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Spatial autocorrelation in plant communities: vegetation texture versus species composition

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Vegetation texture, describing plant communities by the range of characters present in them, can describe functional variation more effectively than using the identities of the species. We ask whether spatial trends, as seen in spatial autocorrelation (SAc), are stronger in vegetation texture. We also ask in what environment SAc is stronger, whether local or over longer distances, and with what measure of distance.

Roadside vegetation was sampled across an orographic region of the South Island, New Zealand, from a high-rainfall zone up to just above treeline (the "Wet" side) and then down into a rain-shadow area (the "Dry" side). Species composition was recorded in quadrats placed in 30 clusters. Five functional plant characters were measured on all species encountered: characters that have been reported in the literature to correlate with light-capture, heat budget and nutrient strategy. SAc was calculated using a saturation-response type of relation in species composition, and also in texture using the five functional characters.

There was significant species-composition SAc in almost all comparisons, but the maximum percentage of variation explained was 25%. The fit was almost always higher using local, short-distance, comparisons than using comparisons over a whole side (Wet or Dry). On average dissimilarity had reached 90% of its asymptote after ca 250 m. It is concluded that the SAc was mainly due to local factors. SAc relations almost always predicted the presence/absence of species more accurately than their abundance. Distances along the road generally gave a very slightly better fit to species composition than surface distances, suggesting that there might be dispersal limitation. On the Wet side, elevation in overall comparisons gave a still better fit, implying environmental control too. The strength of SAc in texture was strongest on the Dry side, and using overall comparisons, abundance weighting and surface distances, but in other cases texture SAc was weaker than SAc in species composition.

It is concluded that the saturation-response formula used here has theoretical advantages over previous approaches. The SAc in this vegetation seems to be caused by a combination of dispersal limitation, broad environmental trends and especially local environmental effects such as disturbance. SAc in texture may have been weaker overall on the Wet side than on the Dry because the main environmental difference across the former is in frost, and characters correlated with frost resistance have not yet been included in texture analyses.

Plant community ecology is based on analysis of heterogeneity in space. Such community heterogeneity occurs on a wide range of scales, probably all (Goodall 1954). Investigations of the relation between scale and differences in the plant community have only recently commenced and it is not yet clear how community differences should be measured for this purpose.

The basic underlying relationship between heterogeneity and scale is spatial autocorrelation (SAc): patches of vegetation that are further apart in space tend to be more dissimilar. After earlier use of univariate methods (Koenig and Knops 1998), methods were introduced by Kleb and Wilson (1999), Nekola and White (1999) and Mistral et al. (2000) to compare whole-community dissimilarity directly with distance. This paper develops these methods in two ways.

Firstly, whilst space is intrinsically 3-dimensional, almost all SAc studies have ignored the third dimension. We examine it here by analysing SAc not only in terms of the surface 2-D plane, but also in terms of elevation.

Secondly, previous work (Nekola and White 1999, Mistral et al. 2000, Palmer 2005) has compared vegetation samples on the basis of their species composition. This is logical; it follows a long history in vegetation analysis and it has yielded useful conclusions. However, some recent thinking is that the functional characters of the species present may be more important than their taxonomic identity (Kolasa and Rollo 1991, Naeem and Wright 2003, Petchey et al. 2004). This suggests an alternative approach to studying vegetation autocorrelation: examining the spatial change in the functional characters of the species present, i.e. the texture of the community (Barkman 1979, Wilson et al. 1994).

Theoretically, dissimilarity should increase, i.e. similarity decrease, steeply with increasing distance at first, but dissimilarity should approach an asymptote close to complete at large distances. For a dissimilarity index on a 0–1 scale it should approach 1.0. We used a model that met these requirements, a saturation-response formula of the same form as the Michaelis-Menton relation but with a variable intercept:

$$\text{Dissimilarity} = \text{Nugget} + b\,\frac{\text{Distance}}{c + \text{Distance}}$$

where Nugget, b and c are fitted parameters, i.e. constants, within a dissimogram of dissimilarity against distance (Fig. 1; Mistral et al. 2000).

