

## Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities

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### Summary

**1.** Understanding the processes by which species sort themselves into communities remains a central puzzle for attempts to maintain biodiversity. It remains unclear whether any single assembly process is generally dominant or whether the influence of contrasting processes varies in a predictable way relative to biotic and abiotic gradients. Abundance-weighted niche overlap between species provides a powerful means of contrasting two major assembly processes – niche complementarity and environmental filtering.

**2.** We examined mean overlap for four vegetative functional traits, relative to that expected when abundances were randomly allocated to species co-occurring in experimental plots in a wet meadow. This provided a test of whether any single assembly process prevailed for the meadow as a whole and across all traits. The effects of mowing, fertilization and dominant species removal, and associated gradients of Simpson's dominance and biomass on the niche overlap of plots, were also examined.

**3.** Niche overlap was higher than expected at random for three of the four traits studied (height, leaf and stem dry matter content, leaf C:N ratio). However, niche overlap was lower than expected for specific leaf area.

**4.** Mowing was the treatment with the greatest effect on both niche overlap and biomass, with overlap significantly lower in the absence of mowing for three of the traits, while biomass was lower in mown plots. For three of the traits there was evidence of a significant decrease in overlap with increasing biomass, but not increasing dominance. None of the significant mowing effects on overlap remained when the effect of biomass had been removed.

**5. Synthesis:** These results suggest that the importance of niche differences between species in structuring grassland communities should increase with increasing biomass and decrease with disturbance in grassland communities. They also emphasize that contrasting community assembly processes may occur for different niche axes, even within a single community.

**Key-words:** coexistence, complementarity, fertilization, functional trait, meadow, mowing, null model, plant population and community dynamics, productivity, removal

### Introduction

Niche complementarities (i.e. niche differences between species) have long been identified as potential key drivers of species coexistence (e.g. Darwin 1859; Gause 1934; MacArthur & Levins 1967; Silvertown 2004), and, more recently, enhanced ecosystem functioning (Loreau & Hector 2001; Scherer-Loren-

zen 2008; de Bello *et al.* 2010b). The limiting similarity principle of MacArthur & Levins (1967) predicts that competition between similar species should produce patterns where co-occurring species are more dissimilar in a niche than expected by chance (Stubbs & Wilson 2004; Mason & Wilson 2006) and where the most abundant species within a community occupy different niches (Mason *et al.* 2008b). Conversely, environmental filtering (related to the 'species sorting' concept of metacommunity research; Leibold *et al.* 2004) selects the suite

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of traits which maximizes the ability to acquire limiting resources given local environmental conditions and in competition with co-occurring species (Grime 2006). This should produce patterns where co-occurring species are more similar than expected by chance (Leibold 1998; Mayfield & Levine 2010) – as frequently revealed by empirical studies (Cornwell, Schwillk & Ackerly 2006; Mason *et al.* 2007; de Bello *et al.* 2009) – and the most abundant species occupy similar niches (Grime 2006).

Despite the conceptual simplicity of the limiting similarity principle, field evidence is somewhat sparse, perhaps due to the influence of confounding factors, such as environmental heterogeneity, on community structure (Mahdi, Law & Willis 1989; Wilson 1999; Silvertown 2004; Stubbs & Wilson 2004). Tests of limiting similarity have mainly combined species niche information with analysis of co-occurrence within (Stubbs & Wilson 2004; Mason & Wilson 2006; Mason *et al.* 2008a) and between communities (Armbruster, Edwards & Debevec 1994; Winston 1995). Examination of the relationship between niche overlap and relative abundance offers a test that removes some of the confounding factors often thought to obscure evidence for limiting similarity (Mason *et al.* 2008b). Relative abundance gives an indication of a species' ability to acquire resources under local environmental conditions and in competition with co-occurring species (Whittaker 1965; Grime 2001). Consequently, in linking functional traits and biomass we can view contrasting assembly processes as opposing pressures impacting on a species' ability to acquire resources. By reframing assembly processes in this way, it becomes apparent that it may be possible for contrasting processes to act along different niche axes, as resource acquisition might be enhanced by trait convergence for some axes and by complementarity for other axes (Leibold 1995; Swenson & Enquist 2009).

Mason *et al.* (2008b) proposed a method for distinguishing between assembly processes by testing whether observed biomass-weighted overlap in functional traits between co-occurring species differs from that expected when species abundances are randomly allocated *within* communities. Lower overlap than expected provides evidence that a species' ability to capture limiting resources is enhanced by complementarity with abundant co-occurring species. Higher overlap than expected provides evidence that the ability to capture resources is enhanced by convergence on an 'optimum' trait value (Mouillot, Mason & Wilson 2007). Thus, by comparing niche overlap to random expectation for independent

functional traits we can test whether similar assembly processes act along separate niche axes.

This study focuses on a wet meadow where fertilizer, mowing and dominant species removal treatments have been applied in a full factorial design. We first tested for evidence that either niche complementarity or environmental filtering is generally prevailing within the experiment, by comparing observed mean abundance-weighted overlap with that expected at random across all experimental plots. We also examined how the ratio of observed to expected overlap varies with experimental treatments and biotic properties, such as standing biomass, to test predictions based on the general hypothesis that niche complementarity should increase as the potential for competition intensifies (Table 1).

