

Evidence for limiting similarity in a sand dune community

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Summary

1 We sought evidence among the plant species of a New Zealand sand dune community that limiting similarity controls the ability of species to coexist. Sampling was at four spatial scales, from a single point up to a scale of 50 m². Twenty-three functional characters were measured on each of the species, covering the morphology of the shoot and root systems and nutrient status, and intended to represent modes of resource acquisition.

2 Patterns of association between plant species at the four scales were examined for any tendency for plants with similar functional characters to coexist less often than expected at random (e.g. if a point has three species, do they have notably different characters?) The observed results were compared with the patterns expected under a null model using a range of test statistics.

3 A test over all characters found that the mean dissimilarity between nearest-neighbour species in functional space, and the minimum dissimilarity, were greater than expected under the null model at the 0.5 × 0.5 m scale. This supports the MacArthur & Levins model, although the actual community did not show an even spread of species over functional space.

4 Limiting similarity effects were seen even more consistently in separate characters when within-species variation was taken into account to calculate measures of overlap. The characters involved were mainly those related to rooting patterns and leaf water control, and thus perhaps reflecting the acquisition of nutrients and/or water.

5 Our results seem to be amongst the most convincing support for the theory of limiting similarity, and the only example involving vegetative processes in plant communities. The characters involved suggest that species can more readily coexist if they differ in their water-use pattern, reducing competition between them.

Key-words: assembly rules, coexistence mechanisms, functional types, niche limitation, root characters

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Introduction

Since the concept of ‘assembly rules’ was proposed (Diamond 1975), ecologists have sought empirical confirmation that rules govern how species associate. Of these rules, one of the most frequently discussed has been the idea that species coexistence is maintained via niche differentiation. MacArthur & Levins (1967) investigated this concept mathematically and developed the theory of limiting similarity, i.e. that there is a limit to how morphologically similar two coexisting species can be, if both are to persist within the same habitat (Fig. 1). Whether this theory operates in plant communities is the focus of this paper.

LIMITING SIMILARITY

Evidence for the theory of niche limitation has been sought in plant species occurrence patterns, some based on the characters of the species but others based on simple presences. While studies on the variance in species richness provide some support for the theory (Wilson *et al.* 1987; Klimes 1995), this is a simplistic approach and the results are open to other interpretations (Leps 1995). More convincing evidence for assembly rules has been found with character-based approaches (e.g. Wilson & Roxburgh 1994; Klimes 1995; Wilson *et al.* 1995; Weiher *et al.* 1998; Watkins & Wilson 2003).

Two types of niche exist: α (alpha) and β (beta), and it is important to clearly define which of these is being addressed (Pickett & Bazzaz 1978; Wilson 1999a). The distinction is partly a question of scale, alpha-niche differentiation being the ways that coexisting and directly

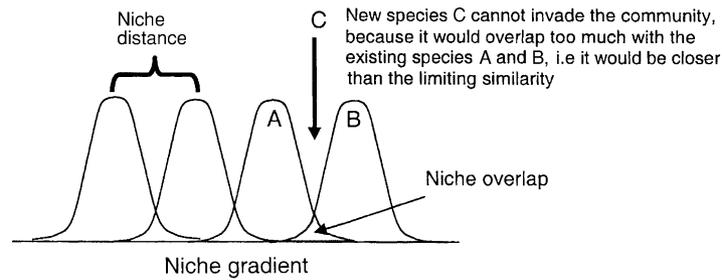


Fig. 1 The concepts of distances between niches, niche overlap and limiting similarity.

competing plants differ in the resources that they use, and beta-niche representing niche differences that comprise plants growing well away from each other, in different environmental conditions. However, it is also a distinction between resources, that are consumed, and environmental conditions, that comprise the environment. This study addresses the α -niche of a plant, which represents the resources utilized by it, and the mechanisms of resource acquisition (e.g. NO_3 use vs. NH_4 use) in one set of environmental conditions, i.e. within a local patch. In order to determine whether or not limiting similarity operates within a plant community, we need a measure of the species niche within the n -dimensional functional-space/niche-space, i.e. in Hutchinson's (1957) n -dimensional hypervolume.

EVIDENCE

Logically, the theory of limiting similarity must operate: so long as species interfere with each other (e.g. compete), one species must have at least a slightly higher competitive ability and, unless they are in different niches, competitive exclusion must occur (though there are other complications in the real world, Wilson 1990). A number of studies have measured the degree of overlap between coexisting species within plant communities (e.g. Pickett & Bazzaz 1978; Cole 1981; Cody 1986). However, few of these have tested whether there is any pattern to these overlaps that is significantly statistically different from random, especially whether the species are more evenly spaced in terms of functional characters because of niche limitation.

