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Abstract. Constrained canonical correspondence analysis was used to compare the elevational distribution of conifer-broadleaved hardwood forests at nine localities on South Island, New Zealand. Elevations of individual species were compared using cover-weighted mean elevations and cover-weighted standard deviations of mean elevation. Mean elevations of floristically similar stands declined with latitude, but was also lower at a locality with a granite substrate than at an adjacent locality with a schist substrate. The mean elevation breadth of frequent species (those in >5% of stands) was greatest at a locality underlain by schist and least at a locality underlain by granite. This is consistent with wide habitat breadth for species in early successional stages, because forest underlain by schist is more frequently disturbed than forest underlain by granite. Elevation breadth of frequent species was less, and species' turnover greater, in South Island conifer-broadleaved hardwood forests than in conifer forests at similar latitudes in the Southern Rocky Mountains, USA.

Keywords: Biogeography; Constrained ordination; Correspondence analysis; Floristics; Gradient analysis.

Nomenclature: Allan (1961); Quinn (1982).

Introduction

Timberline is often used as a reference point for determining geographic variation in the elevation of montane forest zones (e.g. Daubenmire 1943; Troll 1973; Wenhua & Pichuen 1984). However, elevational variation is more complex than can be expressed by a simple relationship with timberline. For three localities in the Southern Rocky Mountains, the elevation of floristically similar forest stands and individual species declined with increasing latitude, but the magnitude of decline between localities varied with relative elevation, and site moisture status (Allen, Peet & Baker 1991). For example, forests on moist, shady sites at Taos, New Mexico, occurred at higher elevations relative to Wet

Mountain Valley, Colorado, than forests on dry, sunny sites. In addition, the elevation breadth of frequent species (found in >5% of stands) increased with latitude, suggesting that the degree of community differentiation decreased with increasing latitude. Elevation breadth may also be related to other factors. For example, species in undisturbed forest may have comparatively narrow elevation breadth because competitive sorting during succession reduces overall habitat breadth (Christensen & Peet 1984; Peet & Christensen 1988). However, few quantitative analyses of geographic variation in such parameters exist.

Conifer-broadleaved hardwood forests are widely distributed on South Island of New Zealand (Fig. 1). Compositional variation in these forests has been related to differences in elevation and stage of forest development after disturbance (Wardle 1977; Reif & Allen 1988). In these forests disturbance is often in the form of landslides, the frequency of which depends on factors such as geologic substrate. Mature stands are often found on comparatively uniform, infertile soils on stable, granite substrates (Reif & Allen 1988). Fractured, schist substrates, however, are subject to frequent landslides with the consequence that seral stands are more frequent on these substrates. In addition, canopy dieback of forest underlain by schist substrates is prevalent, and has been attributed to browsing by introduced, brush-tailed possums (*Trichosurus vulpecula* Kerr.) which prefer seral forest (Reif & Allen 1988).

In this study, compositional variation along the elevation gradient was compared for South Island conifer-broadleaved hardwood forests at nine localities (Fig. 1). Specific objectives were: (1) to compare the compositional variation accounted for by the elevation gradient; (2) to determine elevation differences between the nine localities for floristically similar forest stands and individual species; and (3) to compare the elevation breadth of frequent species (found in > 5% of stands at a locality) along the elevation gradient at the 9 localities.

Methods

Study areas

The nine study localities were selected throughout the montane conifer-broadleaved hardwood forests of South Island to cover a range of latitude, climates, and geological substrates (Table 1; Fig. 1). In these forests, the dominant canopy hardwood species include *Metrosideros umbellata*, *Weinmannia racemosa*, and *Quintinia acutifolia*. At lower elevations (<600 m) these species are associated with the conifers *Dacrydium cupressinum* and *Prumnopitys ferruginea*, and at higher elevations (>800 m) with the conifers *Libocedrus bidwillii* and *Podocarpus hallii*. These forests usually occur in areas with high rainfall (up to 12 000

Table 1. Grid reference, geologic substrate¹, number of relevés, and elevation range sampled for each locality.