## Materials and methods

### STUDY SITE, EXPERIMENTAL TREATMENTS, SAMPLING AND COLLECTION OF TRAIT DATA

The grassland experiment used for this study is part of a long-term project studying the effect of mowing, fertilization and removal of the dominant species (*Molinia caerulea*) on vegetation structure in semi-natural meadows. The experiment was established in 1994 in a full factorial design in a wet meadow in South Bohemia, Czech Republic, Central Europe (see Lepš 2004 for details). Three replicates of each factorial combination of mowing, fertilization and dominant removal were used. Mowing was performed annually in June and fertilization consisted of 65 g m<sup>-2</sup> of commercial NPK (12% N, 19% P and 19% K, since 2003, the commercial fertilizer Cererit was used in the same dosage, with 8% N, 13% P and 11% K) applied in two dosages (50 g m<sup>-2</sup> in autumn and 15 g m<sup>-2</sup> in spring, from 1997 the total dosage was applied in spring). *Molinia caerulea* was manually removed by screwdriver in April 1995 with a minimum of soil disturbance. Subsequent removals were made annually, where required. The size of each plot was 2 × 2 m. Species composition was characterized as the sum of dry biomass across five harvests, taken within 1 year – in April, June (before mowing), August and October 2004, and then in March 2005. At each date, two square quadrats (20 × 20 cm) were harvested and sorted to species-level identification. In total, 10 squares were harvested for each plot. The intention was to obtain an integrative measure of species biomass across different seasons and to account for within-plot heterogeneity.

Lepš (2004) found that correlations between species abundances across years were generally positive, so that the abundance rankings are unlikely to have changed much in response to climatic variability. He also demonstrated that dominant species showed much lower

**Table 1.** Main hypotheses tested and reasoning for each

Hypothesis	Reasoning
Niche overlap should decrease as biomass increases	Competition for light increases with biomass
Niche overlap should decrease with dominance	Presence of one or several competitive dominants may indicate that subordinate species experience more intense competition
Niche overlap should increase with mowing	Mowing reduces biomass and hence light competition and selects for species that can either tolerate or avoid mowing
Niche overlap should decrease with fertilization	Fertilization will tend to increase biomass
Niche overlap should increase with the removal of a competitive dominant	Removal will decrease dominance

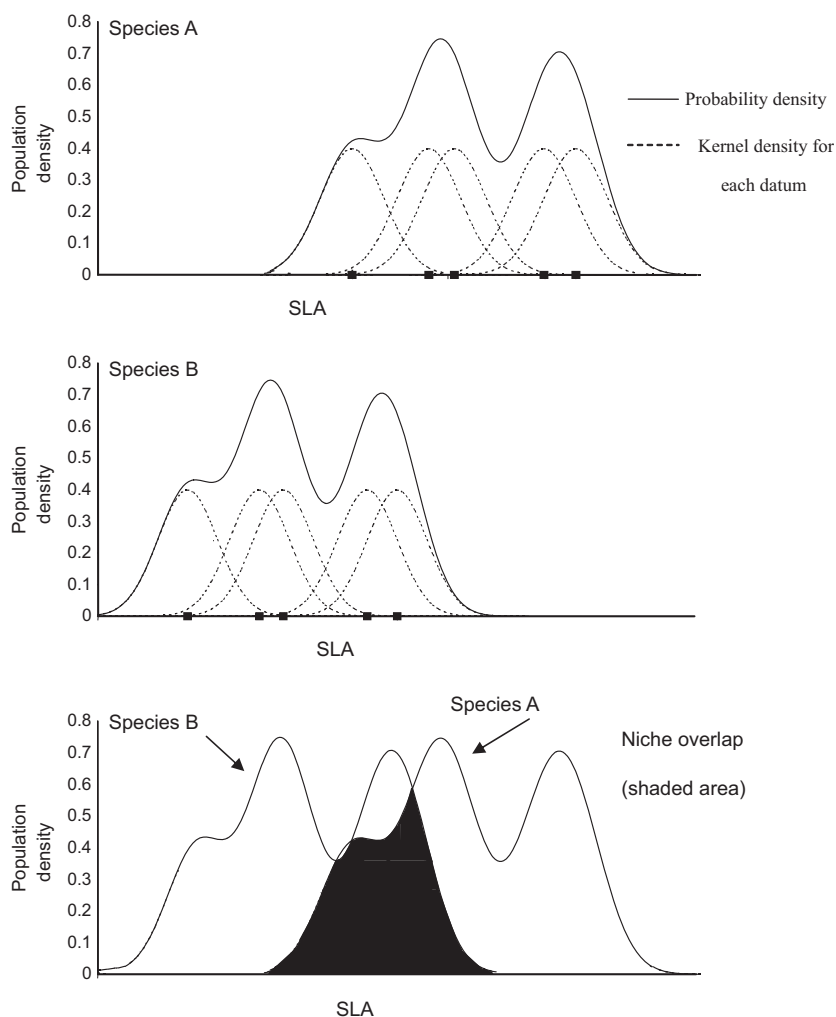
coefficient of variation in biomass across years relative to low-abundance species, so that relative abundance distributions are unlikely to have altered markedly from year to year.