The nugget is the intercept, and is conceptually the dissimilarity at zero distance. This is ecologically interpretable as the unpredictability or randomness of the vegetation at a given point. Because we cannot sample two quadrats at zero distance without resampling the same quadrat, the nugget has to be found by backwards extrapolation. The sum Nugget + b represents the asymptote, i.e. the dissimilarity towards which the vegetation tends as the distance increases and which would be reached at infinite distance. Parameter c controls the rate at which the asymptote is approached. The initial slope, when the distance is small, is b/c but a more intuitive way to represent the shape of the curve is via a derived parameter, the "90% point", i.e. the value of distance at which the dissimilarity reaches 90% of its progress from nugget to asymptote. Our aims in this paper are: 1) given the very few autocorrelation studies at the community level, to move towards generalities. In particular to examine whether the relation differs between environments: here the Wet and Dry sides of a mountain range. 2) To use elevation as an environmental independent variate, and road-distance to give information on dispersal, as well as surface distance. 3) To expand the community-level use of SAc by examining texture as an alternative to species composition. We used roadside vegetation in view of its: a) near-uniform dispersal opportunities, b) uniform management and c) relatively uniform substrate (Wilson et al. 2000).

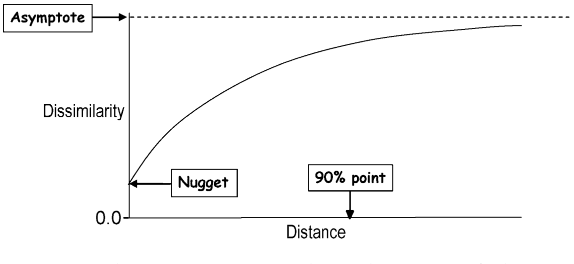

Fig. 1. A dissimogram (Mistral et al. 2000) of the SAc relation and concepts used.

Study sites

Herbaceous roadside vegetation was sampled on two transects within the orographic region of Arthur's Pass, South Island, New Zealand (Fig. 2). The "Wet" transect was on the western side of the Southern Alps and thus exposed to rain-bearing winds (Fig. 3, Table 1); it ran from Arthur's Pass down to near sea level with a considerable increase in minimum temperature but little decrease in rainfall (down to 73% of that at the pass). The "Dry" transect ran from Arthur's Pass eastwards into a dry basin in the rain-shadow of the Southern Alps (beyond this point the elevation increased again); rainfall decreased to 23% of that at the pass, but in the more continental climate minimum winter temperatures were hardly above those at the pass (Fig. 3, Table 1). [They are named "Wet" and "Dry", though clearly the climate was identical when they met at the pass.]

The most frequent species on both sides of the pass included the exotic species *Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus*, *Hypochaeris radicata* and *Trifolium repens*, with *Lotus pedunculatus* also being frequent on the Wet side and *Festuca rubra* on the Dry. The most frequent native species on both sides was *Acaena anserinifolia,* followed by *Coprosma nertera* and *Viola filicaulis* on the Wet side and *Blechnum procerum. Muehlenbeckia axillaris* and *Anaphalioides bellidioides* on the Dry side.

Fig. 2. Roadside 50 m elevation below the summit of Arthur's Pass, on the Dry side.

Methods

Sampling

In order to include variation at a wide range of scales, sampling was performed within clusters of quadrats, and analysed within and between clusters. The 15 clusters on each transect (i.e. 30 in all) were placed at random on the south side of the road within elevational segments of 60 m on the Wet (west) side, and 30 m on the Dry (east) side where the change in elevation was much less. Sampling was restricted to patches with a minimum of 50% vegetation cover, of predominantly herbaceous species, with no evidence of herbicide application. If suitable vegetation was not present at the random location, the other side of the road was used, or, failing that, another random point within the segment.

Each cluster comprised five quadrats at positions 0, 2, 8, 32 and 128 m along the roadside from the random

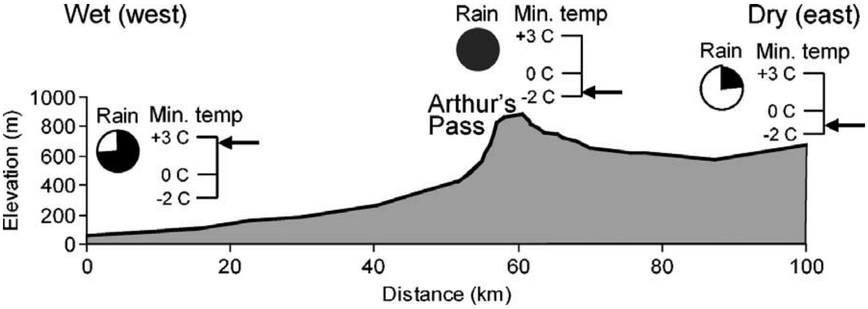

Fig. 3. Section through Arthur's Pass, with rainfall as a proportion of that at the pass, and the mean daily-minimum temperatures in winter (July: Table 1).

