

Variation in invertebrate–bryophyte community structure at different spatial scales along altitudinal gradients

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Abstract

Aim This study assessed changes in diversity and assemblage composition in bryophytes and their associated invertebrates along altitudinal gradients in Australia and New Zealand. The importance of altitude in shaping these communities and for the diversity of both invertebrates and bryophytes was examined at different spatial scales, including local, altitudinal, regional and biogeographical.

Location Samples were taken from four Australasian mountain ranges between 42° and 43°S: Mt Field and Mt Rufus, Tasmania, Australia, and Otira Valley and Seaward Kaikoura Mountains, South Island, New Zealand.

Methods On both Tasmanian mountains, five altitudes were assessed (250, 500, 750, 1000 and 1250 m). At each location (mountain/altitude combination) two sites were chosen and six samples were taken. Six altitudes were assessed on New Zealand mountains (Otira: 250, 500, 750, 1000, 1250 and 1500 m; Kaikoura: 1130, 1225, 1325, 1425, 1525 and 2000 m). Bryophyte substrate was collected, and all samples were stored in 70% ethanol. Invertebrates were extracted from bryophytes using kerosene-phase separation and all invertebrates were identified to family. At each location in Tasmania, all bryophyte species within six 25-cm² grids per site were collected and identified to species. Bryophytes from New Zealand were identified to species from the invertebrate sample substrate because of sampling constraints.

Results Altitude did have a significant effect on diversity, however, no general trend was found along the altitudinal gradient on the four mountains. There were distinct differences in diversity between biogeographical regions, mountains, altitudes and sites. In Tasmania, Mt Field had the highest diversity in invertebrates and bryophytes at 750 m. In contrast, Mt Rufus had consistent low invertebrate and bryophyte diversity along the entire altitudinal gradient. There were also distinctive differences between locations in the composition of invertebrate and bryophyte communities in Tasmania. Along the two altitudinal gradients in New Zealand, Otira had highest diversity for both invertebrates and bryophytes at low altitudes, whereas Kaikoura had highest invertebrate and lowest bryophyte diversity at the highest altitude.

Main conclusions There was an effect of altitude, however, there were no consistent changes in diversity or composition on the four different mountains. There was considerable local and regional variation, and, despite a strong sampling design, no underlying altitudinal trends were detectable. This study demonstrates the importance of examining a range of spatial scales if patterns in community structure along altitudinal gradients are to be studied. The implications of this study are discussed with reference to survey design, taxonomic resolution, climate change and conservation of habitat.

Keywords

Bryophytes, invertebrates, altitudinal gradient, spatial scales, regional diversity, climate change, conservation, Tasmania, New Zealand.

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INTRODUCTION

One of the commonly stated generalizations in relation to patterns of diversity is that there is a general decline in diversity as altitude increases (Begon *et al.*, 1990; Stevens, 1992; Rahbek, 1995, 1997). This is analogous to the patterns thought to occur along latitudinal gradients (Begon *et al.*, 1990; Rohde, 1992; Krebs, 2001), with the decrease in species diversity moving away from the tropics considered to be one of the most general patterns in ecology (Rosenzweig, 1995). Both these general patterns are believed to be a product of an underlying process or processes that are responsible for the species diversity patterns in community structure and diversity (Begon *et al.*, 1990). The generality of species diversity patterns along both latitudinal and altitudinal gradients have been primarily based on studies using vascular plants and birds (e.g. Mark, 1963; Beals, 1969; Kikkawa & Williams, 1971; Whittaker & Niering, 1975; Terborgh, 1977; Ogden & Powell, 1979; Loiselle & Blake, 1991; Hunter & Yonzon, 1993; Wolf, 1994; Pendry & Proctor, 1997; Rahbek, 1997; Shepherd, 1998). However, along both latitudinal and altitudinal gradients other taxonomic groups sometimes show different patterns in diversity, disputing the generality of both these gradient patterns (Janzen, 1973; Turner & Broadhead, 1974; Janzen, 1981; Gauld, 1986; Atkin & Proctor, 1988; Sipman, 1989; Vitt, 1991; Wolf, 1993; Olson, 1994; Tarba, 1994; Hoover & Crossley, 1995).