Plant material for trait measurements was obtained in June 2004 by randomly selecting 10 individuals per species per combination of mowing and fertilizer treatments. Only fully developed, undamaged leaves were selected. For some of the less common species, for some treatment combinations, less than five replicates were available. In these cases, all data recorded for the species at the experimental site were pooled. Species for trait collection were prioritized by relative abundance in experimental plots, to ensure that at least 80% of the total biomass of each plot was represented by species with trait data for each of the treatment combinations. Stem and leaf dry matter content (SDMC and LDMC – respectively the ratio of leaf and stem dry mass divided by the fresh mass), specific leaf area (SLA – the ratio of leaf area to dry weight with units  $\text{mm}^2 \text{mg}^{-1}$ ) and carbon : nitrogen (C:N) ratio were measured following the corresponding protocols of Cornelissen *et al.* (2003) and Garnier *et al.* (2007). SLA represents the ratio of leaf area to dry weight ( $\text{mm}^2 \text{mg}^{-1}$ ). Both SLA and LDMC are among the group of inter-correlated leaf traits, representing a continuum from short- to long-lived leaves across species (Wright *et al.* 2004). Higher SLA is associated with shorter leaf life span, shorter nutrient residence times and higher relative growth rates (Westoby *et al.* 2002). The relationship between LDMC and these traits is generally weaker, and leaves with high

LDMC tend to be relatively tough and more resistant to herbivory and decomposition (Cornelissen *et al.* 2003; Garnier *et al.* 2007). While LDMC is generally negatively related to SLA, global comparative studies have shown that SLA is more strongly related to its other component trait, leaf thickness, than LDMC, and that SLA and LDMC respond quite differently along climatic gradients (Niinemets 2001). Also, the two traits may have different effects on some key plant functions (Cornelissen *et al.* 2003). For example, LDMC is an indicator of photosynthetic rate per unit leaf dry mass, while SLA is also an indicator of photosynthetic rate and construction cost per unit leaf area (Niinemets 1999). Plant height moderates response to both resource availability and disturbance since it relates to both competitive ability and tolerance or avoidance of disturbance and stress (Grime 2001; Westoby *et al.* 2002). Leaf C:N ratio complements the other traits in being very closely correlated with maximum photosynthetic rate per unit leaf dry mass (Cornelissen *et al.* 2003).

#### NICHE OVERLAP CALCULATIONS

For each plot, niche overlap between species was calculated following the kernel function method of Mouillot *et al.* (2005) – a nonparametric method of calculating species population density distributions in niche or functional trait space (Fig. 1). This method attributes a bell-shaped density distribution (the dashed curves in Fig. 1) to each



**Fig. 1.** Use of the kernel density estimator for generation of a probability density distribution for a species in functional space (after Mouillot *et al.* 2005). The black squares represent individual data points (specific leaf area, SLA, measurements). The dashed, bell-shaped curves represent the kernel function associated with each data point. The sum of the kernel functions gives the species' 'probability density' in functional trait space (solid curves). Niche overlap is calculated as the area of overlap between the resulting probability densities (shaded area). Adapted from Mason *et al.* (2008b).

individual datum (in our case to each functional trait measurement) using the kernel function:

$$D_{xX_i} = \frac{e^{-((x-X_i)/h)^2}}{2\sqrt{2\pi}nh}, \quad \text{eqn 1}$$

where  $D_{xX_i}$  is the density (ordinal height of the bell-shaped curve) at functional trait value  $x$  for datum  $X_i$ ,  $n$  is the number of data points (measurements) and  $h$  is the bandwidth (defined as the default value  $1.06\sigma n^{-1/5}$ , with  $\sigma$  being the standard deviation of the trait values following Stine & Heyse 2001).

Species probability density at any functional trait value is calculated as the sum of kernel density functions for each data point (the solid curves in Fig. 1):

$$PD_x = \sum_{i=1}^n D_{xX_i}, \quad \text{eqn 2}$$

where  $PD_x$  is the species probability density at functional trait value  $x$ . Once the density distribution of each species in functional trait space was generated, the niche overlap between each pair of species ( $O_{ij}$ ) was calculated separately for each functional trait as the area of overlap between the population density distributions of each species (which corresponds to the shaded area in Fig. 1) using the following expression:

$$O_{ij} = \int \min(f_{it}(x), f_{jt}(x)) dx, \quad \text{eqn 3}$$

where  $f_{it}$  and  $f_{jt}$  are kernel-generated probability density functions for species  $i$  and species  $j$ , respectively, and  $x$  is a functional trait 'gradient'.

