Are ecotone properties scale-dependent?
A test from a *Nothofagus* treeline in southern New Zealand

C. J. Stowe[1], W. D. Kissling[2], R. Ohlemüller[1] and J. B. Wilson[1,3]

[1] *Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand*
[2] *Landscape Ecology and Biodiversity Conservation, Botanical Institute and Botanical Garden,*
University of Greifswald, Grimmerstr. 88, 17489 Greifswald, Germany
[3] *Corresponding author: bastow@otago.ac.nz*

Keywords: Boundary, Dissimilarity, Exotic species, Heterogeneity, Spatial grain, Species-area relations, Species richness.

Abstract: Species richness, the location of exotic species and heterogeneity (investigated via dissimilarity and via species-area relations) were investigated in relation to spatial scale, in an ecotone between *Nothofagus* forest and sub-alpine shrubland. The rate of change in ordination score as well as tree diameter and the dripline were used to locate the position of the ecotone. Patterns of species richness were largely scale-independent, with species richness lowest in the forest community, intermediate in the ecotone, highest a short distance into the shrubland, and lower again in the shrubland further from the ecotone. High richness just into the shrubland is attributed to the existence of a fine-scale spatial mosaic pattern of vegetation, though the spatial mass effect may have a role. Exotic species were absent in the forest, but occurred sparsely in the ecotone and in the shrubland, possibly with decreasing frequency away from the ecotone. Community pattern, expressed by species-based dissimilarity and species-area curves, also differed. The ecotone community was the most heterogeneous (indicated by higher dissimilarity values and a steeper species-area slope with higher Arrhenius z-values), with the forest the least heterogeneous and the shrubland intermediate. We conclude that z-values are inter-woven with both habitat and spatial scale, and that this argues against a universal relationship between species and area.

Nomenclature: Parsons et al. (1995) unless otherwise indicated.

Introduction

Almost all phenomena in community ecology are scale-dependent (Lavorel et al. 1993), and this may be especially true of ecotones (Gosz 1993). We here examine whether the existence of some commonly suggested features of ecotones are dependent on the spatial scale (i.e., spatial grain) at which they are examined. The majority of definitions of 'ecotone' since Clements (1904) have been based on a sharp transition or boundary between two communities (e.g. Tansley and Chipp 1926, Odum 1983, Laurance et al. 2001). A summary of many definitions might be: "a zone where directional spatial change in vegetation is more rapid than on either side of the zone" (Lloyd et al. 2000).

Several properties have been attributed to ecotones: higher heterogeneity (i.e., beta-diversity; Stanisci et al. 2000), higher/lower species richness (Petts 1990, Zólyomi 1987, van der Maarel 1990) and greater invasion by exotic species (Risser 1995, Lloyd et al. 2000) than in the adjacent communities. There is considerable debate whether such specific ecotone properties exist and, if they

do, in which direction they operate. Scale is part of the definition of an ecotone, so evaluation of ecotone properties may be dependent on the spatial scale at which the vegetation is examined (Kolasa and Zalewski 1995).

We examine in detail an ecotone comprising a sharp altitudinal treeline between *Nothofagus* forest and subalpine grassland/shrubland, probably caused by a temperature switch (Wilson and Agnew 1992). We sampled at five scales (i.e., spatial grains), to determine which features of ecotones exist at which scales, examining species richness, the presence of exotic species, and community heterogeneity as indicated by dissimilarity and species-area relations.

Study area

The study area was at treeline on Bald Hill in the Longwood Range (167°48'E, 46°10'S), South Island of New Zealand. Mean annual rainfall is 1600 mm per year. The range is subject to frequent, strong south-westerly winds and occasional snow in the winter. Mean annual

temperature in the adjacent lowlands is 8-10 °C (McGlone and Bathgate 1983).