Differences in diversity patterns between altitudinal gradients may be due to the effect of variation at other, either smaller or larger, spatial scales. The magnitude of variation at any one spatial scale could impinge on the diversity trend seen at another scale. If diversity is variable at local scales within altitudinal zones, then changes in diversity along altitudinal gradients may be difficult to observe and interpret. However, in most studies of altitudinal gradients, variation at local scales has not been measured. If species diversity varies at larger scales, such as regional or biogeographical scales, then any underlying altitudinal variation may be observable in studies which only sample one altitudinal transect (e.g. Whittaker & Niering, 1975; Walter, 1985; Moeed & Meads, 1986; Leakey & Proctor 1987; McCoy, 1990; Wolf, 1994; Gonzalez-Mancebo & Hernandez-Garcia, 1996), or studies that sample various transects on one mountain (Wright, 1991), or sample different altitudinal gradients and pool the data (Kikkawa & Williams, 1971; Beasley, 1988; Hunter & Yonzon, 1993; Tarba, 1994).

Bryophyte and invertebrate communities are ideal candidates for latitudinal and altitudinal studies as they are found from the tropics to the polar regions and from sea level to above the tree line. However, bryophytes and their associated invertebrate communities have been relatively poorly studied in the past (exceptions include Gerson, 1969, 1982; Lindegaard & Thorup, 1975; Andre, 1983; Booth & Usher, 1985; Kinchin, 1990; Englund, 1991; Smrz, 1992; Suren, 1993; Glime, 1994; Steiner, 1994a,b). As bryophyte communities tolerate a wider range of environmental conditions, and have a longer altitudinal gradient than vascular plants

(Grout, 1908; Lee & La Roi, 1979; Kantvilas & Jarman, 1991; Odasz, 1996), strong generalizations on observable changes in diversity along altitudinal gradients can be made if any patterns do exist. Previously studies have shown that bryophytes reach a mid-altitudinal peak in diversity in the tropics (Gradstein & Pocs, 1989). However, other scales, both smaller and larger, affect the diversity and community structure of invertebrate and bryophyte communities.

The main aim of this study was to assess if there are consistent changes in diversity of invertebrate and bryophyte communities along a series of altitudinal gradients. We examined four scales of diversity, local, altitudinal, regional (between mountains) and biogeographical (between islands) to determine the importance of each in diversity patterns. It was expected that any underlying pattern in diversity along the altitudinal gradients would be seen, even if diversity varied at other scales. The primary emphasis of the paper is on samples collected in Tasmania, Australia, however, opportunistic samples taken from the South Island of New Zealand are included to provide a biogeographical contrast.

The following questions were addressed:

1. Did diversity of invertebrates extracted from bryophytes vary at different spatial scales (local, altitudinal, regional and biogeographical)?
2. Did bryophyte diversity vary at different spatial scales (local, altitudinal, regional and biogeographical)?
3. Was there a measurable underlying altitudinal trend in the diversity of invertebrate or bryophyte communities?

METHODS

Sites were located in Tasmania, Australia and the South Island of New Zealand between 42° and 43°S. Different sampling regimes were conducted in Tasmania and New Zealand because of time and resource constraints for sampling the New Zealand sites. Samples were collected from all sites in Tasmania and New Zealand between 25 and 30 November 1996 to reduce temporal effects of sampling.

In Tasmania, two mountains were chosen, one in the eastern half (Mt Field) of Tasmania and another in the western half (Mt Rufus) of Tasmania. Mt Field sites were all located within Mt Field National Park. Mt Rufus sites were located within Cradle Mountain – Lake St Clair National Park and Franklin – Gordon Wild Rivers National Park. In New Zealand, sites were located in the Otira Valley starting near Arthur's Pass and running down to the west coast, and in the upper Kowhai Valley in the Seaward Kaikoura Mountains on the east coast of the South Island.

Tasmanian sites were located at five altitudes (250, 500, 750, 1000 and 1250 m) on both mountains. The ten different mountain and altitude combinations will be referred to hereafter as 'locations' (e.g. F500 for sites on Mt Field at 500 m or R1250 for sites on Mt Rufus at 1250 m). At each Tasmanian location two 20 × 20 m sites were chosen that were at least 1 km away from each other. Within each site, six 25 × 25 cm quadrats were chosen haphazardly, ensuring that there was greater than 50% bryophyte cover within

each quadrat. Haphazard quadrats were laid because of the uneven spatial distribution of bryophyte beds. The presence of every bryophyte species in each quadrat was recorded, and a sample of every species from each quadrat was collected for species verification. Two 2.5 × 2.5 cm bryophyte samples were nested within each quadrat and placed into 95% ethanol in the field for later invertebrate extraction.