Table 1. Climatic conditions at five positions along the two transects. PET = potential evapotranspiration, calculated using the FAO Penman model.

Side	Site	Elevation (m)	Annual rainfall (mm)	Rainfall/PET	Average of daily-maximum temperature January (°C)	Average of daily-minimum temperature July (°C)
Wet	Western limit[1]	60	3468	6.32	15.8	2.3
	Aickens	385	4409	9.60	14.5	1.0
	Arthur's Pass	802	4721	9.03	12.6	−1.8
Dry	Cass	629	1256	1.80	14.2	−1.2
	Eastern limit[2]	748	1105	1.66	13.7	−1.6

[1]near Turiwhate; [2]Castle Hill.

starting point. Quadrats were 1.0 × 0.5 m in size with the longer side parallel to the road, starting 0.5 m from the roadward edge of vegetation. The species present were recorded by shoot presence/absence and ranked according to percentage cover, 1 for the most abundant, 2 for the second-most abundant, etc. (Visual estimates of abundance are not ideal, but ranks can be estimated more repeatably than absolute values. Moreover, in texture analyses the estimates were used only as weights for the characters. Fully objective estimation of species' abundance can be done only via point quadrats or sorting for biomass, both very time-consuming.) Raw ranks are scaled up to the number of species present in a quadrat, and must be re-scaled to give abundance estimates that are comparable between quadrats; they were therefore transformed to a scale with 1.0 for the most abundant to 1/S for the least abundant, where S is the number of species present in that quadrat. The square was used as a very rough approximation to the dominant species being very dominant. Thus, for species s, with rank Rank_s:

$$\mathrm{Abundance}_s = \left(\frac{S + 1 - \mathrm{Rank}_s}{S}\right)^2$$

Texture

The measurement of characters was based on the Photosynthetic Unit (PSU). For a species with simple leaves, this is the leaf. For a species with compound leaves it is the leaflet (for further definition of the leaflet for this purpose see Smith et al. 1994). For a species with no leaves, but only green stems, the PSU is that stem segment that acts as a leaf. However, for readability the PSU is referred to as "leaf" below. Five characters were measured on each species that was found in any site, where possible on 10 replicate shoots/leaves.

1) Leaf area: measured with a leaf area meter. The area of a leaf is related to heat load and air movement, and hence to the control of leaf temperature, photosynthesis and water retention (Grace 1977, Schulze et al. 1996, Smith et al. 1997).

2) Leaf shape (lamina width: lamina length). The length was defined as the longest axis, and the width as the maximum span perpendicular to this. Leaf shape also affects air movement and heat load, and hence transpiration, gas exchange and temperature (Givnish and Vermeij 1976, Grace 1977, Jordan and Hill 1994).

3) Leaf thickness: measured with a micrometer, avoiding major veins. Leaf thickness is related to water retention and light capture (Bongers and Popma 1988, Mulkey and Wright 1996).

4) Specific leaf weight (SLW): defined as

$$\mathrm{SLW} = \frac{\text{leaf dry weight}}{\text{leaf area}}$$

for an individual leaf. SLW is related to photosynthetic capacity, leaf longevity and stress tolerance. It reflects the investment of carbon and nutrient resources to photosynthetic structure. SLW has been seen as a key to the strategy of a species (Westoby 1998, Hunt and Cornelissen 1997).

5) Leaf lobation: measured as

$$\mathrm{Lobation} = \frac{\text{actual leaf perimeter}}{\text{ellipse perimeter}}$$

where: ellipse perimeter = the perimeter of an ellipse with the measured maximum leaf length and width.

Lobation affects heat load, gas exchange and water retention (Givnish and Vermeij 1976). Each variate was standardised to zero mean and unit variance.

Dissimilarity

In analysing species community composition, two indices were used, both having a 0–1 scale: for abundance information: PD (proportional difference): Appendix, Jongman et al. (1987). For presence/absence information: the complement of the Jaccard coefficient, JD: Appendix, Jongman et al. (1987).

In analysing vegetation texture, the calculations were: quantitative: for a pair of quadrats, the dissimilarity in texture was calculated as the Euclidean distance (Jongman et al. 1987) between weighted means for the five characters in a quadrat, the character value of a species being weighted by its abundance in the quadrat. Thus, for quadrat i, the weighted mean for character c of C characters, WM_{ic}:

$$WM_{ic} = \frac{\sum_{s=1}^{S} x_{cs} a_{is}}{\sum_{s=1}^{S} a_{is}}$$

where: x_{cs} = the character value of character c in species s, a_{is} = the abundance of species s in quadrat i.