The ecotone comprised an abrupt boundary between native forest and native sub-alpine shrubland on a slope of 15-20° and at an altitude of 730 m. The forest community consisted of a pure *Nothofagus menziesii* (silver beech) canopy with an understorey of scattered shrubs. Soils under the beech forest were podzolised yellow-brown earths. The sub-alpine shrubland, on peat soils, was below 2 m in height and was dominated by shrubs *Ozothamnus leptophyllus* (G. Forst.) Breitw. and J. M. Ward, *Brachyglottis buchananii, Dracophyllum longifolium*, and *Coprosma* spp., with interspersed *Chionochloa* tussock grasses and the megaherb *Phormium cookianum*.

Methods

Sampling

Four transects were laid out across the ecotone between *Nothofagus*-forest and subalpine shrubland. The first transect was laid at a random position, perpendicular to the apparent boundary, defining the dripline (i.e., the outer edge of tree branches) as the centre of the transect. The transect extended 40 m into the two neighbouring communities. Three further transects were laid out with the centre lines 10 m apart. Quadrats of five different sizes were placed at regular intervals along the centre line of each transect: 0.5 m × 0.5 m quadrats every 2.5 m, 1 m × 1 m and 2 m × 2 m quadrats every 5 m, and 5 m × 5 m and 10 m × 10 m quadrats every 10 m. This resulted in the 10 m × 10 m quadrats being contiguous, with the smaller ones nested within them.

Shoot presence of all vascular plant species were recorded in all quadrats. Diameter at breast height (DBH)

of the broadest tree with shoot presence in each quadrat was measured to describe the structure of the vegetation. Relative light intensity on a cloudy day (compared to open daylight at the same instant) was measured at 2 m above the ground every 2.5 m on the first transect, using two Li-cor light meters with PAR sensors.

Defining the boundary between forest and subalpine shrubland

To objectively define the centre of the ecotone for the analysis, a combination of three measurements was used:

(1) Mid-point of the ordination scores from Axis 1 of a Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) of the quadrat/species information. Mean ordination score was calculated for the eight 0.5 m × 0.5 m quadrats at each end of the transect, to represent the two communities. The ecotone value was taken as the mean of these, the spatial position of this value was taken as the centre of the ecotone according to plant composition. Quartiles between the community and ecotone values were used to give an idea of the width of the ecotone.

(2) Position of the first 0.5 m × 0.5 m quadrat outside the forest without *Nothofagus*, i.e., the first quadrat with DBH = 0 (Fig. 1).

(3) Position of the *Nothofagus*-tree dripline, defined as the outermost point on the transect overhung by one or more branches of *Nothofagus*.

The average of these measurements was taken as the best estimate for the position of the centre of the ecotone on the transect, and the quadrat nearest to this position was assigned position 0.

Figure 1. Relative light intensity (Transect 1) and maximum diameter at breast height (DBH; mean of all transects) of the largest tree with shoot presence in a 0.5 m x 0.5 m quadrat (in each case of *Nothofagus menziesii*), across an ecotone from forest into subalpine shrubland. Zero distance is defined here as the dripline.
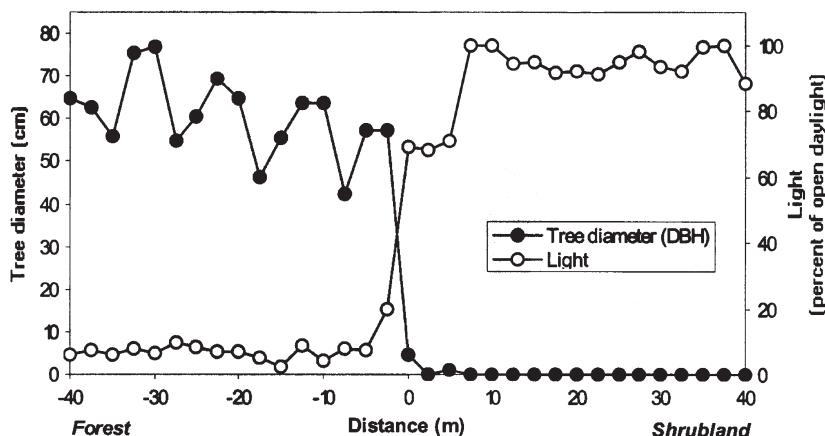
Analysis of species richness and heterogeneity