This method has the advantage that it makes minimal assumptions about the shape of the trait density distribution for a given species population, and thus is less sensitive to departures from normality, especially when analysing skewed distributions (Stine & Heyse 2001). However, a bell-shaped distribution is calculated around each data point, so enough data are needed to provide an adequate estimate of the population standard deviation. The abundance-weighted overlap for each trait, for each community ( $O_c$ ), was calculated thus:

$$O_c = \sum_{i=1}^{S-1} \sum_{j=i+1}^S O_{ij} p_i p_j, \quad \text{eqn 4}$$

where  $S$  is the number of species present in sample  $c$ ,  $O_{ij}$  is the niche overlap between species  $i$  and  $j$ , and  $p_i$  is the proportional abundance of species  $i$ . This index is analogous to the inverse of Rao's quadratic entropy in that it estimates the redundancy fraction of the Simpson index (de Bello *et al.* 2010a).

Community (i.e. plot) niche overlap values were simulated by randomizing relative abundances across species within communities. This randomization retains all processes that produced the observed data except those that affect species' relative abundances. A total of  $10^4$  randomizations were used in all analyses. For each randomization, mean niche overlap across all plots was calculated in the same way as described for the observed data.  $P$ -values were calculated as the proportion of randomizations giving a mean overlap value (taken across plots) as or more extreme than that observed, with these  $P$ -values being doubled to give a two-tailed test. Significance was assumed at  $P < 0.05$ .

For each plot, observed niche overlap was expressed relative to that expected by chance using the Standardized Effect Size (SES, Gotelli & McCabe 2002):

$$SES = \frac{\text{Obs-Exp}}{\sigma_{\text{Exp}}}, \quad \text{eqn 5}$$

where Obs is the functional diversity or niche overlap value obtained from the observed data, Exp is the mean of the randomizations and  $\sigma_{\text{Exp}}$  the standard deviation of expected values. Standardized Effect Size values were used for tests of treatment, biomass and dominance effects on evidence for niche complementarity and environmental filtering, as the variance in simulated overlap values increases as evenness in abundance decreases. Standardized Effect Size corrects for differences between communities in the variance of simulated overlap values and so removes any possible bias arising from the influence of evenness on overlap. Since the permutations only explore a small portion of the data configurations, it is possible SES values might vary between separate simulation tests in the same data set. However, SES values were very stable across separate permutation tests, with values varying by 1% on average between tests using  $10^4$  randomizations each. Results were also very similar when  $10^5$  and  $10^6$  randomizations were used, suggesting that  $10^4$  randomizations are adequate for this method.

#### BIOMASS AND DOMINANCE EFFECTS ON SPECIES RICHNESS AND OVERLAP

The goodness-of-fit of linear, quadratic and log-linear [ $y = \log(x) + c$ ] relationships between biomass, dominance, species richness and niche overlap was compared. Goodness-of-fit was compared using AIC weights (Burnham & Anderson 2002). The Mitchell-Olds-Shaw test for humps and pits (Mitchell-Olds & Shaw 1987) was applied where the quadratic curve received the strongest AIC weight support. This test is intended to examine evidence for a change in the direction of the gradient within the range of the observed data for quadratic relationships. The only evidence for nonlinear relationships was between biomass and species richness so comparisons of AIC weights are not shown in the results section.

The 'glm' function in R (version 2.9.2, R Development Core Team 2009) was used to fit linear and quadratic relationships, while the 'nlm' function was used to fit log-linear relationships. The Mitchell-Olds-Shaw test was performed using the 'MOSTest' function in the 'vegan' package (version 1.16-33).

#### TREATMENT EFFECT ON BIOMASS, SPECIES RICHNESS DOMINANCE AND OVERLAP

PERMANOVA (Anderson & Ter Braak 2003) was used to test the significance of the treatments and interaction between treatments, as some of the responses analysed did not satisfy the assumption of normal distribution of errors, and we preferred to avoid data transformation. PERMANOVA tests the significance of the observed  $F$ -statistic by comparison with  $F$ -values generated using an appropriate randomization procedure. In our case we tested the significance of main effects and interaction effects by randomizing residuals of the response, as suggested by Anderson & Ter Braak (2003) for experiments with eight or fewer treatment combinations. PERMANOVA was also performed for the residuals of niche overlap, species richness and dominance from regression of these responses against biomass, to test whether treatments explained a significant amount of variation independent of their effect on biomass. Levene's test for equal variances (Levene 1960) was used to test for unequal variances between groups in all PERMANOVA analyses. No results were obtained with  $P < 0.1$ , indicating PERMANOVA's assumption of equal variances was not violated.