Locality	Grid reference		Geologic Substrate	No. relevés	Elevation range (m)
Mount Bovis	42°07' S	171°28' E	sandstone	25	370 - 710
Taramakau	42°40' S	171°30' E	granite	188	100 - 1100
Camp Creek	42°42' S	171°33' E	schist	384	170 - 1260
Kokatahi	42°56' S	171°12' E	schist	80	290 - 880
Bonar Range	43°05' S	170°40' E	granite	102	75 - 980
Wilberforce	43°07' S	171°16' E	greywacke/ argillite	49	670 - 990
Wanganui	43°10' S	170°38' E	schist	127	140 - 1010
Fox	43°29' S	170°02' E	schist	174	70 - 1030
Catlins	46°30' S	169°20' E	sandstone/ siltstone	73	5 - 630

¹Geologic substrate from New Zealand Geological Survey (1972).

Fig. 1. Generalised outline of South Island conifer-broadleaved hardwood forest (shaded) and locations of the nine study localities.

mm/yr) and mild temperatures (Wardle, Bulfin & Dugdale 1983).

With the exception of the Mount Bovis and Catlins localities, the forest zone was sampled from alluvial plains (usually <200 m elevation) to the upper limit of forest (woody vegetation >2 m tall; Table 1). On Mount Bovis, a northern outlier of this forest type, conifer-broadleaved hardwood forests occurred only between 370 and 710 m elevation, and *Nothofagus* spp. dominate at both higher and lower elevations. In the Catlins, a southern outlier of this forest type, the highest elevation of conifer-broadleaved hardwood forest is also below the upper limit of forest. For all localities, forest modified by logging or grazing of domestic stock was excluded from sampling, although all forest has been, and continues to be, modified by introduced browsing animals.

Data collection

Relevés used in this analysis were collected during a detailed survey of conifer-broadleaved hardwood forests (Reif & Allen 1988). Relevés were subjectively located to sample the range of forest composition within elevation bands at each locality. Each relevé represented a comparatively homogeneous area, generally from 100 to 400 m². Vascular species present were recorded in four strata, generally based on physiognomy:

1. The *Tree stratum* included emergent trees, canopy trees, and lianas in the main canopy. Where the upper forest layer was less than 6 m, a tree layer was not recorded.
2. The *Sub-canopy tree and shrub stratum* included sub-canopy trees, shrubs, tree ferns, and lianes between 1 and 10 m tall. Where the canopy was less than 6 m tall, it was formed by this layer. If the vegetation was less than 1 m tall (e.g., on recent landslide surfaces) only a ground layer was recorded.
3. The *Ground layer* included all herbaceous and woody species less than 1 m tall.
4. The *Epiphyte stratum* included all epiphytes growing on living and dead trees.

The cover of individual species in each stratum except the epiphyte layer, was estimated using the seven-value scale of Braun-Blanquet (r = solitary, small cover; + = few plants, cover <1.0%; 1 = cover 1 to 5%; 2 = 6 to 25%; 3 = 26 to 50%; 4 = 51 to 75%; 5 = >76%; Mueller-Dombois & Ellenberg 1974), which is a combined estimation of cover and abundance.

Elevation, aspect, and slope were recorded for each relevé. Potential solar radiation was calculated for each relevé using latitude, aspect, and slope (see Frank & Lee 1966).

Data analysis

The data for each species was transformed into a single importance value for each relevé by weighting its cover in each layer, then summing the cover weights over all layers. Species in the epiphyte layer were given a nominal weight of 0.5. The Braun-Blanquet scale was assigned the following cover weights; 'r' was set to 0.1, '+' to 0.5, '1' to 1.0, '2' to 2.0, '3' to 3.0, '4' to 4.0, and '5' to 5.0. Thus, the range of possible importance values was 0.1 to 15.5.

Detrended correspondence analysis (DCA) was used for indirect gradient analysis; this method extracts the dominant compositional gradients from a species-by-relevés data matrix of species' importance values, independently of site variables (Hill 1979; Hill & Gauch 1980; Peet et al. 1988). Canonical correspondence analysis (CCA) was generally used for direct gradient analysis; it extracts the compositional variation attributable to one or more (here only elevation was used) site variables (ter Braak 1986). A bootstrap procedure was used to establish that the elevation constrained first CCA axis, for each locality, was stably represented in the dataset (see Knox & Peet 1989). 100 bootstrap samples of the relevés, at each locality, were used to generate 100 bootstrap first CCA axes (and corrected for selection of arbitrary axis direction by CANOCO).