To calculate heterogeneity, the dissimilarity between quadrats at the same position on adjacent transects was calculated using the complement of the Sorensen (1948) similarity index, often referred to as the complement of the coefficient of community: $D = 1 - 2c/(a + b)$ where c is the number of species shared and a and b are the total number of species in each of the two quadrats. Dissimilarity values along each transect will be affected by the vegetation gradient, but values between quadrats on adjacent transects should mainly reflect mosaic heterogeneity, unrelated to the gradient.

Differences in species richness and in heterogeneity between the forest, the ecotone and the shrubland communities were investigated using one-way analysis of variance and paired t-tests.

Analysis of species-area relations

Mean species richness at each spatial grain was taken from the quadrats nested within each 10 m × 10 m plot, then meaned across the four 10 m × 10 m quadrats at each distance from the ecotone. Species-area curves were calculated for each distance by two models: (1) Arrhenius' (1921)

power function: $S = CA^z$, where S = mean number of species in area A, and C and z are fitted constants; and (2) Gleason's (1922) Exponential model: $S = C + z \log_e A$. These models were extrapolated to an area the size of New Zealand and the results compared to the observed number of species in the native and naturalised exotic vascular flora of New Zealand. This represents a test of the hypothesis that the observed heterogeneity is a local sample of the heterogeneity across the country (Wilson and Chiarucci 2001), and visualizes the implications of the z value.

