Local texture convergence within three communities in Fiordland, New Zealand

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Abstract: The texture of a plant community, i.e. the range of values in functional characters across the species present, integrates the ecological and evolutionary processes that have led to that community's present species composition. The idealistic prediction of ecological theory is that selection for co-adaptation and competitive sorting will lead to convergence in texture between different patches of vegetation with the same environment. This concept has previously been applied at the continental scale; here it is applied for the first time at a within-community scale. Three communities were sampled, all in Fiordland, New Zealand: a predominantly native heathland, a floodplain grassland largely dominated by exotic species but with a considerable native component, and a native sub-alpine grassland with shrubs. The same five functional characters were measured in each community: height, leaf area, specific leaf area, leaf thickness and support fraction. In all three communities, to varying degrees, there was evidence of texture divergence in height, either in the mean or in the distribution. Tall species tended to associate with other tall species, and short species with other short ones. In the sub-alpine grassland, significant texture convergence occurred in leaf area, i.e. each patch tended to comprise a mixture of some small-leaved species and some large-leaved species. It is suggested that convergence may have occurred only in the sub-alpine grassland because of the greater maturity of the vegetation in evolutionary and ecological terms.

**Keywords:** convergence; functional types; grassland; heathland; sub-alpine; texture.

Introduction

"To do science is to search for repeated patterns" (MacArthur, 1972). One of the primary repeated patterns sought in ecological communities has been similarity in the characters of the species in different areas. The concept is two-fold. Firstly, physical filtering will prevent species from occurring in the habitat unless they have the morphology and physiology that allow them to grow there. Secondly, biotic filtering may cause the competitive exclusion of those species that are too similar in functional characters, and hence in niche, to other species present (MacArthur and Levins, 1964, 1967; Schoener 1989). These processes would lead comparable communities in different areas to converge. We here examine the possibility of convergence in texture at the community level (Fig. 1).

The texture of an area of vegetation is the range of values of a character across the species present, especially of characters thought to have significance in determining the niche of different species (Barkman, 1979; Wilson *et al.*, 1994). For example, an area dominated by narrow-leaved plants is different in texture from one dominated by broad-leaved plants. Areas dominated by succulent plants, plants with tap roots, or plants with few stomata differ in texture from areas where the species have the opposite characters. This would be divergence. The opposite situation, where two communities are notably similar in texture, would be convergence. Such convergence has generally been sought between communities in different parts of the globe, such as shrublands in Mediterranean-climate areas (e.g. Mooney *et al.*, 1977; Wiens, 1991; Wilson *et al.*, 1994).

There has been a mistaken view that such convergence has to be due to evolutionary processes.
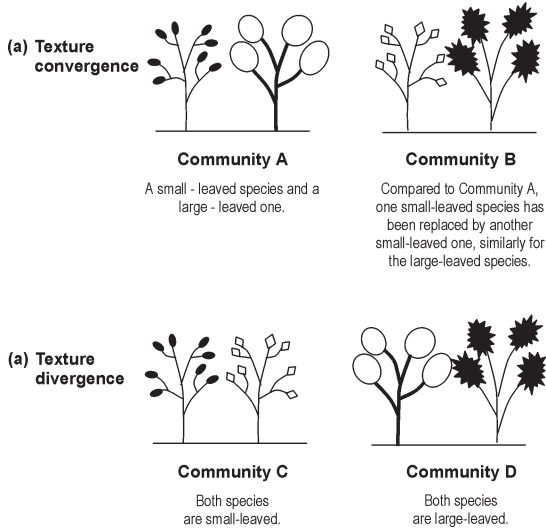
Fig. 1. An schematic illustration of texture convergence/divergence (in both cases, the number of species is too small for statistical significance). (a) Convergence: Two communities that differ in species composition, but have converged in texture by ecological species sorting (i.e. there is **less** variation in leaf size between communities than within). The species balancing each other are drawn differently for identification, but also in practice they would be similar rather than identical in characters. (b) Divergence: Two communities that are different from each other in leaf size, probably because of habitat differences divergence (i.e. there is **more** variation in leaf size between communities than within). [If there is homogeneity within and between communities, the question of convergence/divergence does not arise.]