**Table 2.** Correlations between traits across species and treatment combinations. For each pairwise combination of traits, measurements for each trait from the same species in the same combination of mowing and fertilizer treatment were correlated. Trait codes are as follows: C:N, leaf carbon : nitrogen ratio; Height, plant height; LDMC, leaf dry matter content; SDMC, stem dry matter content

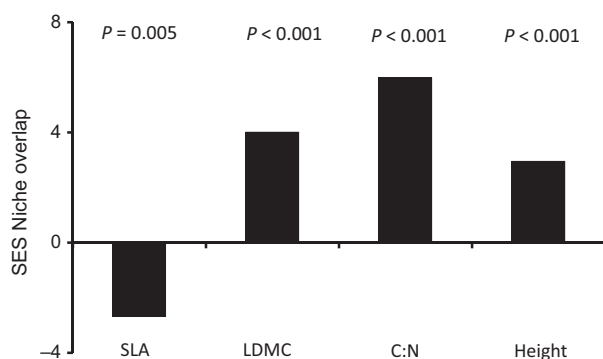
	C:N	Height	LDMC	SDMC
SLA	-0.289	-0.067	-0.249	-0.232
C:N		0.396	0.313	0.262
Height			0.109	-0.028
LDMC				0.703

## Results

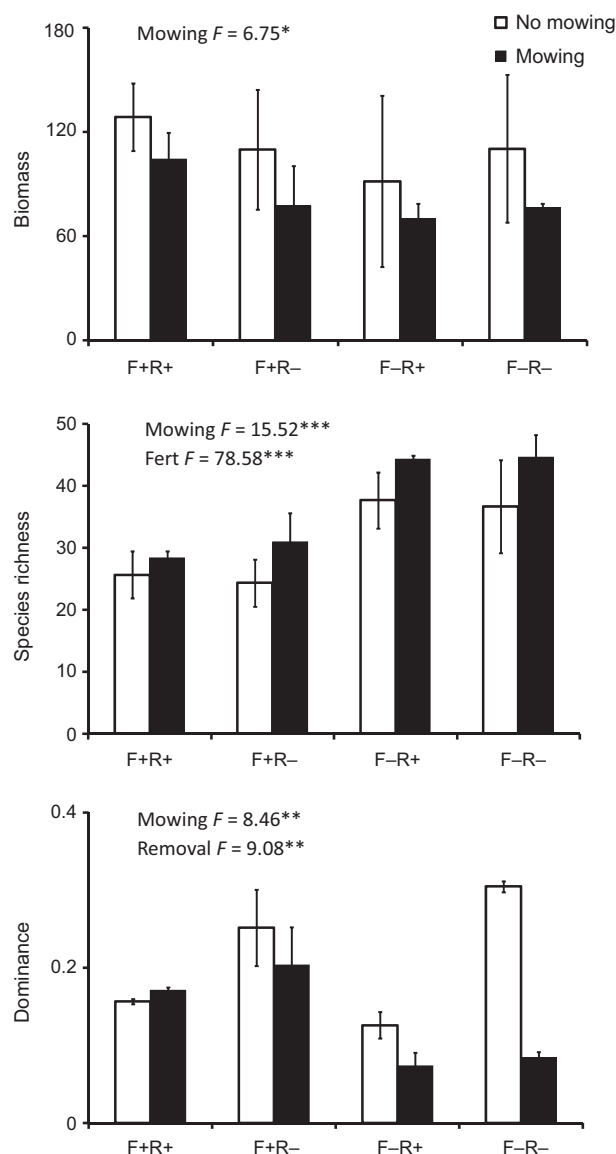
Generally correlations between traits were weak to moderate (Table 2). The only exception was for stem and leaf dry matter content (SDMC and LDMC, respectively). In view of this strong collinearity we have omitted results for SDMC from subsequent analyses. In general, patterns for SDMC were similar to those observed for LDMC.

### NICHE OVERLAP ACROSS ALL PLOTS

Niche overlap was significantly lower than expected by chance for SLA across all samples (Fig. 2). This suggests that, on average, the most abundant species within a plot were more different in SLA than expected. By contrast, overlap for all of the other traits measured was significantly higher than expected by chance (Fig. 2), indicating that the most abundant species tended to be more similar for LDMC, height and C:N ratio. These results suggest that different assembly processes operate for different traits. For SLA, ability to acquire resources (as indicated by relative biomass) is enhanced, having complementary traits to abundant co-occurring species. For the other traits it appears that convergence on particular trait values enhanced resource acquisition.



**Fig. 2.** Standardized Effect Size (SES) values for mean niche overlap for each trait across all plots. *P*-values are the proportion of permutations giving an overlap as or more extreme than that observed. Trait codes are: SLA, specific leaf area; LDMC, leaf dry matter content; C:N, carbon to nitrogen ratio of leaves; Height, maximum height.



**Fig. 3.** Mean and SD for biomass, Simpson's dominance and species richness for all combinations mowing, fertilization and removal treatments. F+ and R+ indicate application of fertilizer and dominant removal, respectively. *F*-statistics and associated *P*-values are from multifactorial PERMANOVA including the three main effects and all possible interaction effects where:  $^*P < 0.05$ ;  $^{**}P < 0.01$ ;  $^{***}P < 0.001$ .

### TREATMENT EFFECTS ON BIOMASS, DOMINANCE AND SPECIES RICHNESS

Mowing was the only significant effect in the three-way PERMANOVA for biomass (Fig. 3), with mowing tending to decrease biomass for all combinations of fertilizer and removal treatments (Fig. 3). Both removal and mowing decreased Simpson's Dominance (Fig. 3), while both mowing and fertilizer had significant effects on species richness. Mown plots had higher and fertilized plots lower species richness than plots where mowing and fertilizer application were absent. There were no significant interaction effects on species richness.