Occasionally, evidence for non-randomness within functional space has been found in animal communities (e.g. Juliano & Lawton 1990; Wiens 1991; Kingston *et al.* 2000). However, the theory applies with equal logic to plant communities, perhaps with more pertinence in view of suggestions that density-independent controls predominate over interspecific competition in some animal communities (e.g. Jonsson *et al.* 1998; Schmidt & Whelan 1999). The best evidence from plant communities has been the work of Armbruster *et al.* (1994), examining tropical plants with specialized insect-pollination mechanisms. Yet for most plants, competition is almost all within the vegetative phase. It is therefore surprising that previous attempts to demonstrate assembly rules based on vegetative plant characters have

been rather unsuccessful (but see Wilson *et al.* 1994; Watkins & Wilson 2003).

While a few studies have claimed to find support for limiting similarity within plant communities, the null models used in several of these have been flawed, in that they randomized all of the species found across a range of environments (Henriques & Hay 1992; Weiher *et al.* 1998). This means that differences between a few communities are being tested multiple times, in effect pseudo-replication. Moreover, some of the test statistics used by Weiher *et al.* (1998) did not necessarily measure the features they intended (see Discussion). Thus, little valid evidence has been produced that limiting similarity in α -niche, deemed inevitable by theory, occurs in plant communities. The aim of this study is to test for it in a New Zealand sand-dune plant community. That is, we ask whether species that are found locally coexisting are more different from one another than would be expected if niches were assigned to the co-occurring species at random.

Methods

VEGETATION SURVEY

The study was conducted at Kaitorete Spit on the east coast of South Island, New Zealand ($43^{\circ}50' \text{ S}$, $172^{\circ}35' \text{ E}$), a sand/gravel barrier complex that lies between a brackish lake and the Pacific Ocean. The mean annual rainfall of *c.* 590 mm, with a coarse sand, leads to a drought-prone environment (Partridge 1992). Kaitorete Spit contains one of the most pristine sand dune communities left within New Zealand, with *Desmoschoenus spiralis* (A. Rich.) Hook. f., a native sand-binding cyperad, found throughout. The vegetation consists of a mosaic of patches, some containing the native prostrate shrub *Carmichaelia appressa* G. Simpson, others containing the short bushes of *Muehlenbeckia complexa* (A. Cunn.) Meissn. or a mixture of grasses and herbs. The site was therefore sampled for species presence/absence at four spatial scales: Area (designed to sample the vegetation coexisting within each of these patches); Quadrat (which aimed to sample the species coexisting beneath a shrub); Mini-quadrat (to measure coexistence between species such as herbs and grasses); and Point (the ultimate measure of coexistence). Nine 50-m² Areas were sampled using 20 0.5 × 0.5 m Quadrats (180 in total). Each of these contained four 0.1 × 0.1 m Mini-quadrats (720

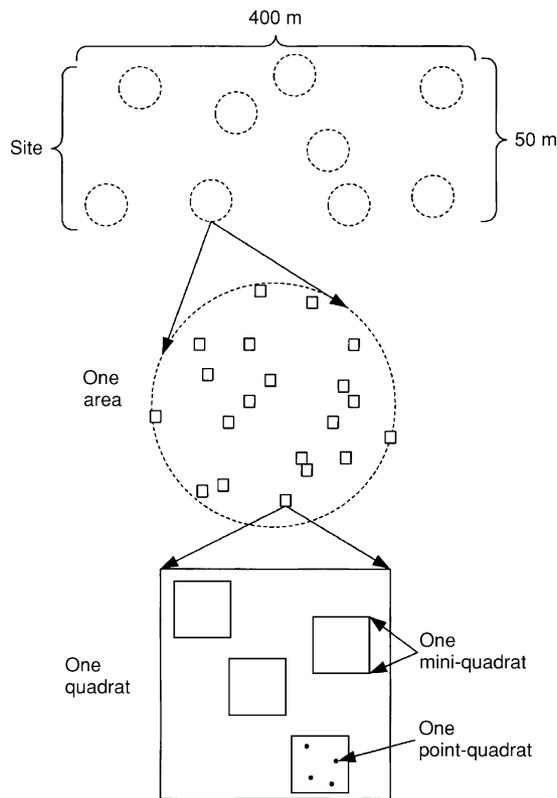


Fig. 2 The sampling design (not to scale): 9 areas, each containing 20 quadrats, each containing 4 mini-quadrats, one of those containing 4 points.

in total), one of which contained four Point (50- μ m tip needles) quadrats (720 in total) (Fig. 2). All area and quadrat placement was by restricted randomization (Greig-Smith 1983). Seedlings (defined for shrub species as individuals shorter than 0.2 m, and for herbs as those still with their cotyledons) were excluded from further analysis, as the functional niche occupied by a juvenile plant is often very different from that of the adult plant (Grime 1979).