In New Zealand a different sampling regime was used to account for the higher altitudinal ranges of the two mountains sampled. At the Otira sites, five altitudes (250, 500, 750, 1000 and 1250 m) were sampled. At each altitude, twelve 2.5 × 2.5 cm samples were taken from a single 20 × 20 m area. At Kaikoura, six altitudes (1130, 1230, 1330, 1430, 1530 and 2000 m) were sampled. Lower altitudes at Kaikoura were not sampled because suitable sites could not be found in the available time. At each altitude six 2.5 × 2.5 cm samples were taken from a single 20 × 20 m area. All samples were put into 95% ethanol for later extraction. Bryophytes within these samples were identified to species.

The invertebrates were extracted from the bryophytes using kerosene-phase separation (Andrew & Rodgeron, 1999). This technique involved washing the preserved samples in 95% ethanol to dislodge the invertebrates from the bryophytes. Kerosene was then mixed thoroughly with the washed sample. The kerosene binds to the cuticle of the invertebrates, which then float to the interface between the ethanol and kerosene once they separate. Invertebrates were collected and identified to family. Bryophytes were identified to species (Scott & Stone, 1976; Scott, 1985; Beever *et al.*, 1992; D. Glenny, unpublished liverwort key). Bryophyte identification was confirmed by expert bryologists familiar with the flora.

When time and taxonomic constraints are present (as in this study) relevant patterns in invertebrate diversity can be measured at the family level with reasonable success; and these can be used as surrogates for species richness (Beattie & Oliver, 1994; Williams & Gaston, 1994). Previous studies have found good correlations between species-level diversity and higher-level diversity for a wide range of taxonomic groups (New, 1994; Williams *et al.*, 1994, 1997; Gaston *et al.*, 1995; Balmford *et al.*, 1996).

Data analysis

For the Tasmanian communities the two samples taken from each quadrat were bulked. Abundance data for Tasmanian invertebrate families were $\log(x + 1)$ transformed to improve the normality of the underlying distribution (Zar, 1984). A three-way ANOVA was used to analyse the data for both abundance and the number of invertebrate families extracted from the bryophyte substrate. The model fitted for Tasmania was Mountain + Altitude + Mountain × Altitude + Site (Mountain × Altitude) + Quadrat [Site (Mountain × Altitude)]. A two-way ANOVA was used to analyse the data for bryophyte family and species richness for each site (quadrats pooled). The model fitted was Mountain + Altitude + Mountain × Altitude + Site

(Mountain × Altitude). Mountain and Altitude were treated as fixed factors, and Site and Quadrat as random. *Post hoc* Scheffe's tests were performed to determine significant differences between paired locations. Multivariate analysis were performed separately on the invertebrate family abundance, and the presence/absence of bryophyte families and species using NPMANOVA (Anderson, 2000), to assess composition changes within the communities along the altitudinal gradient and between mountains. When referring to diversity/richness we are referring only to those invertebrate families and bryophyte species sampled (i.e. observed diversity).

Data from New Zealand for the abundance of invertebrate families were transformed using a $\log(n + 1)$ transformation. A one-way ANOVA was used to analyse both abundance data and the number of taxa extracted from the bryophyte substrate, from each mountain separately. *Post hoc* Scheffe's tests were performed to determine if locations are significant factors. No formal statistical test was performed on New Zealand bryophyte family and species richness. Multivariate analysis were performed separately on abundance of invertebrate families, and presence/absence of bryophyte families and species using NPMANOVA (Anderson, 2000).

RESULTS

Tasmania

A total of 1398 invertebrates from fifty-four invertebrate families from sixteen orders were collected from bryophytes in Tasmania. Acari, Collembola and Diptera were the most abundant orders, collectively comprising 95% (Acari, 45%; Collembola, 41%; Diptera, 9%) of the fauna. Three families [Oribatellidae (Acari), Isotomidae and Brachystromellidae (Collembola)] contributed 58% of the abundance (each family 331, 324, 166 individuals, respectively) of invertebrates collected from bryophytes in Tasmania. Forty-four families (77% of total) contributed only 10% collectively to the total abundance. There were twelve families of Acari, nine families of Collembola, seven Coleoptera families, six families each of Diptera and Hymenoptera, four families of Hemiptera, and one family each of Amphipoda, Thysanoptera, Diplura, Pseudoscorpionida, Symphyla, Geophila, Archaeognatha, Protura, Psocoptera and Paurapoda.