Then the dissimilarity in texture between two quadrats, i and j, DT_{ij}, is:

$$DT_{ij} = \sum_{c=1}^{C} (WM_{ic} - WM_{jc})^2$$

presence/absence: similar to the above, but with weighting 0 (species absent) or 1 (present).

Distances

Distances were measured alternatively, and separate analyses performed, as: 1) surface-distance: straight-line distances between the quadrats on the New Zealand Map Grid Projection combined with the elevation difference using Pythagoras' equation to give the true straight-line surface distance. The maximum surface inter-quadrat distance was 33.0 km on the Wet side and 35.2 km on the Dry side. 2) Road-distance: distance between quadrats along the west→east road over the pass. 3) Elevation: the difference in elevation between the two quadrats, as a measure more related to the environment.

Spatial auto-correlation

These analyses were performed separately on both transects, Wet and Dry, at two levels: 1) local: calculating distance/dissimilarity combinations between all possible pairs of quadrats within each cluster, and accumulating the distance/dissimilarity combinations over clusters before model fitting, but including any comparisons between quadrats in different clusters. 2) Overall: including compardisons between all possible pairs of quadrats, whether in the same cluster or not.

None of the analyses included any comparisons across the pass, because distance would have been a misleading guide to the environment – the largest distances would be between two sites at lower elevation, and thus in some ways similar in environment. Moreover, one of our aims was to see whether there were different autocorrelation patterns in the two environments. The dissimilarity/distance formula was fitted by the simplex method of Press et al. (2002), varying the values of the three parameters to minimise the sum of squares of deviations between the fitted and observed values.

Significance

The distance/dissimilarity pairs are not independent, so significance was determined with a randomisation test, in which the locations of the quadrats were kept constant and the assemblages of species in a quadrat were kept together, but the assemblages were randomised, without replacement, between the positions, thus keeping constant both species correlations and the pattern of inter-quadrat distances (cf. Palmer 2005). The test statistic was the percentage of variation (i.e. sum of squares) explained by the dissimilarity/distance relation. A one-tailed test was used, because it was not conceived that in the real data dissimilarities would be less related to distance than expected by chance.

Results

Species composition

There was highly significant spatial-autocorrelation (SAc) of species composition with surface-distance in all comparisons (Table 2). However, the amount of the variation in species composition that was explained by distance varied from 5.7 to 24.6%. The percentage was consistently higher examining local, i.e. only within-cluster, variation (20.3% mean over the two sides and over abundance and presence/absence) than in overall relations (mean 7.8%). The lower percentage accounted for in the overall analyses (Table 2) indicates that most of the SAc in species composition occurred over short distances, and longer-distance variation only obscured this. The ability of distance to explain the species composition of the community was higher in terms of the occurrence (i.e. presence/absence) of species (mean 15.6% fit over the two sides and local/overall) than the abundance of them (12.6%). The trend was in this direction in all comparisons (Table 2), indicating that the distance-related control of vegetation was on which species were present, more than the abundance of them. The fit was generally higher on the Wet side (15.7% mean over local/overall and abundance/presence–absence) than on the Dry side (12.6%).

All the nuggets for species composition were considerably above 0.0 (Table 2), but no pattern can be seen in the differences between Wet/Dry and local/overall. The abundance and presence/absence nuggets were not far different in value, but nuggets cannot be

Table 2. Species composition spatial autocorrelation, using surface-distances. Pres/Abs = using the presence/absence of species. % explained = the percentage of variation in species composition explained by the distance (i.e. by the autocorrelation model). p = probability of the observed percentage explained or greater under the null model. For other concepts, see Fig. 1.

Comparisons	Side	Measure	% explained	Nugget	Asymptote	90% point (m distance)	p
Local	Wet	Abundance	22.7	0.39	0.70	208	<0.001
		Pres/Abs	24.6	0.47	0.75	162	<0.001
	Dry	Abundance	14.5	0.48	0.74	520	<0.001
		Pres/Abs	19.4	0.47	0.71	177	<0.001
Overall	Wet	Abundance	5.7	0.38	0.71	171	<0.001
		Pres/Abs	9.4	0.50	0.78	300	<0.001
	Dry	Abundance	7.3	0.43	0.77	278	<0.001
		Pres/Abs	9.0	0.47	0.78	255	<0.001

compared between different indices except when they approach 0.0 or 1.0. The similarity of the asymptotes, 0.73 for abundance and 0.75 for presence/absence, taking both sides and local/overall together, has again to be treated with some caution, but for both indices it was consistently and considerably below the maximum dissimilarity of 1.0, indicating that even the distance extremes are within the same community type. The range between the nugget and asymptote, i.e. the total rise of the curve, was small (0.24–0.34), reflecting the rather low percentages of variation explained, since scatter will give a flat curve.