NICHE CHARACTERS

Characters were chosen to reflect the ways in which all potentially important resources (water, nutrients, light, etc.) are acquired and retained by plants (Table 1). This was done in order to enable the plants to inform us of what is important in structuring their community, rather than letting prior prejudices of what forces may be operating within this community predetermine the outcome. These characters were then used to provide a measure of the species functional niche breadth, both individually as uni-variate measures along each character axis, and in consort to provide measures of the distribution of species in multivariate niche space. As not all of the species in this study possess leaves with photosynthetic laminae, 'leaf' characters were based on photosynthetic units (PSUs). For a species with simple leaves this is the lamina; for a species with compound leaves it is the leaflet; and for a species with no leaves

but only green stems, it is the stem segment that acts as a leaf. For ease of reading, 'leaf' is used throughout this paper to describe both true leaves and other types of PSU.

For each of the nine species found, 10 plants were selected at random and each of the chosen characteristics was measured, using standard methods (see References in Table 1). Transformations were used to achieve a distribution close to normal (to avoid undue influence of one tail, rather than because the significance calculated from randomization tests depended on it), and then standardized to zero mean and unit variance.

NULL MODELS

When selecting a null model with which to test a hypothesis, it is essential to keep every feature of the randomized data as it is in the observed data, except the feature that the study aims to test (Tokeshi 1986). This study tests whether there are limitations to coexistence related to the functional characters measured. Therefore, the observed occurrences and abundances of species within points, quadrats and areas were fixed within the randomized communities at those observed, but the observed characters were randomized (Appendix S1 in Supplementary Material). That is, the actual character values measured from species within these communities were retained, not generated *de novo*, but the characters were assigned to species at random without replacement within the null model. By maintaining the observed community structure within all of the randomized communities, any spatial autocorrelation arising from the sampling regime cannot affect the results.

When randomizing the allocation of characters to species, several possibilities exist. Assigning to species completely at random, with no regard to the frequency of the species, could result in giving too much weight in the randomized communities to the characters associated with a very rare species, were they assigned to the occurrences of an extremely common species. To overcome this problem, the characters were randomized within two groups of species: the 50% of species most frequent across the site vs. the remainder. The selection of frequency classes to use is not simple. Too many groups will result in few species within each group, with a resulting loss of power due to the restriction upon the possible randomizations, and too few classes can potentially lead to incorrect weighting of characters. Due to the low species diversity found within this community (nine species), two groups were used as this prevents the rarest characters being allocated to one of the most abundant species while maintaining sufficient power. As the characters of a plant do not act independently of one another, but rather are part of an integrated individual (Diaz *et al.* 1999), in order to maintain biological realism within the randomized communities the characters associated with a species were kept together when randomly assigning the character values to a species within the randomized community, thus preserving the observed character-correlation structure.

Table 1 The characters measured for each species, and their functional importance

Character	Functional importance	Reference to functional significance
Plant height	Light capture; growth strategy	Anten & Hirose (1999)
Number of leaves on the terminal shoot ¹	Light capture; plant architecture	Niklas (1999)
Support fraction ²	Growth strategy; leaf longevity	Anten & Hirose (1999)
Leaf inclination from the horizontal	Light capture; water retention	Anten & Hirose (1999)
Leaf area	Heat load; water retention; gas exchange	Schulze <i>et al.</i> (1996)
Leaf area ratio (LAR = leaf area/total mass)	Growth strategy	Anten & Hirose (1999)
Leaf thickness (measured with a micrometer)	Light capture; gas exchange; water retention	Mulkey & Wright (1996)
Leaf shape (length/width)	Gas exchange; heat load	Givnish & Vermeij (1976)
Leaf lobation: ($\pi \times \text{length} \times \text{width}$)/area	Heat load; gas exchange; water retention	Givnish & Vermeij (1976)
Leaf succulence (fresh mass/dry mass)	Water retention	Kramer (1995)
Specific leaf area (SLA: leaf area/leaf mass)	Photosynthetic capacity; leaf longevity; stress tolerance	Westoby (1999)
Total chlorophyll content of the leaves ³	Light capture; growth strategy	Murchie & Horton (1997)
Chlorophyll <i>a:b</i> ratio	Growth strategy	Murchie & Horton (1997)
Nitrogen content of leaves ⁴	Photosynthetic capacity; leaf longevity	Reich <i>et al.</i> (1991)
Phosphorus content of leaves ⁴	Leaf longevity	Reich <i>et al.</i> (1991)
Number of primary root axes ⁵	Nutrient & water acquisition & storage	Jackson <i>et al.</i> (1999)
Horizontal root system extent	Nutrient & water acquisition	Jackson <i>et al.</i> (1999)
Vertical root system extent	Nutrient & water acquisition	Jackson <i>et al.</i> (1999)
Root diameter of the thickest root	Nutrient storage	Berendse <i>et al.</i> (1999)
Rhizome diameter	Nutrient storage	Jackson <i>et al.</i> (1999)
Presence/absence of tap roots ⁶	Water acquisition	D'az & Cabido (1997)
Presence/absence of tubers ⁶	Nutrient storage	Jackson <i>et al.</i> (1999)
Root profile ⁷	Nutrient & water acquisition	Jackson <i>et al.</i> (1999)

1. A terminal shoot was defined as an entire tiller for grasses and graminoids, and the shoot distal to the lowest leaf remaining on the main stem for shrubs and forbs (Wilson *et al.* 1994).