The species found in all 100 bootstrap samples were used to calculate two measures of stability (Knox & Peet 1989): (1) the median rank correlation of species scores along bootstrap axes with scores on the reference axis (derived from the complete dataset); and (2) the average 'Scaled Rank Variance' (SRV) of species scores across bootstrap axes. SRV values near zero indicate very consistent species ranking, whereas values near 1.0 indicate ranks as variable as random ranks.

Elevation calibration between localities was carried out using the large Camp Creek dataset as the reference locality, because this locality includes many conifer-broadleaved hardwood communities (Reif & Allen 1988) and more than 80% of the species found at each locality were also found at Camp Creek. For this purpose elevation difference was calculated between Camp Creek and the other eight localities. For these paired comparisons, the observed elevation of a stand, for each locality, was contrasted with its predicted elevation at the other locality. The predicted elevation was determined from first axis stand scores of an elevation constrained CCA ordination of stands at the other locality, with those stands having elevation predicted being held passive in the analysis (see ter Braak 1988). A 'passive stand' has no influence on the extraction of ordination axes, but its stand score is generated from a weighted average of the species scores.

Floristically similar stands are based upon the species within a stand that are shared with another locality. Predicted elevations for 'passive stands' were then determined from the relationship between stand scores and observed elevations at a locality. For each comparison, elevation differences were calculated as observed elevation of relevés minus predicted Camp Creek elevation, as well as predicted elevation of Camp Creek relevés at each locality minus their observed elevation. Such two-way comparisons were not made for Mount Bovis, Kokatahi, Wilberforce, and Catlins localities where relevés sampled a narrow elevation range, instead differences were only based on projecting stands from these localities into Camp Creek.

Gradient length from detrended CCA (DCCA) with non-linear rescaling, in SD units (cf., Hill 1979; Hill & Gauch 1980; Eilertsen et al. 1990; Økland 1990), was used as a measure of species' turnover along ordination axes. Species turnover along the elevation gradient was expressed as numbers of SD units of turnover per 1000 m elevation along a DCCA axis constrained by elevation.

Ordinations were run using CANOCO version 2.1 (ter Braak 1988) with default options, except that DCA and DCCA were performed with detrending by segments (Knox 1989; Økland 1990).

Two parameters were used to compare individual species' positions along the elevation gradient: cover-weighted mean position and cover-weighted standard deviation of mean position (see McNaughton & Wolf 1970; Christensen & Peet 1984). The cover-weighted mean elevation is a measure of a species' optimal elevation. The cover-weighted standard deviation of mean elevation is a measure of elevation breadth. Only localities (Taramakau, Bonar Range, Wanganui, and Fox) where relevés sampled from near sea level to the upper limit of forest were used in species' position comparisons with Camp Creek.

Results

Compositional gradients

A comparison of DCA with elevation-constrained CCA ordination results was made for each locality to determine the influence of compositional gradients not accounted for by elevation (Table 2). Axes eigenvalues indicate the amount of variation accounted for by these ordination methods (ter Braak 1988). First DCA and CCA axes eigenvalues for Taramakau, Camp Creek, and Bonar Range indicated that the two ordination methods account for comparatively high amounts of variation at these localities (Table 2). High first CCA axis eigenvalues, relative to the second CCA axis, in-

Table 2. Eigenvalues for first and second DCA and CCA axes from ordinations of all stands at each locality. The CCA ordinations were elevation-constrained so that the first axes maximise the dispersion of species scores with respect to elevation. Also given are Spearman rank correlations (r_s) of first CCA axes stand scores with first and second DCA axes stand scores; * $P < 0.05$; *** $P < 0.001$.