In three of the four comparisons, dissimilarity reached 90% of the asymptotic value in a shorter distance when examining presence/absence (e.g. 162 m for local comparisons, Wet-side) than with abundance (208 m in the comparable case). That is, with increasing distance one community first becomes unrelated to another in terms of the species present, and then at a greater distance becomes unrelated in terms of the abundances of the species. In three of four cases the 90% point occured at a greater distance on the Dry side.

Types of distance

The roads have numerous bends on both large and small scales so the total road-distance on the Wet side (58.16 km) was 1.76 times the surface-distance, and on the Dry side (53.16 km) 1.51 times. However, the road and surface-distances are highly correlated (r = 0.98). Using only local comparisons, there was, as expected, no measurable difference in SAc fit between surface- and road-distances, since there is almost no difference in the two types of distance within the 128 m range of each cluster (Table 3). With overall comparisons (i.e. including between-cluster distances), the percentage of variation in species composition explained was slightly higher with road-distances (Table 3). These differences are small and no significance test is available, but the consistency is notable.

Using elevational distance (Table 3), the ability of local-comparison SAc to explain community variation was lower than for surface- or road-distances, as expected since elevation itself is only a miniscule ecological factor at that scale. In overall comparisons, on the Wet side the percentage of variation explained by elevation was slightly higher than with either surface- or road-distances, but on the Dry side it was lower. The latter is reflected in considerably higher Dry-side nugget dissimilarities (Table 4) than for surface- or road-distances (Table 2). However, the asymptotic dissimilarities were very similar.

The 90% points cannot be compared directly, because those of Table 4 are in metres elevation, not surface distance, but we can see that, as with surface-distances on the Wet side (overall), the asymptote was approached more quickly in species abundance than in presence/absence. It is notable that with elevation the 90% points were much higher on the Wet side than on the Dry side. That is, changes in species composition occurred over a larger elevational range on the Wet side, and this is not attributable to the greater elevational span on that side because the 90% points are small compared to the total span.

Texture

The dissimilarity/distance SAc fit was generally poorer for dissimilarity in texture than for dissimilarity in species composition (mean over all fits = 4.84%, compared to 12.90% for species composition: Table 5 compared to Table 3). However, in all but one case the fit was significantly better than random. This was true whether the characters of the species were weighted by their abundance or not. However, Dry side texture fits with abundance weighting were, in contrast to all the species-composition fits, all closer than with presence/absence weighting (Table 5, cf. Table 3). Another difference from the species-composition fits is that the overall fits were generally closer on the Dry side than on the Wet. The pattern of lower fits with texture was not

Table 3. Spatial autocorrelation in species composition: percentage of variation that is explained by three types of distance: road-distance, surface-distance and elevation, and on the Wet and Dry sides of the mountain pass. Pres/Abs = presence/absence weighting. ***= $p < 0.001$.

Comparisons	Distance measure	Wet side		Dry side	
		Abundance	Pres/Abs	Abundance	Pres/Abs
Local	Surface	22.68***	24.58***	14.51***	19.35***
	Road	22.68***	24.58***	14.51***	19.35***
	Elevation	14.38***	13.13***	10.31***	16.66***
Overall	Surface	5.72***	9.38***	7.30***	8.95***
	Road	5.84***	9.52***	7.36***	9.10***
	Elevation	6.27***	9.72***	5.58***	8.11***

invariable: the best fits for texture, the overall fit by surface-distance and road-distance on the Dry side with abundance weighting (Table 5), were a little higher than the corresponding values with species composition (Table 3).

With overall texture comparisons (Table 5), in some contrast to species composition (Table 3), road-distances (average fit 3.55%) gave no apparent improvement of over surface-distances (average over abundance and presence/absence and over the two sides = 3.56%). Overall comparisons using elevational distances gave better fits on the Wet side, but worse ones on the Dry, as with species composition.

The nuggets, asymptotes and 90% points with texture showed no consistent trends (Table 6).