2. Non-photosynthetic tissue mass as a proportion of the total terminal shoot (Wilson *et al.* 1994).

3. N,H-dimethylformamide extraction, then spectrophotometric measurement at 663.8 nm and 646.8 nm (Porra *et al.* 1989), expressed per unit of fresh weight, on six replicates.

4. Blakemore *et al.* (1987) on one or two replicates.

5. Due to permit restrictions, root characters to represent *Muehlenbeckia complexa* Meissn., *Einadia triandra* (Forst. f) Scott and *Carmichaelia appressa* were measured outside the study site.

6. Because of their 0/1 scale, these characters were not analysed individually, but were included in the multivariate functional space.

7. Root profile was determined by estimating the percentage of roots within 7 depth classes (0–0.02 m, 0.02–0.05 m, 0.05–0.1 m, 0.1–0.2 m, 0.2–0.5 m, 0.5–1.0 m, > 1.0 m). As only *Carmichaelia appressa* had roots deeper than 1 m, and these classes were used as categorical not linear data, no bias arose from assigning all roots greater than 1 m to one depth class.

Test statistics (see below) were calculated for samples at each of the four scales: points, mini-quadrats, quadrats and areas (Fig. 2), and averaged across the site. The frequency of species occurrences at the point and quadrat scale were used as an estimate of the abundance of species at the large-quadrat and area scales, giving both presence/absence and quantitative analyses at these two scales.

TEST STATISTICS (TS)

Because of the paucity of limiting similarity studies on plant communities, it is not clear what form a non-random pattern of niches would take. Therefore, an exploratory approach was taken in this study, using a wide range of test statistics (TSs), as advocated by Fekete *et al.* (1976), protected by a binomial test. In each case, the test statistic was calculated through comparison of the different species co-occurring within a sample, and then compared with the test statistic calculated on the species co-occurring within the randomized community.

Characters do not act independently of one another, and species may separate from one another via a combination of characters (Précisényi *et al.* 1977). The communities were therefore analysed in terms of the distribution of species in multivariate functional space:

TS₁, Mean NN ED: the mean nearest-neighbour Euclidean distance (Jongman *et al.* 1987) between species present in each sample (Fig. 3). The dissimilarity between nearest-neighbours within each sample was weighted by the product of the abundances of those two species in the samples, and the total divided by the number of comparisons. This test statistic provides an indication of how tightly packed the species are: the smaller the mean nearest-neighbour Euclidean distance the more closely packed the species.

TS₂, Min/Max MST link: the minimum link/maximum link in the minimum spanning tree (MST) for each sample. The Euclidean distances between each species pair were used to calculate a minimum spanning tree (MST, Cormack 1971). This test statistic is a measure of the evenness of the species in functional

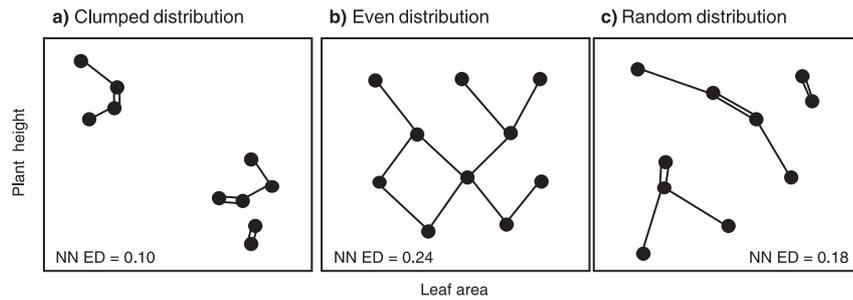


Fig. 3 The Euclidean distances between the nearest neighbours (NN ED) for (a) clumped, (b) even and (c) random distributions. Evenly spaced distributions (centre) will have a greater mean NN ED.

space, a large value indicating that the species in the observed community are spaced evenly. In the extreme case, a value of 1.0 indicates that the shortest link in the MST is equal to the longest link: perfect even spacing. If the species are clumped in Euclidean/functional space, the longest link of the MST will be much greater than the shortest, giving a value closer to 0.0. As this test statistic is a ratio, it will be unaffected by the volume of trait space occupied by the species, providing an estimate of the evenness of species packing that is independent of changes in volume between observed and randomized communities.

TS₃, Minimum ED: the minimum Euclidean distance observed between any of the species within a sample (point, quadrat or area) provides an indication of the absolute limit to the closeness of species packing (Weiher *et al.* 1998).

The average Euclidean distance between all species pairs within each sample and the variance in link length in an MST were also calculated, but they duplicated results from the test statistics above, and are not presented here.