Results

Light, vegetation structure and species composition

Relative light intensity (percentage of open daylight) within the *Nothofagus* forest was 0-10% and in the shrubland 80-100%, with a sharp increase across the ecotone closely reflecting the extent of *Nothofagus* trees (Fig. 1). The DCA ordination shows the change of species composition, with distinct communities at either end of the transect (Fig. 2). The rate of change of species composition across the ecotone differed between transects, from a
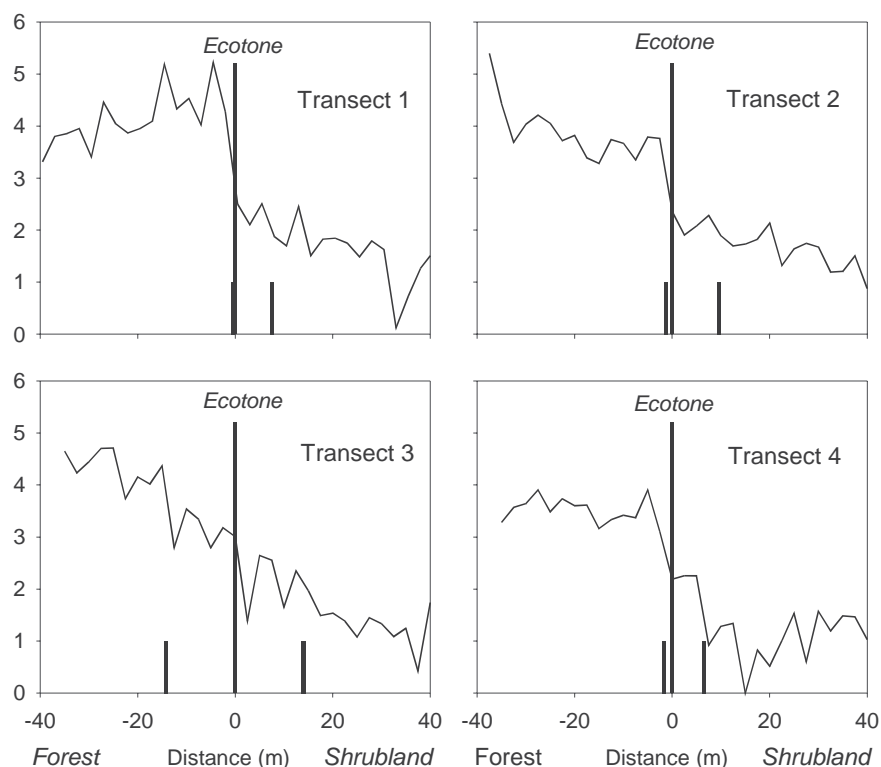
Figure 2. Change in species composition along the four transects as shown by Axis 1 scores from a DCA ordination. The vertical lines indicate the calculated position of the ecotone (defined as distance zero) between the forest and the shrubland communities; the shorter lines indicate the 25 percentiles.
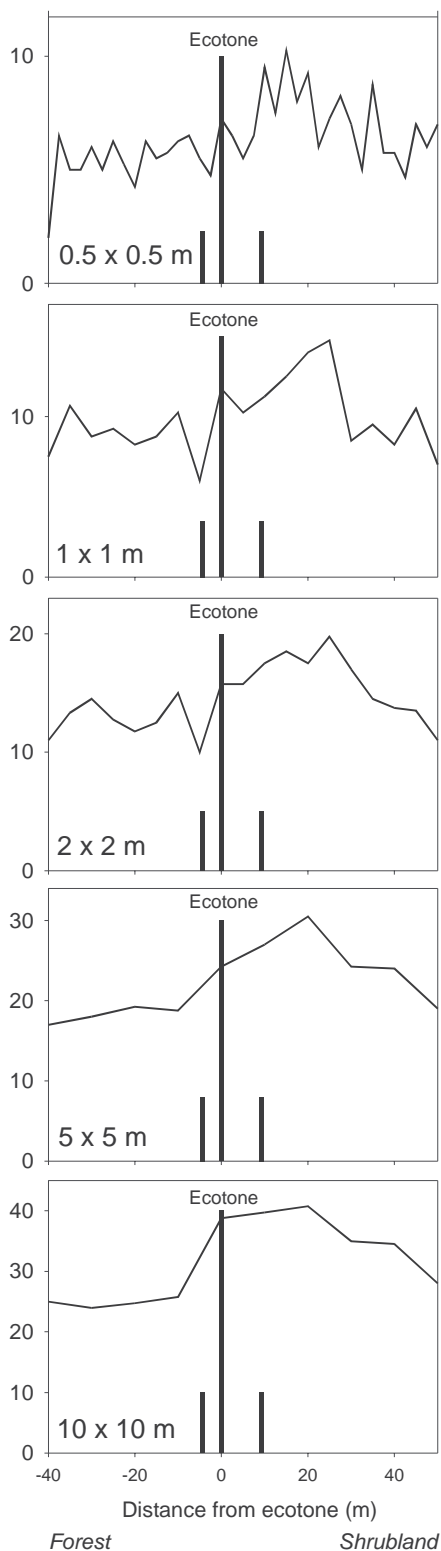
Figure 3. Mean species richness on all transects at five different scales (quadrat size 0.5 × 0.5 m, 1 m × 1 m, 2 m × 2 m, 5 m × 5 m, 10 m × 10 m). The vertical lines indicate the calculated position of the ecotone (defined as distance zero) between the forest and the shrubland communities; the shorter lines indicate the 25 percentiles.

steeper change on Transect 1, to a more gradual change on Transect 3.

Species richness

Mean species richness at all scales was low further into the forest, and except at 0.5 m × 0.5 m almost as low further into the shrubland (Fig. 3; Table 1). There were significant differences ($P < 0.05$) in species richness between communities at all scales except 1 m × 1 m. Shrubland quadrats had significantly higher species richness than forest plots, with richness in the ecotone generally being intermediate. At all scales sampled, species richness peaked 10-20 m beyond the ecotone, in the shrubland community (Fig. 3).

Exotic species

There were no exotic species in the forest. There were a few in the ecotone and shrubland, and they were sparse, with some suggestion of a decrease further into the shrubland (Table 2).