Locality		Eigenvalue		r_s
		DCA	CCA	
Mount Bovis	Axis 1	0.35	0.20	0.71 ***
	Axis 2	0.24	0.33	0.13
Taramakau	Axis 1	0.63	0.44	0.92 ***
	Axis 2	0.26	0.63	0.39 ***
Camp Creek	Axis 1	0.66	0.53	0.96 ***
	Axis 2	0.54	0.57	0.47 ***
Kokatahi	Axis 1	0.57	0.27	0.27 *
	Axis 2	0.25	0.56	0.82 ***
Bonar Range	Axis 1	0.69	0.52	0.95 ***
	Axis 2	0.50	0.58	0.82 ***
Wilberforce	Axis 1	0.54	0.28	0.25
	Axis 2	0.35	0.54	0.84 ***
Wanganui	Axis 1	0.69	0.39	0.10
	Axis 2	0.49	0.69	0.91 ***
Fox	Axis 1	0.61	0.39	0.86 ***
	Axis 2	0.32	0.54	0.40 ***
Catlins	Axis 1	0.54	0.41	0.92 ***
	Axis 2	0.29	0.40	0.12

dicate the importance of elevation relative to other gradients in the datasets from each locality. As expected, rank correlations of first DCA and CCA axes stand scores for these localities indicated that elevation was the dominant compositional gradient. This relationship was found for most localities (Table 2).

The Wanganui, Wilberforce, and Kokatahi localities also had high first DCA axis eigenvalues, but it was their second DCA axis stand scores that correlated significantly with the elevation-constrained first CCA axis stand scores (Table 2). This indicated that elevation was overridden by some other factor as the most important compositional gradient at these localities.

The strong correlations between the ordering of species along bootstrap and reference first CCA axes, as well as the small SRV values (<0.3 ; Table 3) suggest the first CCA axis for each locality is robust with respect to sampling effects. This result supports the use of the elevation gradient as a reference axis to compare the positions of floristically similar stands and species between localities. The first CCA axis for the Bonar Range, Taramakau, and Camp Creek localities, where elevation accounted for a comparatively large amount of compositional variation, were most stable. The first CCA axis

Table 3. Medians (75th and 25th percentiles) of Spearman rank correlations (r_s) between ordering of species on bootstrap and reference first CCA axes, from 100 bootstrap samples of datasets from each locality. Coefficients of variability (SRV) in species ordering along bootstrap axes are variances in ranks, averaged across the n species frequent enough to be present in all 100 bootstrap samples, and divided by the expected variance of a set of n random ranks.

Locality	r_s	SRV
Mount Bovis	0.853 (0.892, 0.801)	0.280
Taramakau	0.967 (0.974, 0.961)	0.062
Camp Creek	0.962 (0.967, 0.954)	0.072
Kokatahi	0.926 (0.945, 0.904)	0.145
Bonar Range	0.972 (0.977, 0.967)	0.062
Wilberforce	0.922 (0.943, 0.905)	0.150
Wanganui	0.951 (0.961, 0.934)	0.100
Fox	0.959 (0.964, 0.951)	0.080
Catlins	0.955 (0.965, 0.947)	0.087

for Mount Bovis, Wilberforce, and Kokatahi localities, where comparatively few relevés sampled a limited elevation range, were least stable.

Elevation of floristically similar stands

As a compositional gradient related to elevation was correlated with one (or both) of the two major compositional gradients at each locality, we used CCA ordination to calibrate elevation of floristically similar stands between localities. The mean elevation of floristically similar stands was lower than at Camp Creek for all localities except Mount Bovis and the Wilberforce (Table 4). The largest decline in elevation was for the most southern and distant locality, the Catlins. Linear regression of mean elevation difference versus latitude of localities (compared with Camp Creek) showed that the elevation of floristically similar stands generally declined with latitude ($R^2 = 0.68$, $P < 0.01$). The decline with latitude was not always consistent. Kokatahi, Wanganui, and Fox localities represent increasing latitude on schist substrates, and by comparison with Camp Creek gave an average decline in elevation of floristically similar stands of -74.6 m, -77.0 m, and -3.3 m, respectively. These represent rates of decline with change

Table 4. Mean elevation difference and associated standard error (S.E.) for floristically similar stands between Camp Creek and other localities¹. Spearman rank correlations (r_s) of observed elevation at a locality with predicted Camp Creek elevation are given (** $P < 0.001$).