To overcome the problem that *TS₁* to *TS₃* average effects shown in several characters, some of which will be niche separators and others not, and also to pinpoint the characters responsible for effects in *TS₁* to *TS₃*, the following univariate test statistics were calculated on each of the characters:

TS₄, Mean NN: the mean absolute difference in character values between nearest-neighbours along the character axis of the species within each sample (Fig. 1, i.e. the univariate equivalent of Ricklefs & Travis (1980) measure of species packing). Species that are more evenly spaced than expected at random will have a greater mean NN than species from a randomized community.

TS₅, Weighted deviance (WD): the mean deviance of the species in the sample from the mean over all the species in that sample, weighted by the abundance of each species (Appendix S1). Compare the 'distance from the origin' test statistic of James & Boecklen (1984). This is a measure of species packing that takes account of the different abundance of different species.

The maximum, minimum and range of characters observed in each sample were also calculated (cf. Weiher

et al. 1998), but the results provided no further insight and are not presented here.

TS₆, Variance/range: the variance in adjacent distances divided by the range of character values. By using adjacent distances (cf. Fig. 1), *TS₆* incorporates all the interspecies distances along the gradient, from one end to the other, into an index of species evenness. Similar *TS*s have been used to test for staggered flowering times (Gleason 1981; Pleasants 1990), but as the range of characters found in the observed and randomized communities can affect the variance, the variance was divided by the range. A community with species evenly distributed throughout character space will have a lower variance/range than species within the randomized communities.

The basic theory of MacArthur & Levins is versed in terms of niche overlap (Fig. 1). Overlap indices can be calculated from the mean and standard deviation of a character for each species in the sample, given the approximation of a normal distribution (Appendix S1; Cody 1975), or for categorical data (here, root profile) using Pianka's (1973) index of niche overlap (Appendix S1).

TS₇, Mean overlap: the mean niche overlap between all pairs of species co-occurring within the sample, which measures the degree of niche overlap between coexisting species.

TS₈, Maximum overlap: the maximum niche overlap between any pair of species co-occurring within the sample.

TS₉, Weighted AN overlap: the mean weighted niche overlap between adjacent-neighbours along the niche gradient. This is a measure of niche overlap that takes account of the different abundance of different species.

TS₁₀, Variance in AN overlap: the variance in the degree of niche overlap between adjacent-neighbours within each sample. This is a measure of the evenness of species packing along the character axis.

The value of the test statistic expected under the null model was calculated as the average value from 10 000 randomizations, and significance (i.e. the probability of the observed result under the null model) as the proportion of randomizations in which the test statistic was equal to that observed, or more extreme, multiplied by 2.0 to effect a two-tailed test. A program to analyse each of the test statistics at each scale was written in C++ and validated with random data (Appendix S1, details of the validation are available from the first author).

Due to the categorical nature of the root profile data, this character was analysed using only the average niche overlap and the maximum niche overlap test statistics. Nitrogen and phosphorus content were not analysed using any of the niche overlap test statistics, as there were insufficient replicates to calculate the SD for a species. Test statistics that use abundance as a weighting were used on both presence/absence and abundance information, except for weighted deviance (TS₅). As multiple comparisons were made on the same data, increasing the chance of a type I error, binomial tests were used to show whether the proportion of significant tests was greater than expected. A test was made separately for each character analysed and at each scale, across all of the test statistics, separately at the *P* = 0.025 level for each tail. Allowance for multiple testing is usually fraught with problems; here it was ecologically necessary to test over several scales and to test several characters, but the binomial tests will probably be conservative because of non-independence between the test statistics.

Results

OVERALL TESTS

Overall, 670 tests were performed (Tables 2–4), giving 54 significant results in the direction of limiting similarity (*P* < 0.00001), and only three in the direction of convergence in characters between coexisting species (fewer than expected at random).

At the point and mini-quadrat scales, the mean nearest-neighbour Euclidean distances were significantly greater than expected at random (TS₁ in Table 2), indicating spacing of co-occurring species in functional space. Further support for a greater spacing between coexisting species at the mini-quadrat scale was seen as greater minimum distance than expected at random (TS₃ in Table 2).