Heterogeneity

Mean heterogeneity across transects was highest and most variable in 0.5 m × 0.5 m quadrats, and decreased in larger quadrats (Table 1). The trend was for the forest to have lowest heterogeneity (Table 1), and at three of the five investigated scales (1 m × 1 m, 2 m × 2 m, 10 m × 10 m) the heterogeneity was higher in the ecotone than in either forest or shrubland. However, heterogeneity was not significantly different (i.e., $P > 0.05$) between the three communities at any spatial scale.

Species-area relations

Both the Arrhenius and Gleason models gave good fits to the observed species richness values. However, the Gleason model gave an inferior fit, explaining 98.7, 95.3 and 96.3% of the variation in the forest, ecotone and shrubland respectively (cf. Table 3). Slopes from the Gleason model for forest, ecotone and shrubland were 2.90, 4.18 and 4.25, which gave extrapolations to the whole of New Zealand of 85.8, 122 and 124.3 – serious underestimates.

Parameter z from the Arrhenius model varied with distance from the ecotone between 0.227 and 0.296, with a mean value over the whole sampled area of 0.264, very close to Preston's (1962) 'canonical' value of 0.26 (Table 3). However, z-values were significantly higher in ecotone and shrubland plots than in forest plots (Table 3). When extrapolated to the New Zealand flora as a whole (Table 3), the Arrhenius model gave predictions from for-

Table 1. Mean species richness and heterogeneity values (dissimilarities, by the complement of the coefficient of community) from forest, ecotone and shrubland communities at different spatial scales. Letters indicate means significantly different from each other by t-test. P-values from one-way analysis of variance.

Spatial grain	Community	Species richness Mean	Species richness P	Heterogeneity Mean	Heterogeneity P
0.5 x 0.5 m	Forest	5.6 a		0.50	
	Ecotone	5.9 ab	0.006	0.61	0.085
	Shrubland	7.3 b		0.62	
1 x 1 m	Forest	9.3 a		0.54	
	Ecotone	9.3 a	0.259	0.62	0.60
	Shrubland	11.3 a		0.57	
2 x 2 m	Forest	13.3 a		0.48	
	Ecotone	13.8 ab	0.019	0.58	0.15
	Shrubland	16.9 b		0.53	
5 x 5 m	Forest	18.3 a		0.39	
	Ecotone	24.3 ab	0.006	0.42	0.64
	Shrubland	26.4 b		0.43	
10 x 10 m	Forest	24.9 a		0.33	
	Ecotone	38.8 b	<0.001	0.38	0.59
	Shrubland	37.5 b		0.35	

Table 2. The occurrence (number of exotic species per distance band) and frequency (mean number of exotic species per quadrat) of exotic species among the four quadrats at each distance across the ecotone from forest to shrubland.

Position (m out from ecotone)	Number of exotic species	Mean frequency out of four transects 0.5 × 0.5 m	Mean frequency out of four transects 10 × 10 m
-40	0	0.0	0.00
-30	0	0.0	0.00
-20	0	0.0	0.00
-10	4	0.0	1.50
0	4	0.125	1.75
10	4	0.125	1.75
20	4	0.125	1.25
30	2	0.125	1.00
40	1	0.0	0.50

Table 3. Species-area relations within 10 m x 10 m quadrats by the Arrhenius model for forest, ecotone and shrubland communities, with z-values (slopes) and the number of species (native and naturalised exotic vascular plants) predicted by extrapolation for the whole of New Zealand, compared to the actual number. Letters indicate significant differences between communities by t-test (one-way analysis of variance for z: P = 0.0112; for predicted number of species: P = 0.002).