Analyses of invertebrate families suggest that communities were structured differently between mountains, altitudes and the mountain–altitude locations (Fig. 1, Table 1a, Table 2). Few consistent trends along the altitudinal gradient of both mountains were found for invertebrate abundance and richness. In total, more invertebrates were extracted from bryophytes at Mt Field (1031 individuals) than at Mt Rufus (367 individuals, Table 1a, Abundance: Mountain). However, there was no effect of altitude, nor any interaction between mountain and altitude for invertebrate abundance (Table 1a, Abundance: Mountain, Altitude, Mountain × Altitude; Fig. 1a,b). There was a significant difference among sites [Table 1a; Abundance: Site (Mountain × Altitude)] as well as high variation within sites indicated by the

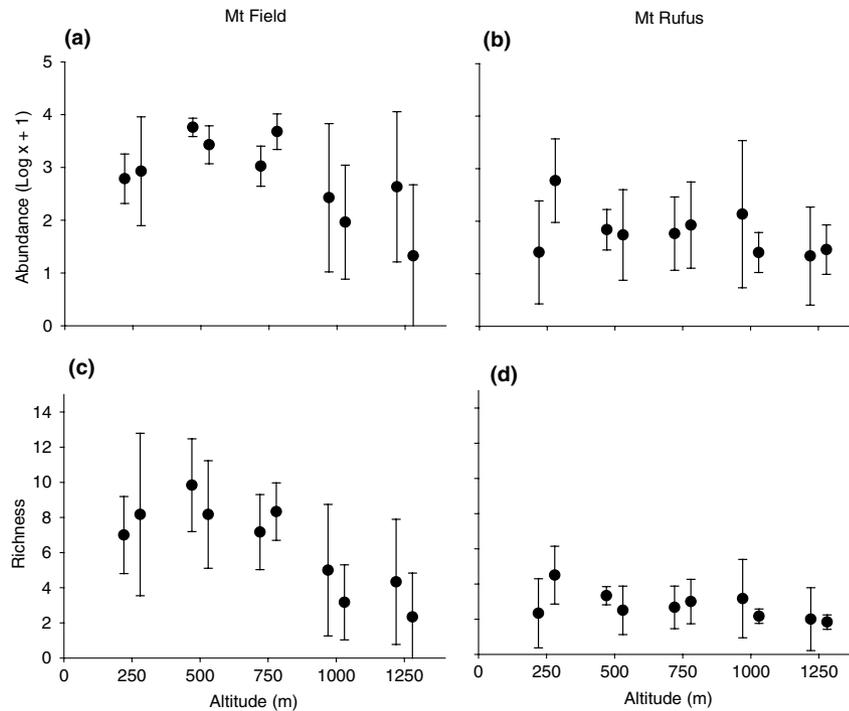


Figure 1 Invertebrate taxa collected from bryophytes along an altitudinal gradient in Tasmania. (a) and (b) show abundance [$\log(x + 1)$] per site ($n = 6$) from Mt Field and Mt Rufus, respectively. (c) and (d) show taxa richness of invertebrates per site ($n = 6$) from Mt Field and Mt Rufus, respectively. Mean (\pm SD) are shown.

Table 1 (a) ANOVA table for invertebrate abundance and richness extracted from bryophytes in Tasmania along an altitudinal gradient. (b) ANOVA table for bryophytes family richness and bryophyte species richness collected in Tasmania along an altitudinal gradient. (c) Non-parametric analysis of variance (NPMANOVA) table for invertebrate taxa community composition, bryophyte family composition and bryophyte species composition collected in Tasmania along an altitudinal gradient

Factor	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
(a)							
		Abundance		Richness			
Mountain	1	21.81	<0.01	66.84	<0.01		
Altitude	4	2.25	0.136	8.79	<0.01		
Mountain \times Altitude	4	1.70	0.226	4.58	0.01		
Site (Mountain \times Altitude)	10	2.01	0.04	1.08	0.38		
Quadrat [Site (Mountain \times Altitude)]	100						
(b)							
		Bryophyte families		Bryophyte species			
Mountain	1	14.04	<0.01	36.1	<0.01		
Altitude	4	6.15	<0.01	4.35	0.03		
Mountain \times Altitude	4	3.48	<0.01	5.6	0.01		
Site (Mountain \times Altitude)	10						
(c)							
		Invertebrates		Bryophyte species		Bryophyte families	
Mountain	1	3.47	<0.01	16.41	<0.01	14.04	<0.01
Altitude	4	1.87	<0.01	6.52	<0.01	6.15	<0.01
Mountain \times Altitude	4	1.33	0.05	4.31	<0.01	3.46	<0.01
Site (Mountain \times Altitude)	10						

SD boxes and 95% confidence intervals in Fig. 1a,b), which may have contributed to the lack of a statistical interaction between mountain and altitude locations.