DIVERGENCE OF CO-OCCURRING SPECIES

Amongst the leaf characters within this community, considerable support for the theory of limiting similarity

Table 2 Results from the functional-space test statistics. Bold type indicates significant results in the direction that suggest the presence of limiting similarity, i.e. the species were evenly spaced along the niche gradient (Obs/Exp > 1). Obs = observed test statistic; Exp = expected (see Methods); NS = non-significant; PA = presence/absence data; Quant. = quantitative data. *Binomial tests indicate that there are more significant results than expected by chance

Test statistic	Scale	PA/Quant.	Obs/Exp	<i>P</i>	
TS ₁ Mean NN ED	Points	PA	1.20	0.048	Obs > Exp
	Mini-quadrats	PA	1.20	0.027*	Obs > Exp
	Quadrats	PA	1.04	NS	
		Quant	1.1	NS	
	Areas	PA	0.89	NS	
		Quant	1.2	NS	
TS ₂ Min/Max MST	Points	PA	0.99	NS	
	Mini-quadrats	PA	0.99	NS	
	Quadrats	PA	0.96	NS	
	Areas	PA	0.81	NS	
TS ₃ Minimum ED	Points	PA	1.18	NS	
	Mini-quadrats	PA	1.20	0.024*	Obs > Exp
	Quadrats	PA	1.02	NS	
	Areas	PA	0.73	NS	

Table 3 Results from the distance measures. Bold type indicates significant results in the direction that suggests limiting similarity, i.e. the species were evenly spaced along the niche gradient. SLA = specific leaf area; LAR = leaf area ratio; Diam. = diameter; V. root ext. = vertical root extent; H. root ext. = horizontal root extent. Other abbreviations as in Table 2

Test statistic	Scale	Clumped	Spaced
TS ₄ Mean NN (PA)	Points	–	Root diam. V. root ext.
	Mini-quadrats	–	V. root ext. H. root ext. Leaf thickness* SLA* P content*
	Quadrats	–	–
	Areas	–	–
TS ₅ Weighted deviance (Q)	Quadrats	–	H. root ext. LAR* Leaf thickness* SLA*
	Areas	–	V. root ext. SLA* LAR*
TS ₆ Variance/range (PA)	Points	–	–
	Mini-quadrats	SLA	No. 1° axes
	Quadrats	SLA	–
	Areas	–	–

Table 4 Significant results from niche-overlap test statistics. Bold type indicates results in the direction that suggests the presence of limiting similarity, that is species were spaced along the niche gradient. Supp. frac. = support fraction; other character abbreviations as in Tables 2 and 3

Test statistic	Scale	Clumped (Obs > Exp)	Spaced (Obs < Exp)
TS ₇ Mean overlap	Point	–	Leaf area* Root profile*
	Mini-quadrat	–	Leaf thickness* Supp. frac.* SLA* Root profile*
	Quadrat	–	–
	Area	–	Leaf thickness [Q] Supp. frac.* [Q]
TS ₈ Maximum overlap	Point	–	Root profile* Leaf area*
	Mini-quadrat	–	Leaf thickness* Supp. frac.* SLA* Root profile*
	Quadrat	–	Leaf thickness* [Q] Leaf succulence [Q] SLA* [Q] Root profile [Q] LAR* [Q]
	Area	–	Supp. frac.* [Q] SLA* [Q] Root profile [Q] LAR* [Q]
TS ₉ Weighted AN overlap	Point	–	Leaf area*
	Mini-quadrat	–	Supp. frac.* Leaf thickness* SLA*
	Quadrat	–	Supp. frac. [PA/Q*] Leaf thickness* [Q]
	Area	Plant height [PA]	Supp. frac. [PA/Q*]
TS ₁₀ Variance in AN overlap	Point	–	–
	Mini-quadrat	–	–
	Quadrat	–	Supp. frac. [PA/Q*]
	Area	–	Leaf area [PA/Q]

was found. For leaf thickness and SLA (specific leaf area), the mean distances between nearest-neighbours observed within the mini-quadrats were greater than expected for a random assortment of species from the same pool (TS₄ in Table 3). The weighted deviance (TS₅) was also significantly higher for these two characters, at both the quadrat and area scales for SLA, and at the quadrat scale for leaf thickness (Table 3). Significantly low overlap between coexisting species was observed at two or more scales in leaf thickness, support fraction of the terminal shoot, and SLA (TS_{7–9} in Table 4). The variance in niche overlap of adjacent neighbours was less than expected for support fraction, terminal shoot and leaf area (TS₁₀ in Table 4). These results are consistent with the results described above (TS₄ and TS₅), and support the concept of niche limitation.

The species found coexisting within this community also seem to be separated with respect to their rooting characters at all scales, at least to some degree. At the point and mini-quadrat scales, both the mean niche overlap (TS₇) and the maximum niche overlap (TS₈) of the rooting profiles were less than expected at random (Table 4). A significantly lower-than-random maximum niche overlap (TS₈) was also observed for root profile at both the quadrat and the area scales (Table 4), and the results from both horizontal and vertical root extent were always in the direction of greater spacing between coexisting species than expected at random (Table 3). While the degree of niche overlap (Table 4) or amount of spacing (Table 3) between species for the number of primary root axes was not significantly different from that expected at random, the variance in distance between species was lower at the mini-quadrat scale (TS₆ in Table 3). Thus, overall the rooting characters also show support for the concept of niche limitation.