Position	Number of quadrats	% of variation explained	z	Predicted number of species for NZ	Actual NZ
Forest	16	99.5	0.242 a	5020 a	4126
Ecotone	4	99.7	0.296 b	23500 b	4126
Shrubland	16	99.8	0.278 b	16443 b	4126

est plots ranging from 3399 to 5951 species, close to the true number of 4126 vascular plant species (Williams and West 2000). Extrapolation from the ecotone quadrats considerably over-estimated the New Zealand flora, and extrapolations from the shrubland community were also high (Table 3).

Discussion

The patterns one observes in nature are dependent on the spatial scale of investigation (Wiens 1989). This is likely to be especially true of ecotones, since they are intrinsically spatial phenomena (Gosz 1991). Therefore, any 'rules' proposed for the ecological processes and at-

tributes we may find in ecotones are suspect unless the spatial scale of the phenomenon is considered.

Species richness

Several authors have proposed that species richness should be higher in ecotones than in the adjacent communities (Petts 1990, Odum 1983, Zólyomi 1987). Mechanisms that have been suggested for such an effect are the spatial mass effect (Shmida and Ellner 1984), a vegetation mosaic in ecotones (Risser 1995), greater productivity, and greater environmental fluctuation (Dabrowska-Prot et al. 1973). However, it is not clear that greater productivity or environmental fluctuation are actually attributes of ecotones, nor whether they would cause an increase in species richness (Lloyd et al. 2000). The opposite proposition, that species richness will be lower in ecotones, has also been attributed to greater environmental fluctuation (van Leeuwen 1966, van der Maarel 1976). Empirical studies have found species richness to variously be greater, lower, or intermediate in ecotones (Lloyd et al. 2000).

Thus, some arguments predict higher richness at the ecotone itself, but in fact richness is greater just beyond it in the shrubland (Fig. 3). The higher heterogeneity demonstrated at the ecotone suggests the effect could be due to a small-scale vegetation mosaic in the shorter vegetation just beyond the ecotone. Climate change, leading to an up-slope invasion by forest species, could produce a similar effect (Kullman 1993). However, even with no climate change, the spatial mass effect could give this pattern. Species from the shrubland will tend to disperse to the forest but not survive in the shade, but species from the forest could disperse into the shrubland and perhaps remain until an unusually hard frost kills them. Of 14 forest species (species that are 1.5 or more times more abundant in the forest than in the shrubland), eight extend into the shrubland; of 38 shrubland species, only seven extend into the forest. The stray forest species add to the thirteen shrubland species that appear in the first 10 m upslope from the ecotone. The lower species richness higher up the slope, away from the ecotone, may also be due to a harsher climate there, towards an exposed ridge.

Our definition of an ecotone is 'a zone where directional spatial change in vegetation is more rapid than on either side of the zone'. Change in species composition is shallow on some transects, compared to the sharp change in tree sizes and light (Figs. 1, 2) suggesting that the spatial mass effect does occur, especially outwards into the shrubland.

Exotic species

It has been suggested that exotic species are especially likely to occur within ecotones, both anthropogenic and natural (Risser 1995). Here, there were no exotic species in the forest, a few in the ecotone, and perhaps slightly fewer further into the shrubland, which could again be attributed to the harsher climate there. This is weak evidence for the occurrence of exotic species in ecotones.

Heterogeneity

It has been suggested that ecotones typically comprise a small-scale vegetation mosaic (Pound and Clements 1900; Risser 1995), perhaps because moving towards the ecotone conditions will become marginal for some species, resulting in increased sensitivity to local site conditions and suitable habitat therefore becoming fragmented. Such mosaics have occasionally been documented, for individual species (e.g., Neilson and Wullstein 1983) and for communities (Meiners and Pickett 1999).

The mosaic effect depends on the spatial scale at which the system is viewed - what is an ecotone when viewed at one scale may break into a mosaic at smaller scales. We found no statistically-significant trend to greater heterogeneity (i.e. higher beta-diversity) in the ecotone, though at three of the five spatial scales sampled, heterogeneity was highest in the ecotone (Table 1). Forest plots showed lowest heterogeneity. Stanisci et al. (2000) found the opposite pattern in a *Fagus*-forest/*Juniperus*-shrubland ecotone, with heterogeneity at a minimum in the ecotone. They explain this with a well defined transitional zone of shrubby vegetation around the forest edge, with extensive species exchange leading to uniform species composition in the ecotone. The *Nothofagus* tree line investigated here is obviously much sharper. Whether there is heterogeneity in an ecotone may differ between types of ecotone.