Discussion

Community-wide analysis of spatial autocorrelation

The measurement of spatial autocorrelation (SAc) has been used to investigate plant communities increasingly over the past two decades (Legendre 1993). The term “spatial autocorrelation” was taken from univariate methods, but it is appropriate to multidimensional ones. The term “Distance decay” has also been used, but whether the pattern is decay or increase depends on whether similarity or dissimilarity is used, and a major tradition in the SAc literature is to use an index that rises from a nugget intercept to a “sill” asymptote (Jongman et al. 1987). In early work it was unclear how to apply the concept of SAc to multivariate data (Koenig and Knops 1998). The first studies used traditional semivariograms and autocorrelograms (Jongman et al. 1987), applying them to vegetation by examining one variate at a time, such as plant height (irrespective of species) and species diversity H′ (Kuuluvainen et al. 1998). Another approach was to use ordination to reduce community variation to one or a few variate(s). Thus, Meisel and Turner (1998) used principal components analysis to reduce grass, forb, vine, wood, bare ground and leaf litter cover categories to two factors for SAc analysis by semivariance, Galiano (1983) used reciprocal averaging, analysing the first axis for SAc by two-term local variance, and Palmer (1988) used DCA to reduce the variation in five communities in North Carolina, USA, to one axis in semivariograms. This approach discards the variation that is not represented by the first (or first few) axis (axes). We never know how many axes represent ecologically-meaningful and spatially-correlated variation. Including too many axes, or all the variation as is done here, cannot give a bias, only add noise. In fact, all variation in species composition must have a cause, so we could argue that none of the variation is noise and none should be ignored.

Since plant communities are intrinsically multivariate, an approach using multivariate dissimilarity is

Table 4. Elevation-based spatial autocorrelation in species composition: overall comparisons. % explained = the percentage of variation in species composition explained by the distance (i.e. by the autocorrelation model). Pres/Abs = presence/absence weighting.

Side	Measure	% explained	Nugget	Asymptote	90% point (m elevation)	p
Wet	Abundance	6.27	0.51	0.71	57.7	<0.0001
	Pres/Abs	9.72	0.60	0.78	84.0	<0.0001
Dry	Abundance	5.58	0.57	0.77	17.7	<0.0001
	Pres/Abs	8.11	0.60	0.79	29.1	<0.0001

Table 5. Texture spatial autocorrelation: percentage of variation in community texture explained by three types of distance: road-distance, surface-distance and elevation. Pres/Abs = presence/absence weighting. ns = p > 0.1, * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

	Distance measure	Wet side		Dry side	
		Abundance weighting	Pres/Abs weighting	Abundance weighting	Pres/Abs weighting
Local	Surface	6.74**	8.16**	8.85**	6.09*
	Road	6.74**	8.16*	8.85**	6.09*
	Elevation	6.18*	8.88*	5.18**	1.06 ns
Overall	Surface	1.49*	1.52*	9.46***	1.77*
	Road	1.54*	1.58*	9.33***	1.76*
	Elevation	1.87***	2.27***	1.51**	1.12*

more appropriate. Kleb and Wilson (1999), in Canadian prairie and *Populus tremuloides* forest, fitted a linear relation of the Jaccard similarity of two sites *versus* the log of their distance apart, and Mistral et al. (2000) in New Zealand forest, mire and road-centre vegetation used a similar plot. This has the theoretical problem that at very large distances the fit would predict a negative similarity, or a dissimilarity >1.0, and moreover the nugget cannot be calculated because the x-axis never reaches zero. Nekola and White (1999), in American *Picea* spp./*Abies balsamea* forests, used a linear plot of the log of Jaccard similarity against distance. This gave an approximately linear relation with their data, and no prediction of a similarity >1.0, though that would have been possible. However, to achieve this they needed to omit comparisons with zero similarities, which ignores useful information and could introduce bias. In all these analyses a linear relation is not logically tenable since: a) it can predict similarities/dissimilarities outside the range of the index (0–1 with Jaccard and PD), b) there is no reason to expect a linear relation, and c) in all four communities examined by Mistral et al. (2000) the relation was non-linear. Theoretically, dissimilarity should increase (i.e. similarity decrease) steeply with increasing distance at first, but it should approach an asymptote close to 1.0 at large distances, when there are no species in common. An equation of the saturation-response type but with an intercept, as used here, can achieve this, though extrapolation from the observed distances can give an asymptote well below 1.0, as often seen here, or even above 1.0. With a very regular pattern a non-monotonic relation can in theory be found (Fortin and Dale 2005). However, in none of our analyses was there any indication of such patterns, nor have any other workers found them in vegetation sampling. There would have been a danger of a non-monotonic fit had we included both sides of the pass in an analysis, but we avoided that. The most likely alternative formula to the one we used, an exponential one, gave a slightly worse fit (ca 2% worse) to the data.