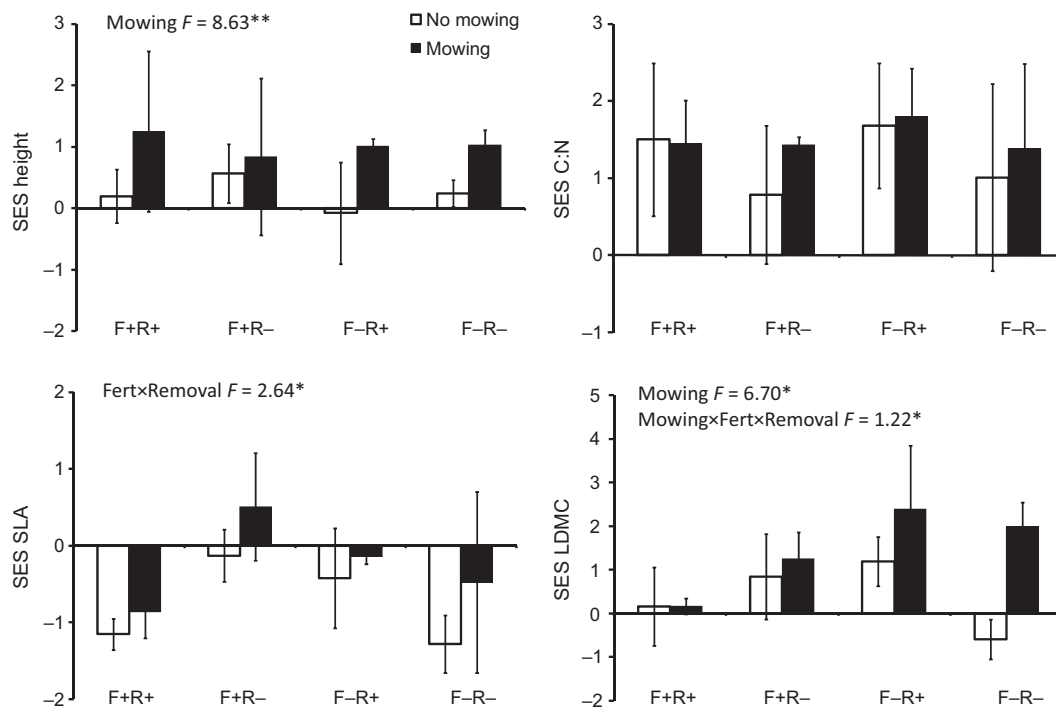
## TREATMENT EFFECTS ON NICHE OVERLAP

Mowing had a significant positive effect on SES niche overlap values for LDMC and height at  $P < 0.05$ , with lower overlap in unmown plots (Fig. 4). The only significant interactions were between fertilizer and removal for SLA and the three-way interaction for LDMC. The fertilizer  $\times$  removal interaction was driven by reduced overlap for SLA where fertilizer and removal were either both applied, or both absent. The three-way interaction for LDMC was apparently driven by low overlap in unmown plots where fertilizer and removal were both absent. Once the effect of biomass had been removed (i.e. by taking the residuals from regression of overlap values on biomass), the only significant effect was the

fertilizer  $\times$  removal interaction effect on SLA (Table 3). These results suggest that much of the influence of mowing on niche overlap for LDMC and height was explained by its effect on biomass.

## BIOMASS, SPECIES RICHNESS, DOMINANCE AND NICHE OVERLAP

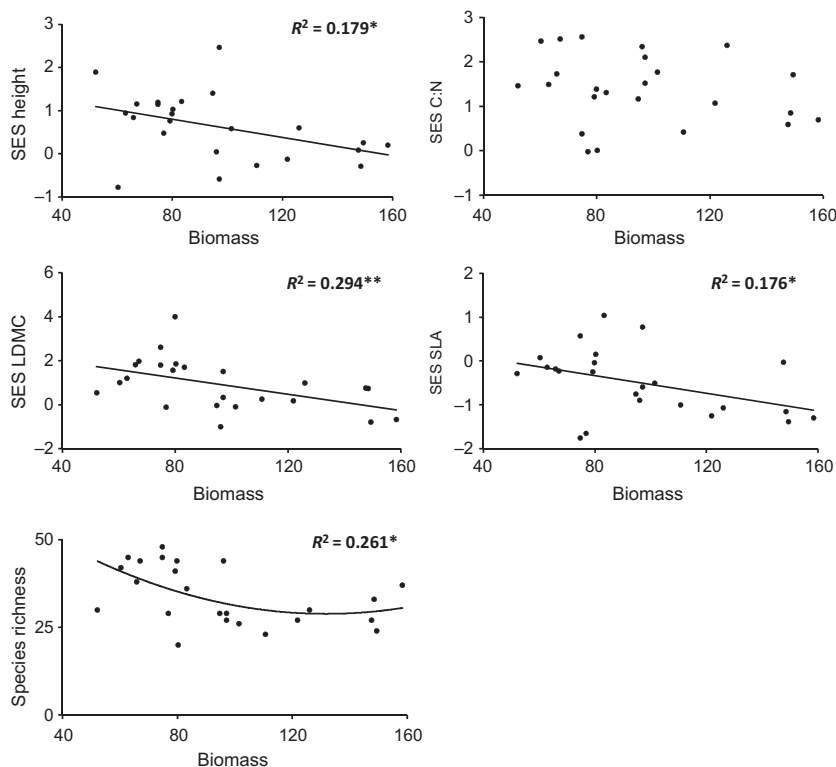
Biomass was negatively correlated with species richness, with the quadratic curve receiving the strongest support (Fig. 5). The Mitchell-Olds–Shaw test gave no support for a hump or pit within the range of biomass values observed, indicating that the decline in species richness with increasing biomass