Locality	Mean (m)	S.E. (m)	r_s
Mount Bovis	32.1	17.6	0.67 ***
Taramakau	-86.8	7.5	0.85 ***
Kokatahi	-74.6	16.7	0.44 ***
Bonar Range	-72.0	5.8	0.87 ***
Wilberforce	1.1	12.9	0.57 ***
Wanganui	-77.0	6.7	0.81 ***
Fox	-3.3	7.8	0.80 ***
Catlins	-247.1	15.0	0.76 ***

¹ Comparisons of Mount Bovis, Kokatahi, Wilberforce, and Catlins with Camp Creek were one-way because relevés sampled a narrow range of elevations at these localities.

in latitude of -324.3 m, -163.8 m, and -4.0 m per °lat., respectively. There were also differences between adjacent localities. For example, on average, floristically similar stands were found 86.8 m lower on granite at the Taramakau than on schist at adjacent Camp Creek < 5 km away.

Stepwise, multiple linear regression of stand elevation differences against observed elevation and solar radiation indicated differences were little influenced by a stands topographic position. Partial coefficients of determination were 0.25 ($P < 0.001$) for elevation in the Kokatahi and Catlins comparisons with Camp Creek, and 0.19 ($P < 0.001$) for solar radiation in the Wilberforce comparison with Camp Creek. All other partial coefficients of determination were < 0.10 .

Spearman rank correlations between predicted Camp Creek elevations and observed elevations at each locality were highest for the Taramakau and Bonar Range (Table 4), indicating that these localities had compositional variation with elevation similar to that at Camp Creek. The lowest correlation was for the Kokatahi.

Elevation of individual species

The mean differences in species elevation (cover-weighted mean elevation of species at each locality minus Camp Creek cover-weighted mean elevation) for widely distributed species (found on $> 5\%$ of relevés at each locality) showed that individual species were found at lower elevations at four localities than at Camp Creek (Table 5). As for floristically similar stands, the largest mean difference was found between the adjacent Camp Creek and Taramakau. In addition, the optimal elevation of widely distributed species at the Taramakau and

Table 5. Mean differences in optimal elevation (cover-weighted mean elevations of individual species at each locality minus Camp Creek cover-weighted mean elevations) for widely distributed species (found on > 5% of relevés at each locality) at localities with relevés over a wide elevational range, with associated standard errors (S.E.). N = Number of species. Spearman rank correlation (r_s) of species' optimal elevations at each locality with Camp Creek optimal elevations are given (*** $P < 0.001$).

Locality	N	Elevation difference (m)		r_s	
		Mean	S.E.		
Taramakau	83	-126.3	9.6	0.92	***
Bonar Range	83	-72.4	6.2	0.95	***
Wanganui	91	-92.7	12.6	0.79	***
Fox	89	-109.2	11.5	0.81	***

Bonar Range (on granite) were more closely correlated with those at Camp Creek (on schist) than were those at the Wanganui and Fox (on schist; Table 5).

Mean elevation breadth of frequent species (found on > 5% of relevés at a locality) was least at the Bonar Range (granite substrate) and widest at Fox (schist substrate; Table 6). As expected, species' turnover along the elevation gradient (from DCCA ordination of 102 randomly selected relevés from each locality, to equal the total of 102 relevés sampled at the Bonar Range) was greatest at the Bonar Range and least at Fox (Table 6). For the other three localities, species' turnover varied in the order expected from the magnitude of mean elevation breadth; although, there was little difference in mean elevation breadths at these localities.

Discussion

Elevation was usually strongly correlated with the dominant compositional gradient at localities examined in this study, as has often been reported for mountain-land forests (e.g. Whittaker 1967; Peet 1981; Allen, Peet & Baker 1991). Variation in composition along this gradient was most similar at Camp Creek, Taramakau, and Bonar Range (Tables 4, 5). The most distant locality compared with Camp Creek (Catlins; Table 4) did not have the least similar variation in composition along the elevation gradient. At Kokatahi and Wanganui, elevation correlated only with the second axis of compositional variation, even though relevés sampled a wide range of elevation. Both these localities are underlain by schist, where landslides and canopy mortality are comparatively frequent disturbances (Reif & Allen 1988). As relevés sampled a wide range of forest response to these disturbances, this response may form the dominant

Table 6. Mean elevation breadth (cover-weighted standard deviation of mean elevation) of frequent species (found on > 5% of relevés at a locality), with associated standard errors (S.E.), and gradient length from elevation-constrained ordination of 102 relevés from selected localities. N = number of species.

