = 0.975$, $n = 35$; Annette Kolb, pers. comm.). Nevertheless, we were able to estimate realized niche breadth for only two environmental gradients and therefore cannot rule out the possibility that smaller species have narrower fundamental niches than taller species.

Trait organization and productivity

We found evidence that species organization according to maximum height changed significantly and directionally along a gradient of potential forest productivity (Fig. 2), providing support for the finding by Weiher et al. (1998) that a gradient of productivity can influence species organization according to an important functional trait. The mean of species maximum height became increasingly higher than expected by chance with increasing potential forest productivity (Fig. 2a) and the skew of species maximum height became increasingly lower than expected by chance with increasing forest plot productivity (Fig. 2b).

As with our general results, these results may be interpreted as support for the prediction that competitive filtering of species is more important in more productive communities (Grime 1979, Sammul et al. 2000, Brooker et al. 2005). Thus, in productive communities, a size-advantage in competition may be accentuated, with taller species increasingly over-represented and smaller species increasingly under-represented as a consequence. If a size-advantage in competition for light is more important in more productive forests, more productive forests should, on average, have more closed canopies. We tested this prediction and found that canopy openness for a subset of these forests (estimated using hemispherical canopy photographs and GLA software; Frazer et al. 1999), is not significantly lower in more productive forests ($n = 152$, $r = 0.063$, $p = 0.438$; Schamp and Aarssen unpubl.). While this test is limited in nature, it does not provide support for the interpretation that increased competition for light in productive forests leads to the competitive exclusion of a greater number of small species.

While our co-occurrence analysis suggests that small species are not competing more intensely than tall species in this region, it is likely that the reduced representation of smaller species in productive forests results from an increased importance of competition in general, both between tall and small species, but also among small species, contributing to the observed changes in species organization according to size with increasing potential forest productivity (Fig. 2)

Trait organization and disturbance

There was no relationship between disturbance level and the organization of species into forests according to maximum

species height (Table 3). This did not support the prediction that an increased level of disturbance would reduce the relative importance of competition in structuring forest communities (Weiher and Keddy 1995), and is consistent with the assertion that competition can still be important in the presence of disturbance (Tilman 1987). One possible explanation is that forest plots were not generally found near the forest edge, where the effects of disturbance on community structure can be high (Oliveira-Filho et al. 1997). Therefore, gaps generated by disturbances in our study forests may generally be captured by species from the surrounding forest resulting in relative abundance changes, but little change in the list of species present. It is possible that analyses that weight trait scores by abundance may have revealed this effect (Stubbs and Wilson 2004, Schamp et al. 2008).

Limitations to our data on disturbance may also have contributed to this result. For example, the weighting system used to generate the disturbance index may have underestimated the effects of some disturbance classes, while overestimating the effects of others. This is especially true for disturbance classes that are biased in their probable effects on the mortality of plants of different size. For example, the impact of wood harvesting, which concentrates mortality on tall species (i.e. trees), would likely have a strong effect on the species size distribution compared with disturbance from trails, which largely affect smaller species. Further study is required to examine whether, and how disturbance impacts upon the organization of species according to important functional traits (Weiher and Keddy 1995, Grime 2006).

Conclusions and implications

Our results identify and quantify a new non-random pattern of plant species organization among forests in southern Ontario, Canada, according to maximum species height. These results provide a baseline for comparison with forest communities in other regions, and for comparison with other habitat types. Our results do not fit clearly into the framework of trait convergence or divergence (*sensu* Weiher and Keddy 1995, Stubbs and Wilson 2004, Grime 2006), but instead reveal a new pattern wherein relatively smaller species are under-represented in forest plots. We found evidence supporting a role for competition in driving these patterns, and that this role appears to be emphasized in more productive communities. We found no conclusive evidence of limiting similarity among coexisting forest species, in contrast to previous findings that coexisting wetland species are more different in height than expected (Wieher et al. 1998) and less different in height than expected in sand dune communities (Stubbs and Wilson 2004). Perhaps this indicates a tendency for differences in maximum species height to contribute less to niche separation in forest communities where height may be an advantage in competition for light. It is possible that size differences between species may contribute to both competitive interactions and niche separation (i.e. limiting similarity) within forest communities, which may explain difficulties

in distinguishing between mechanistic explanations for our results. This possibility is supported by recent theoretical predictions that evolution under competition can lead to both increased similarity (i.e. convergence) and increased differentiation (Scheffer and van Nes 2006).

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