**Fig. 4.** Mean and standard deviation for niche overlap Standardized Effect Size (SES) values for each of the traits, for all combinations of mowing, fertilization and removal treatments. F+ and R+ indicate application of fertilizer and dominant removal respectively. SLA, specific leaf area; LDMC, leaf dry matter content; C:N, carbon to nitrogen ratio of leaves; Height, maximum height.  $F$ -statistics and associated  $P$ -values are from multifactorial PERMANOVA including the three main effects and all possible interaction effects where: \* $P < 0.05$ ; \*\* $P < 0.01$ .

**Table 3.** PERMANOVA results for treatment effects on residuals from regression on biomass of standardized effect size values for abundance-weighted niche overlap for each trait. Trait codes are as follows: SLA, specific leaf area; LDMC, leaf dry matter content; C : N, carbon to nitrogen ratio of leaves; Height, maximum height.  $F_{\text{obs}}$  is the observed  $F$ -statistic for each effect and  $P$  is the proportion of permutations giving an  $F$ -value equal to or greater than that observed. Significant results are highlighted in bold

Effect	SLA		LDMC		CN		Height	
	$F_{\text{obs}}$	$P$	$F_{\text{obs}}$	$P$	$F_{\text{obs}}$	$P$	$F_{\text{obs}}$	$P$
Mowing	0.693	0.414	1.793	0.184	0.145	0.685	3.695	0.07
Fertilization (Fert.)	1.795	0.197	0.603	0.434	0.065	0.801	1.800	0.216
Removal	0.873	0.372	0.253	0.637	2.585	0.132	0.006	0.947
Mowing $\times$ Fert.	0.008	1	1.348	0.201	0.001	1	0.086	0.973
Mowing $\times$ Removal	0.111	0.953	0.229	0.873	0.152	0.929	0.425	0.714
Fert. $\times$ Removal	<b>2.190</b>	<b>0.038</b>	0.768	0.482	0.000	1	0.307	0.814
Mowing $\times$ Fert. $\times$ Removal	0.820	0.29	0.866	0.265	0.068	0.997	0.329	0.906



**Fig. 5.** Species richness and Standardized Effect Size (SES) values for niche overlap for each of the traits against total biomass. SLA, specific leaf area; LDMC, leaf dry matter content; C:N, carbon to nitrogen ratio of leaves; Height, maximum height.

was monotonic. Dominance was significantly positively correlated with biomass, with removal and non-removal plots having different linear regression coefficients (results not presented).

Biomass was significantly negatively correlated with SES niche overlap values for SLA, LDMC and height at  $P < 0.05$ . Thus, for three of the four traits studied there was evidence that niche overlap decreased with biomass. In each case there was no AIC weight support for rejecting the linear model (Fig. 5). There was no evidence for relationships between niche overlap and either Simpson's Dominance or species richness. There was no relationship between dominance and species richness when removal was applied, but without removal there was a significant negative relationship between dominance and species richness.

## Discussion

Mean niche overlap was higher than expected at random for LDMC, leaf C:N ratio and height, and lower than expected for SLA. There was also strong evidence for decreasing overlap with increasing biomass and in the absence of mowing, with the effect of mowing being largely due to its effect on biomass. These results, altogether, suggest that traits that are often thought to capture similar aspects of plant ecological strategy (Cornelissen *et al.* 2003; Wright *et al.* 2004) may reveal evidence of contrasting assembly processes, and that niche complementarity appears to increase with increasing competition for light. Below we discuss the potential mechanistic basis for our results in more detail, and place them in the context of existing literature.