The need now, as Palmer (2005) says, is for more research in more communities and at broader scales. For this, Tobin (2004) advocated sampling subregions more densely for more accurate fitting at smaller distances, and we achieved this by sampling at both within- and between cluster scales, and also by a roughly geometric spacing of points within local clusters. However, at the large distances it is questionable whether we are describing plant communities, or their reaction to geographical differences.

Table 6. Texture spatial autocorrelation, using surface-distances. % explained = the percentage of variation in species composition explained by the distance (i.e. by the autocorrelation model). Pres/Abs = presence/absence weighting. ∞ = the relation is indeterminate since fitting did not converge.

Comparisons	Side	Distance measure	% explained	Nugget	Asymptote	90% point (m distance)	p
Local	Wet	Abundance weighting	6.74	0.42	0.73	199	0.002
		Pres/Abs weighting	8.16	0.32	0.58	76	0.005
	Dry	Abundance weighting	8.85	0.58	0.99	710	<0.001
		Pres/Abs weighting	6.09	0.40	0.65	140	0.037
Overall	Wet	Abundance weighting	1.49	0.42	0.75	228	0.028
		Pres/Abs weighting	1.52	0.40	0.63	422	0.031
	Dry	Abundance weighting	9.46	∞	∞	∞	<0.001
		Pres/Abs weighting	1.77	0.40	0.73	226	0.009

Strength of spatial autocorrelation in plant communities

Kleb and Wilson (1999) found that in Saskatchewan prairie there was significant SAc, but in nearby forest SAc was weak and non-significant (Spearman's rank correlation between similarity and distance, $r_s = -0.07$ in spring and -0.18 in summer). Nekola and White (1999) found that in their North American forests up to 80% of the variation in species composition could be explained by distance, though the fit was much lower in other comparisons. In contrast, Palmer (2005) found that the SAc relation was weak in tropical rain forest in Costa Rica. Our maximum fit was 25% (Table 3), though there was significant SAc in almost all comparisons, at both the local (short distances) and overall (short and longer) scales. There are differences between these studies in distance range, sampling method, quadrat size, measure of similarity/dissimilarity, climate and vegetation type. It is therefore too early to make generalisations on where SAc will be strong and where it will be weak, beyond the obvious conclusion that it will be stronger when there are strong environmental trends, because the vegetational response to those will overwhelm local effects.

Spatial range: local versus overall comparisons

Almost consistently the local SAc fit was closer than the overall one (Table 3 and 5). This indicates that local factors such as soil, disturbance and plant form were more important determinants of the species composition, and generally of the texture, than climate. The local nature of the SAc is also indicated by 90% points of a few hundred metres (Table 2 and 6), and the similar mean 90% point in local analysis (mean 267 m) and overall ones (mean 250 m). A number of the species present are clonal (e.g. *Hieracium pilosella*, *H. prealtum*, *Hydrocotyle moschata*, *H. novae-zelandiae* and *Trifolium repens*) and this can cause local SAc. Differences in the adjoining vegetation may be a cause, since forest can affect roadside vegetation next to it, probably via the spatial mass effect, i.e. plants getting a foothold but not necessarily establishing long term (Ullmann et al. 1995). The greater difference between local and overall fits on the Wet side (Table 3 and 5) may be caused by differences in topography due to roadmaking in the narrow valley there, disrupting the larger-scale relations.

Environment versus dispersal limitation as the cause of SAc

Spatial autocorrelation can be caused by further sites being different in environment and hence in species composition/texture (e.g. along a climatic gradient) and/or by limits to dispersal (Nekola and White 1999). It is difficult to separate these effects, and here they are potentially confounded by a general rise in elevation up to the pass and a general decrease thereafter (Fig. 2), though the correlation between surface distance and elevation is actually low (on each side: $r = 0.20$).