Invertebrate family richness collected from Mt Field sites (forty-four families) was significantly higher than sites at Mt

Rufus (thirty families, Table 1a, Richness: Mountain; Fig. 1c,d). Richness did vary significantly with altitude, Mt Field and Mt Rufus had distinct altitudinal diversity patterns (Table 1a; Richness: Mountain \times Altitude) but the analysis indicates that there was also a consistent underlying

Table 2 Presence of invertebrate taxa extracted from two sites at locations along an altitudinal gradient on Mt Field and Mt Rufus, Tasmania. Membership in one of three general groups (a–c) is included, based on presence/absence on mountain altitudinal gradients (see text for explanation). The number one indicates the presence of the bryophyte species at one location, two indicates the species was present at both locations

Family	Order	Mt Field					Mt Rufus				
		F250	F500	F750	F1000	F1250	R250	R500	R750	R1000	R1250
Isotomidae	Collembola	2	2	2	2	2	2	1	2	1	
Entomobryidae	Collembola	2	2	1	1		1	1	1	1	
Brachystomellidae	Collembola	2	2	2	2	1	1	1	2		
Mixonomatidae	Acari	2	2	1	1	1	1				
Oribatellidae	Acari	1	2	2			2	2	1		1
Galumnidae	Acari	1	1		1				1	1	
Ceratopogonid	Diptera	2	1	2				1			
Chironomidae	Diptera	2	2	2		2	1	2	2	1	1
Staphylinidae	Coleoptera	1	1				1	1			
Tomoceridae	Collembola	1			2			1	2		
Opipiidae	Acari	1	1	2		2	2				
Microzetidae	Acari	1		1	1	2	2	1		2	1
Apididae	Hemiptera	1	2	1	1			1			
Scelionidae	Hymenoptera	1				1	1				
Eulophidae	Hymenoptera	1									1
Paronellidae	Collembola	1								1	
Cepheidae	Acari		1	1					1		1
Sminthuridae	Collembola			1	1	1	1	1		1	
Onychiuridae	Collembola		2			1				1	1
Taxa 1	Coleoptera		1		1		1		1		
Curculionidae	Coleoptera					1					1
Cecidomyiidae	Diptera			1							1
Acerentomidae	Protura				1			2			
Neelidae	Collembola	1	1		1						
Neanuridae	Collembola	2		2							
Adelphacaridae	Acari	1			1						
Thripidae	Thysanoptera	1				1					
Tipulidae	Diptera	1									
Amphipod	Amphipod	1									
Ptiliidae	Coleoptera	2									
Paurapoda	Paurapoda	1	1		1						
Taxa 2	Diplura	1									
Psyllidae	Hemiptera	1									
Pseudoscorpionida	Pseudoscorpionida	1									
Mycobatidae	Acari	1	1	1	1						
Adelphacaridae	Acari				1						
Taxa 3	Hymenoptera		1								
Phthiracridae	Acari		1	1		1					
Carabodidae	Acari		2	2	1						
Lathridinae	Coleoptera			1							
Scarabedidae	Coleoptera		1								
Taxa 4	Geophila		1	1							
Checicoidae	Hymenoptera			1							
Taxa 5	Symphyla			1		1					
Coccoidea	Hemiptera										1
Taxa 6	Hemiptera					1					1
Myrmicinae	Hymenoptera					1					1
Carabidae	Coleoptera						1				
Myrmaridae	Hymenoptera						1				
Meinertellidae	Archaegnatha							1			
Psychodidae	Diptera								1	2	1
Cymbaeremaeidae	Acari							1			
Phoridae	Diptera									1	
Average Taxa richness/site (n=2)		18.5	19	17.5	15	13	13.5	10	8.5	7	7.5
Taxa richness/location		28	22	21	19	17	14	13	11	10	9
Taxa richness/mountain				46					29		
Total taxa richness							53				

altitudinal pattern (Table 1a; Richness: Altitude). Highest invertebrate richness was at the low- and mid-altitudes of Mt Field, with the locations F500 and F750 having signifi-

cantly more taxa than F1000, F1250, R250, R500, R750, R1000 and R1250 (Scheffe's *post hoc* test: all comparisons $P < 0.01$).