Species-area relations

Species-area relations can provide evidence on community structure (Yodzis 1978) and have been used as an expression of heterogeneity (Wilson and Chiarucci 2000). We discuss the Arrhenius model because: (1) it gave a better fit for the communities, (2) it gave closer predictions to the observed species richness of New Zealand, and (3) previous extrapolations of species-area curves have used the Arrhenius model (Kilburn 1966, Dony 1977, Wilson and Chiarucci 2000).

The slope of the species-area curve depends on the rate at which new species are encountered as sample area increases: more heterogeneous areas accumulate species

faster than homogenous areas. If the relatively solid areas of the adjacent communities were giving way to increasingly smaller community patches of the two communities at the ecotone, indicating a spatial mosaic, there would be a steeper species-area curve (i.e., higher values of z). This is in fact what we found for the ecotone vegetation (Table 3). As a result, extrapolating species richness from the ecotone to an area the size of New Zealand yielded an expected value almost six times size of the flora. In contrast, extrapolation from the more homogenous forest community gave an estimate close to the actual value (Table 3). This could be taken to mean that ecotones are atypical in the landscape, and that broad-scale variation is only within-community variation writ large, but this concept remains controversial (Wilson and Chiarucci 2000, Hill 2001, Wilson and Chiarucci 2001). Since z-values reflect both habitat and spatial scale there may be no universal relationship between species and area at larger spatial scales.

Conclusion

Our study has shown no evidence for scale-dependent species richness patterns and little evidence for scale-dependent heterogeneity across a treeline ecotone. There was evidence for greater species richness, but just above the ecotone in the more favourable light environment of the shrubland, possibly due to the spatial mass effect. The few exotic species were possibily concentrated in the ecotone. Heterogeneity was highest between ecotone plots at three of the five investigated scales. This is confirmed by the species-area relations at the ecotone. The observed properties across this pronounced *Nothofagus*-forest/subalpine shrubland ecotone are consistent across the entire investigated range of scale.

References

Arrhenius, O. 1921. Species and area. *J. Ecol.* 9: 95-99.

Clements, F.E. 1904. *Studies in the Vegetation of the State. III. The Development and Structure of Vegetation.* The Seminar, University of Nebraska.

Dabrowska-Prot, E., J. Luczak and Z. Wojcik. 1973. Ecological analysis of two invertebrate groups in the wet alder wood and meadow ecotone. *Ekol. Polska* 21: 753-809.

Dony, J. G. 1977. Species-area relationships in an area of intermediate size. *J. Ecol.* 65: 475-484.

Gleason, H.A. 1922. On the relation between species and area. *Ecology* 3: 158-162.

Gosz, J.R. 1991. Fundamental ecological characteristics of landscape boundaries. In: M.M. Holland, P.G. Risser and R.J. Naiman (eds.), *Ecotones: the Role of Landscape Boundaries in the Management and Restoration of Changing Environments.* Chapman and Hall, New York. pp. 8-30.

Gosz, J.R. 1993. Ecotone hierarchies. *Ecol. Applic.* 3: 369-376.

Hill, M. O. 2001. Do plant communities exist? A reply to Wilson and Chiarucci. *J. Veg. Sci.* 12: 143-144.

Hill, M.O. and H. G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.

Kilburn, P. D. 1966. Analysis of the species-area relation. *Ecology* 47: 831-843

Kolasa, J. and M. Zalewski. 1995. Notes on ecotone attributes and functions. *Hydrobiologia* 303: 1-7.