However, the ecological processes of species sorting can also lead to convergence, because species that are too similar to each other will be competitively excluded (as envisaged by MacArthur and Levins, 1964, 1967). Evolutionary convergence must be initiated by ecological processes in order for there to be a selection differential (Wilson, 1999). Such ecological convergence, if indeed it occurs, could occur between sites that are geographically very close, i.e. within a 'community' (Fig. 1a). In fact, texture convergence will probably be most clearly evident when examining patches within a community, since they share the same species pool. We do not assume that character-based competitive exclusion occurs. Rather, this is the hypothesis that we test.

The study of texture convergence is related to examination of guild proportionality (Wilson, 1989; Wilson and Roxburgh, 1994; Wilson and Whittaker, 1995) and limiting similarity (Armbruster *et al.*, 1994; Weiher *et al.*, 1998). The texture convergence approach to community structure as used in our study has three advantages over the latter two approaches: (1) Texture calculations can be based on either presence/absence or abundance information, whereas guild proportionality and limiting similarity have almost always used just presence/absence information; (2) Texture approaches use a continuous scale for the plant characters, unlike guild approaches which necessarily split continuous variation into arbitrary ranges; (3) Texture examines the total range of character values in the community, not just information on close neighbours as is used in the limiting similarity approach.

There have been only a few studies of texture convergence using an explicit null model that allows significance to be calculated. Those studies have generally compared sites remote from each other, allowing some evaluation of evolutionary processes (e.g. Schluter, 1986; Wiens, 1991), but none of these has examined within-community convergence, the level at which, we argue, convergence due to ecological sorting can best be seen. We examined variation within three communities, to make such a test. The hypothesis we test is that patches of a community will be more similar in texture than expected under a null model. Our null model is that within each site species co-occur without any constraint caused by their characters. Almost all answers in ecology are dependent on the spatial sampling scale (i.e. spatial grain) at which they are investigated (Wiens, 1989b). We examine texture convergence at a range of spatial scales, for the first time.

Study sites

Three study sites were selected, each with no obvious discontinuity in environment (Table 1).

Heathland: This site is situated close to Lake Te Anau. Charcoal, common on the soil surface and within the soil, is evidence of past fires. Scattered trees of *Leptospermum scoparium* form an open grassland/shrubland. The soil is derived from glacial moraine and outwash gravels (Department of Scientific and Industrial Research, 1968).

Floodplain grassland: The site is situated on a river terrace adjacent to the Eglinton river. The vegetation has been lightly grazed by domestic stock. The soil is alluvial in origin (Department of Scientific and Industrial Research, 1968). The vegetation is dominated by exotic grasses (e.g. *Agrostis capillaris* and *Anthoxanthum odoratum*) with many indigenous species (e.g. *Muehlenbeckia axillaris* and *Gonocarpus micranthus*).

Sub-alpine grassland: This site, in the Gertrude Valley, may have been subject to occasional disturbance by rock and snow avalanche, and alluvial

Table 1. Characteristics of the three sites.

	Heathland	Floodplain grassland	Sub-alpine grassland
Latitude	45º 16′ 25″ S	44º 58′ 04″ S	44º 45′ 40″ S
Longitude	167º 47′ 47″ E	168º 00′ 47″ E	168º 00′ 42″ E
Location name	Te Anau Downs	Knobs Flat	Gertrude Valley
Altitude (a.s.l.)	240 m	350 m	800 m
Soil type	Yellow-brown loam	Yellow-brown loam	Recent alluvial
Soil organic content	9.0 %	15.6 %	6.2 %
Number of vascular plant species	50	16	29
Number of native species	40	10	28
Species richness per 0.25 m^2	12.7	6.4	10.1

deposition. The soil is stony. The vegetation is dominated by *Chionochloa pallens* tussock grasses, with herbaceous species such as *Ranunculus lyallii* and *Anisotome haastii*, and the shrub *Hebe cockayneana*, under and between the tussocks. Nearby patches of *Nothofagus menziesii* forest indicate that this site is below regional treeline, but frost may prevent succession of the site's vegetation to tall forest.