CONVERGENCE OF CO-OCCURRING SPECIES

While most of the results from this study support the concept of limiting similarity between coexisting species, in a few aspects the coexisting species were more similar to one another than expected at random (Tables 3 and 4). Co-occurring species had a significantly greater overlap in plant height at the area scale, though not when the abundances of the species were taken into account (TS₉, Table 4). There was a greater variance in adjacent distances for SLA (TS₆, Table 3), though other test statistics indicated limiting similarity for this character, i.e. lower overlaps (Table 4) and greater distance between the mean values of adjacent species and weighted deviance (Table 3). None of these indications of similarity between coexisting species were significant after binomial correction.

Discussion

OVERALL TESTS

The overall tests (Table 2) were performed first to seek general patterns and as another guard against the problem of multiple tests, additional to the binomial tests. They gave good evidence for spacing at the point and mini-quadrat scales, in Mean NN ED (TS₁) and Minimum NN ED (TS₃, Table 2). Table 2 is not full of significant results. This should not worry us because the statistical power at the point scale is restricted by the low number of species at any one point, and at the area and perhaps quadrat scale competitive exclusion may not be complete, and because microenvironmental differences may intrude, making niche limitation hard to see. Moreover, whilst these tests include, we believe, some characters that are related to the actual niches, they

inevitably include others that are not, which will have a diluting effect on the overall test.

Previous workers have found it difficult to demonstrate niche limitation in plant communities above environmental noise, which leads to significantly *high* overlap between coexisting species, the opposite direction from that expected under limiting similarity. The paucity of results in this direction in our study can probably be attributed to our more advanced sampling scheme. However, unlike many of the tests suggesting separation, none of the indications of similarity remained significant after binomial correction.

INDIVIDUAL CHARACTERS: SHOOT

The theory we are testing, that of coexisting species being less similar to one another than expected when random species are selected from a broader regional pool, has been in the literature from the original formulation of 'limiting similarity' of MacArthur & Levins (1967) to the 'community-wide character displacement' of Leibold (1998). The theory has been difficult to test because of problems in formulating the null model, but we have found good evidence: coexisting species were spaced with respect to leaf area (TS₇₋₉, Table 4). This is similar to Cody's (1986) conclusion, from a study of the niche overlap of leaf morphology in protead communities, that species with similar leaf sizes were less likely to be found coexisting. While the measure of similarity used by Cody is unusual, being related to the degree of sexual dimorphism, and his null model is unclear, this study is one of the few that have demonstrated a greater functional spacing between species in plant communities.

Species co-occurring at several scales were spaced in support fraction, using various measures of overlap (Table 4). This can be seen as effective stratification. The species with low support fraction, by definition, allocate less of the carbon within their shoot into presenting their leaves, and more into manufacturing leaves. Those with high support fraction allocate more into presenting their leaves, probably placing them higher and in the light. This result most likely reflects the coexistence of small herbs and grasses with the taller shrubs (e.g. *Einadia triandra* growing under the *Carmichaelia* bushes). Leaf thickness, and the related character SLA, also demonstrated spacing, mainly at the mini-quadrat scale. That is, within a 10 cm × 10 cm quadrat there tended to be a mixture of species with different leaf thickness (e.g. the thick leaves of *Desmoschoenus spiralis* and the thin leaves of *Acaena agnipila* Gand.), again suggesting niche differentiation in light capture.

INDIVIDUAL CHARACTERS: ROOT

Evidence for local limiting similarity at Kaitorete Spit was found in a large suite of characters related to the acquisition and retention of water and nutrients. Effects were strong in characters reflecting rooting depth (e.g.

root profile, maximum root diameter and horizontal and vertical root extent), suggesting competition for water as a structuring force (Jackson *et al.* 1999). Some of the leaf characters demonstrating spacing, such as SLA and leaf thickness, are related to the water retention ability of the plant (Parkhurst & Loucks 1972; Kramer 1995; Mulkey & Wright 1996). The Kaitorete dunes, like most dune systems, are deficient in both nutrients and water (Peace 1975), but since plant N and P content showed few tendencies to be either clumped or spaced, and the sand at Kaitorete is coarse, our results suggest that competition for water is important in limiting species assembly at Kaitorete Spit. Experiments would be necessary to examine this further.

CONTEXT

In summary, significant tendencies for locally co-occurring species to be functionally spaced and with a low overlap (even after allowing for multiple tests) were seen in many characters (Tables 3 and 4), especially in support fraction, leaf thickness, SLA and root characters. Limiting similarity is operating within this community. While species within this community may also be partitioned by aspects of plant niches not investigated in this study (e.g. temporal partitioning and microhabitat variation), this does not negate the support for limiting similarity found here. A few other studies have convincingly demonstrated such effects in plant communities. Ranta *et al.* (1981) found greater spacing of co-occurring species in the flowering time of bumblebee-pollinated plants (in two out of seven pollinator-types at one site, and three out of six types at another site). Armbruster *et al.* (1994) demonstrated a lower variance in the reproductive characters of co-occurring trigger plants in a western Australian plant community. Our investigation and these two rigorous investigations confirm that functional spacing can be detected within plant communities.