Kullman, L. 1993. Pine (*Pinus sylvestris* L.) tree-limit surveillance during recent decades, central Sweden. *Arctic Alp. Res.* 25: 24-31.

Laurance, W.F., R. K. Didham and M.E. Power. 2001. Ecological boundaries: a search for synthesis. *Trends Ecol. Evol.* 16: 70-71.

Lavorel, S., R. H. Gardner and R. V. O'Neill. 1993. Analysis of patterns in hierarchically structured landscapes. *Oikos* 67: 521-528.

Lloyd, K.M., A. A. M. McQueen, B. J. Lee, R. C. B., Wilson, S. Walker and J. B. Wilson. 2000. Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. *J. Veg. Sci.* 11: 903-910.

McGlone, M.S. and J.L. Bathgate. 1983. Vegetation and climate history of the Longwood Range, South Island, New Zealand, 12 000 B.P. to the present. *N. Z. J. Bot.* 21: 293-315.

Meiners, S.J. and S.T.A. Pickett. 1999. Changes in community and population responses across a forest-field gradient. *Ecography* 22: 261-267.

Neilson, R.P. and L.H. Wullstein. 1983. Biogeography of two southwest American oaks in relaton to atmospheric dynamics. *J. Biogeogr.* 10: 275-297.

Odum, E.P. 1983. *Basic Ecology.* Saunders College Publishing, Philadelphia.

Parsons, M.J., P. Douglass and B. H. Macmillan. 1998. Current names list for wild gymnosperms, dicotyledons and monocotyledons (except grasses) in New Zealand as used in herbarium CHR. Manaaki Whenua - Landcare Research, Lincoln, New Zealand.

Petts, G.E. 1990. The role of ecotones in aquatic landscape management. In: R. J. Naiman. and H. Décamps (eds.), *The Ecology and Management of Aquatic-terrestrial Ecotones,* UNESCO, Paris. pp. 103-140.

Pound, R. and F. E. Clements. 1900. *The Phytogeography of Nebraska,* 2nd ed. Botanical Seminar, Lincoln.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43: 185-215 and 410-432.

Risser, P.G. 1995. The status of the science examining ecotones - A dynamic aspect of landscape is the area of steep gradients between more homogeneous vegetation associations. *Bioscience* 45: 318-325.

Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55

Sorensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of vegetation on Danish commons. *Biologiske Skrifter*, 5(4), 1-34.

Stanisci, A., D. Lavieri, A. Acosta and C. Blasi. 2000. Structure and diversity at Fagus timberline in central Italy. *Community Ecol.* 1: 133-138.

Tansley, A.G. and T. F. Chipp. 1926. Aims and methods in the study of vegetation. British Empire Vegetation Committee, London.

Van der Maarel, E. 1976. On the establishment of plant community boundaries. *Ber. Deutsch. Bot. Ges.* 89: 415-443.

Van der Maarel, E. 1990. Ecotones and ecoclines are different. *J. Veg. Sci.* 1: 135-138.

Van Leeuwen, C. G.1966. A relation theoretical approach to pattern and process in vegetation. *Wentia* 15: 25-46

Wiens, J.A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385-397.

Williams, J.A. and C. J. West. 2000. The ecology and management of environmental weeds: foreword. *Austral J. Ecol.* 25: 423-424.

Wilson, J.B. and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Adv. Ecol. Res.* 23: 263-336.

Wilson, J. B. and A. Chiarucci. 2000. Do plant communities exist? Evidence from scaling-up local species-area relations to the regional level. *J. Veg. Sci.* 11: 773-775.

Wilson, J.B. and A. Chiarucci. 2001. Self-similarity and phantoms: a response to Hill. *J. Veg. Sci.* 12: 299.

Yodzis, P. 1978. Competition for space and the structure of ecological communities. Lecture Notes in Biomathematics 25. Springer-Verlag, Berlin.

Zólyomi, B. 1987. Coenotone, ecotone and their role in preserving relic species. *Acta Bot. Hung.* 33: 3-18.