Methods

Sampling methods

At each site, 50 quadrats, each 0.5×0.5 m, were placed by restricted randomisation (Greig-Smith, 1983), i.e. a random quadrat was placed within each of 50 sub-areas. Nested within each quadrat was a 0.2×0.2 m quadrat, and within that a 0.1×0.1 m quadrat. Each of these nested quadrats was divided into 0.05×0.05 m sub-quadrats, giving 100, 16 and 4 sub-quadrats respectively at the three scales. In each sub-quadrat the shoot presence (i.e. the presence, at least overhanging the quadrat, of some above-ground part) of all vascular plant species was recorded. This gave an estimate of the abundance of each species as local shoot frequency at three spatial scales. In the heathland site, areas with shrubs of *Leptospermum scoparium* greater than 3 m in height were excluded, to exclude obvious heterogeneity. Soil samples were collected (0-15 cm depth) from five quadrats at each site, and organic content determined by loss on ignition at 500°C.

Character measurement

The basic photosynthetic unit varies between species in its morphological origin: leaf, leaflet or green stem. Measurements were therefore based on the PSU (photosynthetic unit: Wilson *et al.*, 1994; Smith *et al.*, 1994), here defined more precisely as 'the smallest photosynthetic structure for which some independent movement of position or angle is possible'. 'Leaf'

hereafter refers to the PSU. Characters were selected for this study which have been considered crucial to the location or form of the PSU (and thus the potential niche of the species in a community in terms of light capture):

Plant height (cm): The maximum height of a plant of the species found within the study area. It has been suggested that height is the main determinant of above-ground interactions between species, and of their niche (Davies *et al.*, 1998; Westoby, 1998).

Support fraction: The ratio of weight of support material (i.e. non-leaf) to total weight within the terminal shoot, where the latter is defined as the shoot distal to the lowest leaf remaining on the main stem (Wilson *et al.*, 1994). The support fraction indicates the relative allocation to support *versus* photosynthetic tissue for the function of light capture.

Leaf area (cm^2): The area of an individual leaf, measured with a leaf area meter. Leaf area is related to the control of leaf temperature, to air movement, and hence to photosynthesis (Grace, 1977; Smith *et al.*, 1997).

Specific leaf area (SLA: cm^2 g^{-1} dry wt): leaf area / leaf weight for an individual leaf. This has been seen by many as a key to the strategy of a species, being related to relative growth rate (Hunt and Cornelissen, 1997; Westoby, 1998).

Leaf thickness (mm): Measured across the smallest of the three axes on fresh leaves with a micrometer, avoiding major veins. Leaf thickness is related to water, nutrient and light regimes (Bongers and Popma, 1988).

Except for height, samples (*c.* 10) were taken from a random selection of the quadrats, and the mean calculated for each character.

Statistical analysis

Null model

Convergence and divergence have to be judged against a null model in which neither effect is present. The null model used here was based on the null hypothesis that species are distributed without regard to other species present, especially without regard to their characters. The model was effected by a randomisation test (Manly, 1997). Within each site, the model took the character values of the observed species and assigned them to species (in terms of abundance patterns across quadrats) at random (Wilson and Smith, 2001). Thus, the occurrences of each species in each quadrat, and their abundances in those quadrats, were retained. The character values were also retained, but the model randomised which character value was associated with which species. The randomised communities were then compared with the observed data.