The invertebrate community composition differed between mountains, along the altitudinal gradient, and between mountain–altitude locations (Table 1c; Invertebrates, Table 2). Of the fifty-four invertebrate families collected from bryophytes, twenty-three families were found on both mountains at various altitudes (Table 2; group A), four of which were only found once on each mountain. Twenty-three invertebrate families were found exclusively at Mt Field locations (group B), with twelve families found at only one location. Interestingly, six of the invertebrate families extracted from bryophytes were unique to Mt Rufus locations (group C), five of which were only found at one location.

Forty-one bryophyte species, from thirty families, were collected from Tasmania (Table 3). Twenty-two species (from sixteen families) were mosses and nineteen species (from fourteen families) were liverworts. Most bryophyte families were represented by only one species, with the exception of three families with three species each (Dicranaceae, Lepidoziaceae and Geocalyceae), and six families with two species (Sematophyllaceae, Lembophyllaceae, Amblystegiaceae, Grimmiaceae, Lepyrodontaceae and Plagiochilaceae).

Bryophyte species richness was higher in total at the Mt Field locations (thirty-six species, Fig. 2a) than at the Mt Rufus locations (nine species, Fig. 2b; Table 1b, Bryophyte Species: Mountain). There was significantly more bryophyte species at F750m locations (Table 1b, Bryophyte Species: Mountain \times Altitude) compared with F1250m, R1000 and R1250 (Scheffes *post hoc* $P = 0.045, 0.014$ and 0.014). However, the analysis also indicates that there was a consistent underlying altitudinal pattern (Table 1b; Bryophyte Species: Altitude).

In a similar trend to the bryophyte species richness, bryophyte family richness was higher in total at Mt Field locations (twenty-six species, Fig. 2c) than at Mt Rufus locations (seven species, Fig. 2d; Table 1b, Bryophyte Families: Mountain). F750 had the highest bryophyte family richness (Table 1b, Bryophyte Families: Mountain \times Altitude) which differed significantly from R500m, R750, R1000 and R1250 (Scheffe's *post hoc* $P = 0.02, 0.03, 0.03$ and 0.03 , respectively). As with both the invertebrate family richness and bryophyte richness there was a consistent altitudinal pattern (Table 1b, Bryophyte Families: Altitude).

Similar to the invertebrate taxa, the communities of bryophyte species were structured differently between mountains, altitudes and mountain–altitude locations (Table 1c, Bryophyte Species; Table 3). Similar trends were found for the bryophyte families (Table 1c, Bryophyte Families). Only four bryophyte species (the mosses *Campylopus clavatus*, *Racomitrium crispulum*, *Grimmia pulvinata* and *Andreaea mutabilis*) were common to both mountains (Table 3: group A). They occurred within the alpine areas (1000 and 1250 m) of Mt Field, but were more cosmopolitan on Mt Rufus. Thirty-two bryophyte species were unique to Mt Field locations (group B), with twenty-three species unique to one location, eight of which were liverwort species unique to F750 m. Locations at Mt Rufus had five

unique species (group C), three moss species (*Gymnostomum calcareum*, *Polytrichum commune* and *Campylopus introflexus*) found at various locations, and two liverwort species (*Cephaloziella arctica* ssp. subantarctica and *Herzogobryum teres*) each unique to one location. One feature of the altitudinal gradient consistent to both mountains in Tasmania was the change in growth form from the low altitudes to high altitudes. Bryophytes found at low- and mid-altitudes (250–750 m) had growth forms that were mainly upright, and leaves dark green in colour and generally large. This is in comparison with high-altitude species (1000 and 1250 m) that were prostrate (<1 cm tall), densely clumped, and either reddish in colour or with hairs on the leaves.

When comparing the invertebrate communities to bryophyte communities, several similarities were apparent. In general, there were distinct changes along the altitudinal gradient, but these changes were not consistent. Mt Field had a invertebrate and bryophyte diversity than Mt Rufus. Along the Mt Field altitudinal gradient invertebrate diversity was highest in sites at the low- and mid-altitudinal region up to F750m. Bryophyte family and species richness was higher at F750m, because of the high number of unique species (especially liverworts) occurring at this location. All sites along the Mt Rufus altitudinal gradient were low in both invertebrate richness and bryophyte richness, however, the composition of these communities showed slight changes.