Palmer (2005) found that in the tropical rain forest that he sampled, most of the SAc could be attributed to the spatial pattern of the environment, implying that, in that community, dispersal limitation was not a significant factor up to the 2 km maximum analysed. In our study with distances up to 35 km, and that of Nekola and White (1999) up to ca 5750 km, dispersal limitation may be significant. This could apply especially to the exotic species on the roadsides studied here which have had only ca 150 yr since introduction to New Zealand to disperse through the area, though Wilson et al. (1992) found that only four out of 24 roadside species surveyed showed evidence of dispersal limitation and none of them were frequent in our survey. The generally better fit of species composition with road-distances compared to surface-distances (overall comparisons; Table 3) points towards some rôle for dispersal along road corridors. Examination of the explanatory power of elevation, well correlated with the climate within each side, also offers evidence. Within a cluster, changes in elevation are small and probably a proxy variate for distance, and we consider only overall comparisons. In these, elevation exhibited a relationship with both species composition (Table 3) and texture (Table 5) that was closer than with surface- or road-distances on the Wet side, but lower on the Dry. A strong rôle for the environment is implied. Smith et al. (1994) found no simple relationship between elevation and texture, but here the improvement in fit with elevation compared to surface distance on the Wet side was seen especially in texture, be it with very poor fits. The explanation is probably that on the Wet side the environmental variation is in frost (Fig. 1), which will be well correlated with elevation, but the main environmental trend on the Dry side is the rain shadow effect, more related to distance.

The overall conclusion, as in the study by Briers and Biggs (2005) with pond invertebrates, is that both environmental and pure distance effects are operative in determining species composition.

Spatial autocorrelation in different conditions: the Wet side versus the Dry side

The lesser SAc fit, in local comparisons, to the species composition on the Dry side (15–19%; Table 3) compared to the fit on the Wet side (22–25%) may be due to more frequent disturbance by vehicles, humans, rabbit grazing, incidental sheep grazing, etc., or to slower recovery (succession) after disturbance in a more hostile environment. Possibly the vegetation recovers well enough in texture (Table 5), but different species are present. The Dry side comprises a larger proportion of exotics (49% of occurrences versus 35% on Wet side), and incomplete equilibrium among them could also cause lower SAc.

In four out of eight comparisons using surface-distance, there was stronger SAc on the Wet side. The other four cases, in which there was stronger SAc on the Dry side, were in: local comparisons, in texture, with abundance weighting (Table 5), overall comparisons, in species composition, with abundance weighting (Table 3), overall comparisons, in texture, with presence/absence weighting (Table 5) and overall comparisons, in texture, with abundance weighting (Table 3).

Thus, when any two out of: a) overall comparisons, b) texture and c) abundance weighting obtained, there was a better fit on the Dry side. This effect reached its peak when "a", "b" and "c" all obtained, i.e. with overall comparisons in texture using abundance weighting, when the fit was about six times closer than on the Wet side.

Texture

There has been no previous study of spatial autocorrelation in texture. Here, SAc in texture followed the same general trends as SAc in species composition, but it was consistently weaker. The concept of texture is that there are alpha (i.e. resource) niches, which can be filled by species with similar characters though not necessarily the same specific identity. This would make texture more predictable than species composition. Even though the range in texture might be less the noise would be considerably less. The concept of texture originated with Barkman (1979). It was applied in other terms to comparisons of fauna between continents, and it was used to examine texture convergence by Wilson et al. (1994) and Smith et al. (1994). The same idea is now used widely under the concepts of functional types and species redundancy. What explains its relative failure here?

One explanation is dispersal limitation as discussed above, i.e. that species with the appropriate characters have not yet reached all sites, though that should affect species composition more than texture. The other explanation is in the nature of the characters measured. The ones used here would be characterised as "soft" sensu Díaz et al. (2004), though they are well related to the functioning of the plant in terms of light capture and water conservation – who could doubt that a thin leaf with a large area will capture more light but maybe use it less efficiently, and tend to lose water faster? Such leaf characters should be especially important in the drought-prone environment of the Dry side. We would expect the abundance-weighted analysis to be a more accurate representation of texture, and we would expect light and water availability to vary over longer distances. These were indeed the conditions in which the texture fit was best – Dry side, abundance weighting, overall comparison (9.46% with surface-distances: Table 5). This was in spite of SAc in species composition being weaker on the Dry side. Probably disturbance/historical factors had more influence on which species were present, but the environment controlled the type of species, and hence the texture.

On the Wet side, with generally lower overall texture fits and higher texture nuggets, there is little change in the water regime (Fig. 3) and probably little in sunlight hours. The gradient there is one of frost, and frost-tolerance is conferred by characters that we did not measure, and are not so easy to measure, such as the proportion of intercellular space, the permeability of the cell membrane, septae in the leaves and the presence of sites or substances within the cells that promote or delay the formation of ice crystals (Sakai and Larcher 1987).

It must be the aim in community ecology to move beyond species identities to the texture of the community, i.e. to generalise from name-based comparisons to the characteristics of the plants that interact with the environment. Our study is only a preliminary step along that path, and progress should come by using a wider range of functional characters.

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