Test statistic and significance test

The test statistic, used to compare the observed assemblage of species with assemblages produced by the null-model randomisations, was that of Wilson *et al.* (1994). Calculated for each character separately, it measures the deviance (D) in that character (i.e. the amount of variation) between the quadrats within a site. For character i:

$$D_i = \sum_{j=1}^{J} \left| x_{ij} - x_{i.} \right|$$

where: x_{ij} = the mean of character i over the species in quadrat j (out of J quadrats)
$x_{i.}$ = the mean of character i over all species in all J quadrats.

In calculating the mean of a character in a quadrat, each species can be weighted either equally (thus examining only species presence/absence) or by abundance, in this case by frequency (Wilson *et al.*, 1994). Analyses were performed with both weightings. Analyses were also performed with abundance transformed as the square root and as the rank, but both showed results generally intermediate between presence/absence and abundance, and are not presented.

The value of D calculated from the observed data is D_{obs}. The values calculated for 2000 randomised datasets (D_{rand}) were meaned to give the expectation under the null model, D_{exp}. The observed deviance was compared with that expected under the null model using the index of Wilson *et al.* (1994):

$$RV_{tex} = \frac{D_{obs}}{D_{exp}}$$

This index takes the values:
- \> 1   when difference between quadrats is greater than expected under the null model, i.e. texture divergence,
- = 1   when difference between quadrats is exactly that expected on average under the null model,
- \< 1   when difference between quadrats is less than expected under the null model, i.e. texture convergence.

Patches of a community may converge (or diverge) in the distribution of characters as well as in their mean values (Fig. 2). Using the method of Wilson and Smith (2001), the distribution was examined. In this method, graphs are made for each character, with the species in order of their character values from largest to smallest (as in Fig. 2), but constructed of histogram-type bars, with the width of each bar proportional to the abundance (here local frequency) of the species. To calculate the difference in distribution between two quadrats, their graphs are standardized to the same mean and overlaid. The test statistic for the difference in distributions is the area between the two graphs (Wilson and Smith, 2001). The calculations of RV_{tex} above were repeated using the test statistic for the distribution.

The proportion of D_{rand} values more extreme than D_{obs}, multiplied by 2 to effect a 2-tailed test, gives the probability of the observed result under the null model, i.e. P.

Results

In the heathland site, there was texture divergence in mean height ($RV_{tex} > 1.0$), significant at the smallest spatial scale (0.01 m²) with presence/absence weighting and significant at all spatial scales when weighting by abundance (Table 2). That is, there was more variation between quadrats in the mean height of the species than expected at random. There was some indication of similar effects in the distribution of heights, significant at the largest spatial scale when using abundance. Mean leaf thickness in the heathland showed a tendency to converge between quadrats ($RV_{tex} < 1.0$), which was consistent across the six combinations of spatial scale and measures of abundance, but in no individual case was it significant. (Standard methods for combining probabilities cannot be used, because the tests are not independent.)

In the floodplain grassland site, there were effectively no significant departures from the null model (one, in plant height, at $P = 0.042$ out of 60 analyses), i.e. no converge or divergence was apparent.