New Zealand

In total, 3289 individual invertebrates were collected from New Zealand (1209 from Otira and 2087 from Kaikoura). As with Tasmania, the majority (97%) of invertebrates collected from bryophytes in New Zealand consisted of Collembola (60% of total), Acari (28%) and Diptera (9%). Forty-five invertebrate families were collected from New Zealand. Twelve of these families were Acari, eight Collembola, four Diptera and Hemiptera, three Coleoptera, two Hymenoptera and one family each of Lepidoptera, Dermaptera, Protura, Diplura, Araneae, Isopoda, Pseudoscorpionida, Thysanoptera, Symphyla, Geophila, Polydesmida and Spirobioda. Of the overall invertebrate community sampled from bryophytes in New Zealand, 73% of the total abundance was attributed to three families from two orders: Entomobryidae (Collembola) – 1361 individuals, Brachystomellidae (Collembola) – 502 and Oribatellidae (Acari) – 450. In contrast, 39 families (87% of taxa) collectively contributed only 10% to the overall abundance.

The mountains showed different trends along the altitudinal gradient. On the Otira gradient invertebrate diversity was highest at low altitudes (Fig. 3a,b), lowest at the mid-altitude (O750), and slightly higher at O1000, and O1250m. This variation was significant for invertebrate richness (ANOVA $F_{5,66} = 4.86, P < 0.01$) but not for invertebrate abundance (ANOVA $F_{5,66} = 1, P = 0.43$). Invertebrate abundance at location O750 differed significantly from O250 and O500 (Scheffe's *post hoc* test $P = 0.01$ for both).

Table 3 Presence of bryophyte species, families and bryophyte type (moss or liverwort) from two sites at locations along an altitudinal gradient on Mt Rufus, Tasmania. Membership in one of three general groups (a–c) is included, based on presence/absence on mountain altitudinal gradients (see text for explanation). The number one indicates the presence of the bryophyte species at one location, two indicates the species was present at both locations

Species	Family	Type	Mt Field					Mt Rufus					
			F250	F500	F750	F1000	F1250	R250	R500	R750	R1000	R1250	
<i>Campylopus clavatus</i> (R. Br.) Wils.	Dicranaceae	Moss	2	2	2	1	1	2	2	1	2	2	1
<i>Racomitrium crispulum</i> (Hook. F. & Wils.) Hook. F. & Wils.	Grimmiaceae	Moss				1	2			1			2
<i>Grimmia pulvinata</i> (Hedw.) Sm. ex Sm. & Sowerby	Grimmiaceae	Moss				1	2			1			2
<i>Andreaea mutabilis</i> Hook. F. & Wils.	Andreaeaceae	Moss				1	1			1			1
<i>Wilkea extenuata</i> (Brid.) Crum	Sematophyllaceae	Moss			2								
<i>Rhaphidobrychium amoenum</i> (Hedw.) Mitt	Sematophyllaceae	Moss			2								
<i>Thuidium sparsum</i> l (Hook. F. & Wils.) Jaeg.	Thuidiaceae	Moss			1								
<i>Psychomnion aciculare</i> (Brid.) Mitt.	Psychomniaceae	Moss			1								
<i>Distichophyllum microcarpum</i> (Hedw.) Mitt.	Hookeriaceae	Moss			1								
<i>Racomitrium convolutaceum</i> (C. Muell.) Reichdt.	Racomitriaceae	Moss			1								
<i>Lembophyllum divitum</i> (Hook. F. & Wils.) Par.	Lembophyllaceae	Moss			1								
<i>Hypnodendron vitense</i> Mitt.	Hypnodendraceae	Moss			1								
<i>Lepidobryum pyriforme</i> (Hedw.) Wils.	Bryaceae	Moss			2								
<i>Dicranoloma bilalerier</i> (Brid. ex anon.)	Dicranaceae	Moss			2								
<i>Acrocladum chilamydophyllum</i> (Hook. F. & Wils.) C. Muell. & Broth.	Amblystegiaceae	Moss			2								
<i>Lepidodon lazurus</i> (Hook.) Mitt.	Lepidodontaceae	Moss			1								
<i>Lepidozia ulothrix</i> (Schwaegr.) Lindenb.	Lepidoziaceae	Moss			2								
<i>Phaeoceros laevis</i> (L.) Prosk.	Anthocerotaceae	Liverwort			1								
<i>Chioscyphus coarctus</i> (Hook.) Nees	Geocalycaceae	Liverwort			1								
<i>Campylohaete arbuscula</i> (Sm.) Reichdt	Lembophyllaceae	Moss			2								
<i>Calliergonella cuspidatum</i> Loeske	Amblystegiaceae	Liverwort			1								
<i>Hypnum cupressiforme</i> Hedw. var. <i>cupressiforme</i>	Hypnaceae	Moss			2								
<i>Gackstroemia weindorferi</i> (Herzog) Grolle	Lepidoaenaceae	Liverwort			2								
<i>Lepidozia laevifolia</i> (Hook. F. & Taylor) Taylor	Lepidoziaceae	Liverwort			1								
<i>Kurzia compacta</i> (Steph.) Grolle	Lepidoziaceae	Liverwort			1								
<i>Marsupidium surculosum</i> (Nees) Schiffn.	Acrobolbaceae	Liverwort			1								
<i>Chioscyphus leucophyllus</i>	Geocalycaceae	Liverwort			1								
<i>Plagiochila retrospectan</i> (Nees) Nees	Plagiochilaceae	Liverwort			1								
<i>Plagiochila denticulata</i>	Plagiochilaceae	Liverwort			1								
<i>Riccardia cochleata</i> (Hook. f. & Taylor) Kuntze	Aneuraceae	Liverwort			1								
<i>Chioscyphus lentus</i>	Geocalycaceae	Liverwort			1								
<i>Bryum campylotheicum</i> Tayl.	Bryaceae	Moss			1								
<i>Drepanocladus uncatius</i> (Hedw.) Warnst.	Amblystegiaceae	Moss			1								
<i>Ditrichum punctulatum</i> Mitt.	Ditrichaceae	Moss			2								
<i>Ischyrodon lepturus</i> (Tayl.) Scheiße	Fabroniaceae	Moss			1								
<i>Breutelia elongata</i> (Hook. F. & Wils.) Mitt.	Bartramiaceae	Moss			1								
<i>Gymnostomum calcaratum</i> Nees & Hornsch.	Pottiaceae	Moss			1								
<i>Polytrichum commune</i> Hedw.	Polytrichaceae	Moss			1								
<i>Campylopus introflexus</i> (Hedw.) Brid.	Dicranaceae	Moss			2								
<i>Cephalozia arctica</i> ssp. <i>subantarctica</i>	Cephalozeliaceae	Moss			1								
<i>Herzogobryum teres</i>	Gymnomitriaceae	Moss			1								
Average bryophyte species/site (n=2)			6.5	9	14.5	8	4	4	5	2.5	3	3	2.5
Bryophyte species/location			7	11	17	10	6	6	5	3	5	3	3
Bryophyte species/mountain					36					9			
Total bryophyte species													41