Locality	N	Elevation breadth (m)		Gradient Length (SD/1000m)
		Mean	S.E.	
Taramakau	111	171.3	5.4	3.3
Camp Creek	129	166.7	3.8	4.1
Bonar Range	104	144.1	5.8	4.2
Wanganui	104	164.9	5.7	3.2
Fox	116	189.9	5.3	2.7

axis of compositional variation at these localities. Although we did not quantify this relationship, such an interpretation is a plausible hypothesis for the differences in the hierarchy of gradients found between apparently similar localities.

Although increased latitude was usually accompanied by the expected decline in elevation of floristically similar stands, this relationship showed considerable complexity, reflecting the influence of other factors. The similar elevation for the more southern Wilberforce may reflect its location on the inland, dry eastern slopes of the southern Alps in contrast to Camp Creek which is on the high-rainfall west slope. This corresponds with the increases in timberline described from west to east and from coast to interior by Wardle (1985). Because of the limited range of elevations sampled at the Wilberforce, its comparison with Camp Creek was one-way and perhaps not as robust as two way comparisons. The lower elevation of floristically similar forest on the isolated Taramakau granitic domes compared with that at nearby Camp Creek on the main axial range is a robust result, and is consistent with vegetation zones being lower on isolated peaks than on extensive mountain ranges ('Massenerhebung' effect). This effect has been noted on mountains in the European Alps and in the tropics (Richards 1952).

In contrast to Southern Rocky Mountain forests, little of the elevation differences of floristically similar stands between localities was related to relative elevation or, for a given elevation, differences in potential solar radiation (cf., Allen 1988; Allen, Peet & Baker 1991). Potential solar radiation influences soil moisture regimes, and elevation differences can reflect the interaction between elevation and moisture gradients (Peet 1988; Allen, Peet & Baker 1991). However, in the high-rainfall, conifer-broadleaved hardwood forests of South Island, New Zealand, potential solar radiation did not appear, with the possible exception of the

Wilberforce, to influence elevation differences between localities in the same way (cf. Kirkpatrick et al. 1988). This result supports Wardle's (1985) view that timberline in New Zealand is little influenced by climatic factors that reflect local site conditions such as aspect and topography.

The classification of New Zealand forests has been considered difficult because of the broad ecological amplitude of many species (Dansereau 1964). The mean elevation breadths of frequent species from five localities in this study were all less than 200 m, whereas similarly calculated mean elevation breadths for three localities in the Southern Rocky Mountains were all greater than 200 m (Allen, Peet & Baker 1991). This pattern was also supported by species' turnover along the elevation gradient (analysed by DCCA), which ranged between 2.7 and 4.2 (SD/1000 m) for the South Island localities and between 2.5 and 3.1 for the Rocky Mountain localities. The narrower elevation breadths in New Zealand conifer-broadleaved hardwood forests, admittedly only one dimension of compositional variation, would suggest greater community differentiation than in Rocky Mountain forests. This comparison does not support Dansereau's (1964) view that New Zealand species have exceptionally broad ecological amplitudes.

Of the three schist localities for which elevation breadth was calculated in this study, the most southern (Fox) had the highest elevation breadth, with the other two localities having similar values (Table 6). For the Southern Rocky Mountain forests, elevation breadth of frequent species also increased with latitude (Allen, Peet & Baker 1991). However, competitive sorting of species during succession reduces habitat breadth and increases compositional differentiation (Christensen & Peet 1984; Peet & Christensen 1988; Zhang 1988). Because localities underlain by schist are more frequently disturbed than those underlain by granite, it may be expected that species' turnover along compositional gradients would be greater for granite localities than for schist localities. This is consistent with elevation breadth being least and species' turnover being greatest for the Bonar Range (granite) and the opposite for the Fox (schist); but the pattern is unclear for the other localities (Table 6).

This study of shifts in elevation of both species and floristically similar stands has shown considerable complexity, at least in part, related to geology, disturbance, and latitude. This supports the need to examine geographic variation in vegetation using several datasets to identify local gradients which can be used to form a multi-dimensional framework for analysis of large-scale patterns (Peet 1978; Allen, Peet & Baker 1991). Few such studies exist, yet the increasing number of datasets

available may eventually allow modelling of vegetation response to elevation and other factors as a basis for predicting response to environmental change.

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