In the sub-alpine grassland, height tended to diverge between quadrats ($RV_{tex} > 1$), in both mean and distribution (Table 2; with the exception of the mean at
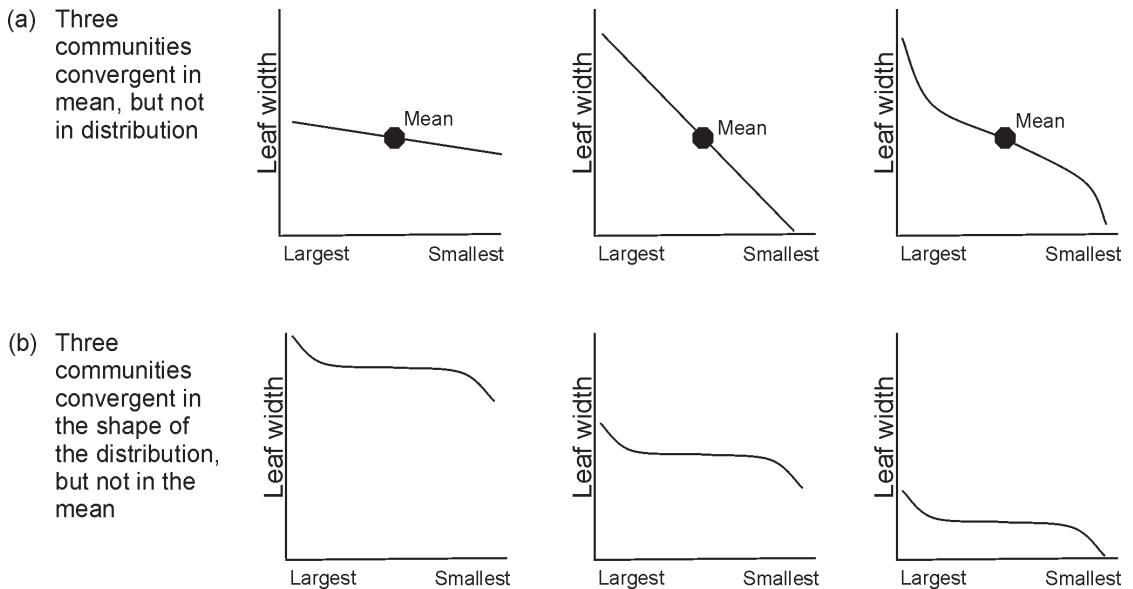
Fig. 2. Comparison between means and distributions. Suppose we arrange species of a community in order of decreasing leaf width. They may converge in (a) mean, or in (b) distribution.

0.24m^2 scale with presence/absence weighting). This tendency was significant in distribution at the smallest spatial scale using weighting by either presence/absence or abundance (frequency), and at the medium scale with abundance. In contrast, leaf area converged between quadrats, in both mean and distribution, and this tendency was significant for most combinations of scale and abundance-measure.

Discussion

We have to be cautious about drawing conclusions from the significant results when they are so scattered. At the floodplain grassland site, we could conclude that there is no community structure present, and there was little evidence of it at the heathland site either. However, the sub-alpine grassland showed 12 significant tests out of 60. The number of significant results would have been increased had we used a 1-tailed test for convergence [as Armbruster *et al.* (1994) did in examining limiting similarity]. However, we believe that in ecology it is rarely obvious in which direction an effect will be found, and therefore a 2-tailed test is necessary. The cases of divergence that we observed justify this approach.

At all three sites, the three nested spatial scales showed similar trends, even if effects were sometimes significant at one scale and not at another. It seems that,

at least within the range of scales that we used, our conclusions about texture convergence/divergence are not critically dependent on the scale examined.

Texture divergence in height in the heathland is readily interpretable, since the vegetation comprised a shrub savannah, even after exclusion of the taller vegetation, with grass/heath vegetation between shrubs, e.g. of *Leptospermum scoparium*, *Halocarpus bidwillii* and *Cyathodes juniperina*. Any particular genotype will show a plastic response to shade, growing taller. This is not the effect observed here. The result we have found is that, within this community, intrinsically tall species tend to associate, as do intrinsically short ones. It is interesting that there is some evidence for a divergent trend with species heights in all three sites.

Almost all environments are patchy (Goodall, 1954). This patchiness is usually reflected in species composition. Often, it is reflected in the characters of the plants: patches with species of one type, versus patches with species of another type. This is texture divergence. One could argue that texture divergence should be the expectation because of the physical filter (Keddy, 1992), not the randomness expressed in the null model. Such texture divergence driven by environmental heterogeneity is in the opposite direction from the texture convergence expected from community assembly theory. It will therefore obscure any texture convergence, and make the latter difficult to find, and the more notable when it is found, as with leaf size

Table 2. Texture convergence ($RV_{tex} < 1.0$) or divergence ($RV_{tex} > 1.0$), and 2-tailed probability (P), in three communities in Fiordland, New Zealand, sampled at three spatial scales (i.e. three quadrat sizes), with species weighted by either presence/absence (P/A) or abundance.