MECHANISM

Greater spacing between coexisting species could have a variety of explanations. Plastic effects undoubtedly occur, the characters of a species changing from one quadrat to another, but since we used in our calculations a single overall character mean and/or distribution for each species, such effects cannot be the explanation for our results. Precisely the same argument applies to microevolution (Turkington & Harper 1979): the process may occur, but it cannot explain our results. Both these processes would tend to obscure rather than explain our results. Evolutionary effects on the scale of a flora of a whole site are similarly not being examined, because our null model includes the site flora.

The coexistence of many species within a community can be due to weak interspecific interactions (Kokkoris *et al.* 2002), but this model cannot be invoked to explain the results of the present study as it cannot explain the

significant spacing of species observed within niche space. Our results must therefore be a demonstration of ecological sorting: small-scale non-random assortment in ecological time. That is, an invading species is more likely to succeed if it has an α -niche that is on a part of the niche gradient that is less occupied by the species locally present. If the invading species is closer along this niche gradient to the species already present, the invasion is more likely to fail, or alternatively, to lead to the extinction of one of the existing species. Armbruster (1995) speculated that such character-based ecological sorting would occur more often in vegetative characters, and we have demonstrated such an effect.

Fargione *et al.* (2003) found that invasion in an experimental grassland was limited by the abundance of species in the same functional group as the invader: C3 or C4 grass, legume or non-legume forb. Our study validates this effect with work in a natural community, by including smaller spatial scales, and by using more precise characterization of the functional niche of the species.

OVERLAP AND POSITION TEST STATISTICS

The different test statistics can give different indications of limitations to species coexistence, and we can relate these differences to the ecological processes. The most consistent indication here of niche limitation was seen using overlap test statistics (Table 4). These are tests close to the original theory of MacArthur & Levins, which is reassuring. If there were enough species present in the pool to populate the niche gradient, or there had been evolution within the site flora to fill the gradient, the distance between adjacent species along the niche gradient would be consistent, i.e. spacing would be regular (Abrams 1983). The only example of this in the present study was for the number of primary root axes, at the mini-quadrat scale (TS₆, Table 3).

In the absence of such a perfect species pool, there may be gaps in occupation of the gradient, but still signs of species spacing. Complex situations can arise. For example SLA in the mini-quadrats was demonstrated to be clumped by TS₆ (variance/range), but spaced by TS₄ (mean NN), TS₇ (mean overlap), TS₈ (max. overlap) and TS₉ (weighted AN overlap). There is a similar pattern in quadrats, though the test statistics involved are not the same: using all characters, there was a high mean nearest-neighbour distance at the two smaller scales (TS₁, Table 2), but spacing was not even (TS₂).

It is often necessary to take an exploratory approach, as we do not know what form the non-random pattern of niches in the community will take. The choice of test statistic can be crucial, not only to explore the ecological meaning of any non-random spacing, but also to avoid misleading conclusions. For example, when Weiher *et al.* (1998) measured the variance of distances between coexisting species along a character axis, their measure calculated this for nearest-neighbour distances. They intended this to give a low value for a spaced dis-

tribution, but, because nearest-neighbour relations can be reciprocal, it can also give a low value for clumps with even spacing within them. Using distances between species adjacent both ways along the gradient, as in the present study, overcomes this. Moreover, the test statistic used as a measure of evenness by Weiher *et al.* (1998) is subject to limitations of interpretation with changing range.

MODELS AND REALITY

We would not expect real communities to be very like the models, because of factors such as disturbance, but there should be a trend in that direction. There is a danger of doing too many tests, but we would most expect to find evidence of MacArthur & Levins' ecological sorting:

1. at a small scale;
2. using all characters (i.e. with the Euclidean distance measures); and
3. using mean AN (adjacent neighbours).

This suggests that the most direct test of the MacArthur & Levins theory in this sand dune community would be using TS₁ and TS₃ (Table 2), at the point and mini-quadrat scales. With this combination, the theory was supported (though with TS₃ the test was powerful enough to show significance only with the latter scale). The strongest evidence for the presence of assembly rules found to date has been from salt marsh, lawn and grassland communities, and at a fine scale, from a point up to 360 mm² (Watkins & Wilson 1992; Klimes 1995; Wilson & Whittaker 1995); our present study extends the upper limit to 50 m².

Schoener (1974) reminded us that while evidence of spacing of niches supports the argument that competition can contribute to community structure, it provides little insight into the relative importance of other processes, such as herbivory. However, there has been very little firm evidence of non-random spacing in communities (Wilson 1999b), and we believe that the present study provides one of the clearest examples to date of limiting similarity operating within a plant community.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC898/JEC898sm.htm>

Appendix S1 Flowchart of computer algorithm used for the analysis of the results.

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