## CONTRASTING ASSEMBLY PROCESSES

The clear evidence of opposing assembly processes for related trait axes suggests that much of the debate over whether one or another community assembly process dominates (e.g. Etienne & Olff 2005; Mason *et al.* 2008b; Wilson 2007) may have been misguided. Grime (2006) did propose the idea that divergence should be common in reproductive traits with convergence predominating for vegetative traits (i.e. those relating to resource use and acquisition and growth rate) in plant communities. Also, past authors have demonstrated theoretically that competition can cause convergence for niche axes related to habitat selection and divergence for axes related to resource acquisition (Leibold 1995). However, this is the first work we are aware of to show opposing tendencies for different vegetative traits that are often thought to capture similar aspects of plant strategy. The ability to detect contrasting patterns for different traits adds to the growing body of work demonstrating the power of combining abundance data with information on different niche axes in revealing community assembly processes (Mouillot, Mason & Wilson 2007; Mason *et al.* 2008b; Vergnon, Dulvy & Freckleton 2009). Approaches that include only abundance data have difficulty in distinguishing between competing assembly processes (e.g. niche vs. neutral processes; Chave 2002), while those examining the relationship between functional traits and species co-occurrence often struggle to deal with confounding effects such as environmental heterogeneity and dispersal limitation (Stubbs & Wilson 2004). Our method, focusing on relative abundance in local communities at small spatial scales, also avoids many

of the confounding factors that hinder species-pool filtering approaches (e.g. Tofts & Silvertown 2000).

Despite the contrasting results we observed, for three of the four traits studied there was strong evidence of environmental filtering, suggesting that convergence on trait values that maximize resource acquisition under local conditions and in competition with other species was the dominant assembly process. This is consistent with the predictions of the theoretical frameworks proposed by both Grime (2001) and Tilman (2004). These results suggest that abundant species tend to have similar tissue density (LDMC is an indicator leaf tissue density; e.g. Wilson, Thompson & Hodgson 1999; Shipley & Vu 2002), nutrient status (C:N ratio) and height. Convergence in height is understandable as competition for light is size-asymmetric (taller species are disproportionately advantaged). Convergence for tissue density and nutrient status suggests that there is strong pressure for similar resource use dynamics (slow and tight vs. fast and leaky; e.g. Wilson, Thompson & Hodgson 1999). This is expected, as the local physical and competitive environment strongly influences the relative ability of species differing in resource use strategy to acquire resources, especially when nutrients are limiting (e.g. Wilson, Thompson & Hodgson 1999). It is unlikely that the dominance of tall species is also responsible for the patterns observed in other traits, as height was very weakly correlated with all other traits (Table 2), except C:N ratio, and even this correlation was only of moderate strength ( $r = 0.396$ ).

The contrasting result for SLA is curious, given that leaf tissue density is a component of SLA (Niinemets 1999). However, it has been recognized that these two traits may not always capture the same plant functions (Cornelissen *et al.* 2003). In our study SLA and LDMC were relatively weakly correlated ( $r = -0.249$ ), suggesting that both supplied a high degree of independent information from each other. The other component of SLA is leaf thickness. A global study (Niinemets 1999) demonstrated that SLA is more closely related to thickness than to density and was negatively related to photosynthesis and construction costs per unit area via this relationship. SLA is also positively related to photosynthesis per unit dry mass because of its negative relationship with density.

The contrary results for SLA and LDMC could be due to divergence in light capture strategies between species. Sun leaves tend to have lower SLA than shade leaves since they are often limited by assimilative capacity, while shade leaves tend to be light-limited (Hallik, Niinemets & Wright 2009). Consequently, return on investment will be maximized by increasing per-unit-area assimilative capacity for sun leaves, and by increasing leaf area for the lowest cost possible per unit area for shade leaves. Divergent patterns in light capture strategy have been demonstrated in meadows (Hirose & Werger 1995; Anten & Hirose 2003), indicating that niche complementarity for light capture is possible in grassland communities.

#### BIOMASS AND COMPLEMENTARITY

The evidence for increasing niche complementarity with increasing total community biomass is logical if we interpret

the biomass gradient as a shift in the balance between nutrient and light competition. At low biomass, light competition will be less intense (Wilson & Tilman 1993), perhaps causing pressure for divergence in light capture strategy to decrease. Furthermore, competition for light is size asymmetric (Vojtech, Turnbull & Hector 2007), so that light competition may often provide a harsher constraint on the occurrence and abundance of some species, than competition for below-ground resources. Mowing was the dominant factor influencing biomass, and was the key driver of variation overlap for LDMC and height (in all cases overlap was lower in the absence of mowing). Mowing had a strongly significant positive effect on species richness in our study, suggesting the associated decrease in biomass may have reduced competitive exclusion between functionally similar species. However, the negative effect of fertilization on species richness was even stronger than the positive effect of mowing, with no concomitant impact on niche overlap, suggesting that the relationship between mowing and niche overlap may not be attributable to reduced competitive exclusion alone. There was a high degree of plasticity in SLA, LDMC and height for some dominant species in response to mowing (results not shown). This trait plasticity generally caused them to become more similar in these traits when mowing was applied than when it was absent. Thus, plastic responses may partially explain the decrease in overlap with increasing biomass and in the absence of mowing.

It is unclear whether this trend for decreasing overlap with increasing biomass would continue beyond the highest biomass values recorded in this study. Consequently, it is impossible to claim that this will be a general pattern observable in woody as well as non-woody vegetation. However, given the consistency of the effects we observed, it would be interesting to test whether it occurs in other contexts. It would also be interesting to test for the trends observed here using natural gradients of biomass and disturbance.

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