		Spatial scale 0.01m²				Spatial scale 0.04m²				Spatial scale 0.25m²			
		P/A		Abundance		P/A		Abundance		P/A		Abundance	
	Character	RVtex	P	RVtex	P	RVtex	P	RVtex	P	RVtex	P	RVtex	P
Heathland													
Mean	Height	**2.30**[1]	**0.046**	**2.85**	**0.037**	1.30	ns	**2.57**	**0.035**	1.08	ns	**2.29**	**0.040**
	Support fraction	1.28	ns[2]	0.88	ns	2.23	ns	1.58	ns	2.15	ns	1.51	ns
	Leaf area	0.86	ns	0.81	ns	1.00	ns	0.98	ns	0.48	0.072	0.61	ns
	SLA	0.69	ns	0.76	ns	0.64	ns	0.82	ns	0.69	ns	0.76	ns
	Leaf thickness	0.74	ns	0.73	ns	0.66	ns	0.48	0.070	0.81	ns	0.51	ns
Distribution	Height	2.12	ns	2.48	0.094	1.52	ns	2.40	0.061	1.15	ns	**2.30**	**0.012**
	Support fraction	2.09	ns	1.61	ns	2.12	ns	1.63	ns	2.09	ns	1.61	ns
	Leaf area	0.50	ns	0.48	ns	0.93	ns	0.83	ns	0.50	ns	0.48	ns
	SLA	1.59	ns	3.75	ns	1.61	ns	2.94	ns	1.59	ns	3.75	ns
	Leaf thickness	0.79	ns	0.66	ns	0.64	ns	0.57	ns	0.79	ns	0.66	ns
Floodplain grassland													
Mean	Height	1.10	ns	1.25	ns	**1.43**	**0.042**	1.11	ns	0.98	ns	1.18	ns
	Support fraction	0.92	ns	1.27	ns	1.22	ns	1.37	ns	1.09	ns	1.44	ns
	Leaf area	0.97	ns	1.08	ns	1.18	ns	1.02	ns	0.93	ns	1.13	ns
	SLA	1.36	ns	1.51	ns	1.36	ns	1.26	ns	1.30	ns	1.61	ns
	Leaf thickness	1.90	ns	1.45	ns	1.53	ns	1.39	ns	2.07	ns	1.57	ns
Distribution	Height	1.05	ns	1.23	ns	1.20	ns	1.15	ns	1.08	ns	1.23	ns
	Support fraction	0.91	ns	0.99	ns	1.04	ns	1.15	ns	0.96	ns	1.06	ns
	Leaf area	1.01	ns	1.04	ns	1.02	ns	0.96	ns	0.99	ns	1.06	ns
	SLA	1.12	ns	1.36	ns	1.11	ns	1.11	ns	1.07	ns	1.23	ns
	Leaf thickness	1.68	ns	1.53	ns	1.24	ns	1.28	ns	1.62	ns	1.45	ns
Sub-alpine grassland													
Mean	Height	1.33	ns	1.54	ns	1.30	ns	1.55	ns	0.92	ns	1.52	ns
	Support fraction	1.15	ns	1.10	ns	1.01	ns	1.25	ns	1.08	ns	1.11	ns
	Leaf area	0.73	0.058	**0.65**	**0.010**	0.17	ns	**0.12**	**0.004**	**0.19**	**0.015**	**0.13**	**0.016**
	SLA	1.05	ns	0.93	ns	1.10	ns	0.95	ns	1.04	ns	0.88	ns
	Leaf thickness	0.98	ns	0.94	ns	0.88	ns	0.86	ns	0.51	ns	0.59	ns
Distribution	Height	**1.49**	**0.014**	**1.70**	**0.008**	1.27	ns	**1.63**	**0.018**	1.15	ns	1.66	0.085
	Support fraction	1.24	ns	1.28	ns	1.21	ns	1.32	ns	1.11	ns	1.34	ns
	Leaf area	**0.74**	**0.006**	**0.69**	**0.002**	0.19	0.093	**0.11**	**0.022**	**0.18**	**0.008**	**0.14**	**0.021**
	SLA	1.02	ns	0.90	ns	1.17	ns	0.98	ns	1.10	ns	0.94	ns
	Leaf thickness	0.85	ns	0.89	ns	0.92	ns	0.90	ns	0.44	0.071	0.50	ns

[1]Significant results (i.e. $P < 0.05$) are indicated in bold. P values between 0.1 and 0.05 are shown for information, but are not interpreted as significant.
[2]ns = not significant at $P = 0.10$.

(area) in the sub-alpine grassland. Of course, there are many species in common between the observed 50 quadrats of an area. However, this is equally true of the randomised datasets. It therefore cannot be the cause of the convergence seen. The ecological meaning is that, to the extent that there is species turnover between quadrats, when a particular small-leaved species is absent from (or at low frequency in) a quadrat, it tends to be replaced by another small-leaved species, and when a particular large-leaved species is absent from a quadrat it tends to be replaced by another large-leaved species (Fig. 1).

There have been many problems in the search for texture convergence. Most texture convergence work

has been done at the inter-continental scale, but many of the issues apply equally at the much smaller scale examined here. In comparing continents of similar climate, there is always inexact climate matching, leading to possible texture divergence, which could obscure convergence. Exactly the same problem occurs with micro-environmental differences between quadrats. Mooney *et al.* (1977) and Keeley (1992) suggested that hypotheses of convergence were untestable. However, tests against null models already existed (e.g. Schluter, 1986), and have been developed further since (Wilson *et al.*, 1994; Wilson and Smith, 2001). Overlap in species composition can be a minor problem with inter-continental work (with cosmopolitan species, or with exotics). This problem becomes much more severe on a within-community scale. A method that retains such overlap in the null model (Wilson *et al.*, 1994) solves this problem for presence/absence data. There are further problems when using abundance information to weight the species (Smith *et al.*, 1994), which have only recently been overcome (Wilson and Smith, 2001). In continent-scale studies, it can be questioned whether the selective forces are the same in different areas (Wiens, 1989a), but our local study seems to avoid this problem. There is also a problem in continental-scale studies of whether differences in the genetic pools might prevent convergence; again our local study avoids the problem. However, lack of equilibrium might be an issue. Weins (1989a) emphasised there may not have been sufficient time for evolutionary adjustment to have occurred at the continental scale, and this problem might be mirrored at the local scale in lack of time for ecological sorting since the last disturbance.

The heathland area may have been forest-covered in the past, and is probably held back from succession to forest (found nearby) by occasional fires, though the poor soil probably contributes to slow reinvasion by *Nothofagus*. The floodplain grassland is probably kept as grassland by valley frost, perhaps helped by occasional flooding. The grazing represents ongoing disturbance (but all areas will suffer grazing by feral animals, especially deer). The sub-alpine grassland site is probably disturbed by river and/or landslip gravels every hundred years or so, but it may have been some time since the last disturbance. The relatively undisturbed status of the sub-alpine grassland in ecological time, and perhaps its longer history in evolutionary time (being almost 100% native), may have allowed time for ecological species sorting to occur, giving greater community structure and development of texture convergence, the only case of which was observed here.

Assembly rules are hard to find (Wilson, 1999). The demonstration of texture convergence here, be it in only one character in one site, shows that these rules do exist.

Acknowledgements

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