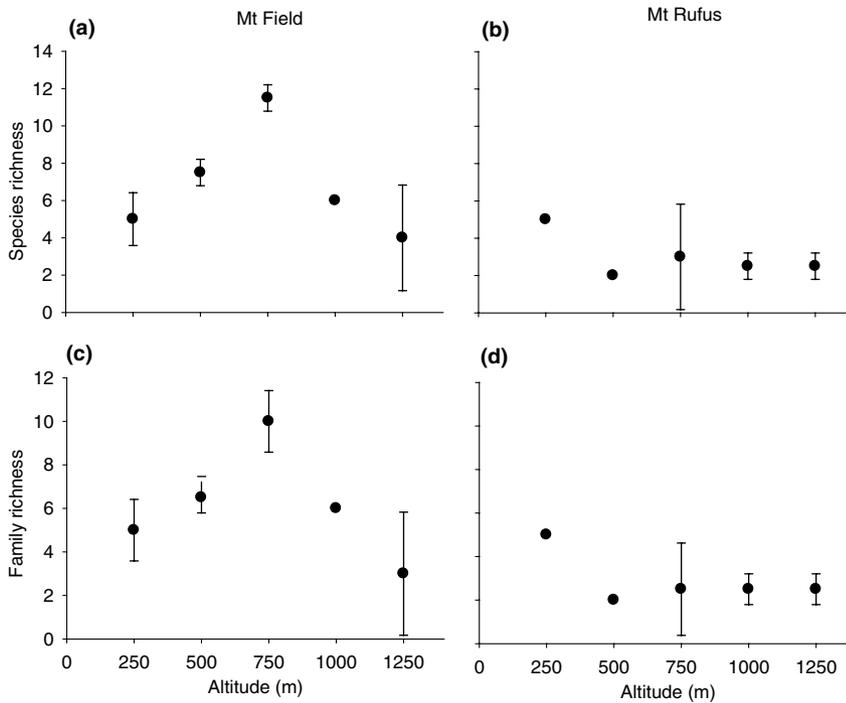


Figure 2 Bryophyte species richness along an altitudinal gradient in Tasmania. (a) and (b) show family richness from Mt Field and Mt Rufus locations, respectively ($n = 2$). (c) and (d) show species richness from Mt Field and Mt Rufus locations, respectively ($n = 2$). Mean (\pm SD) are shown.

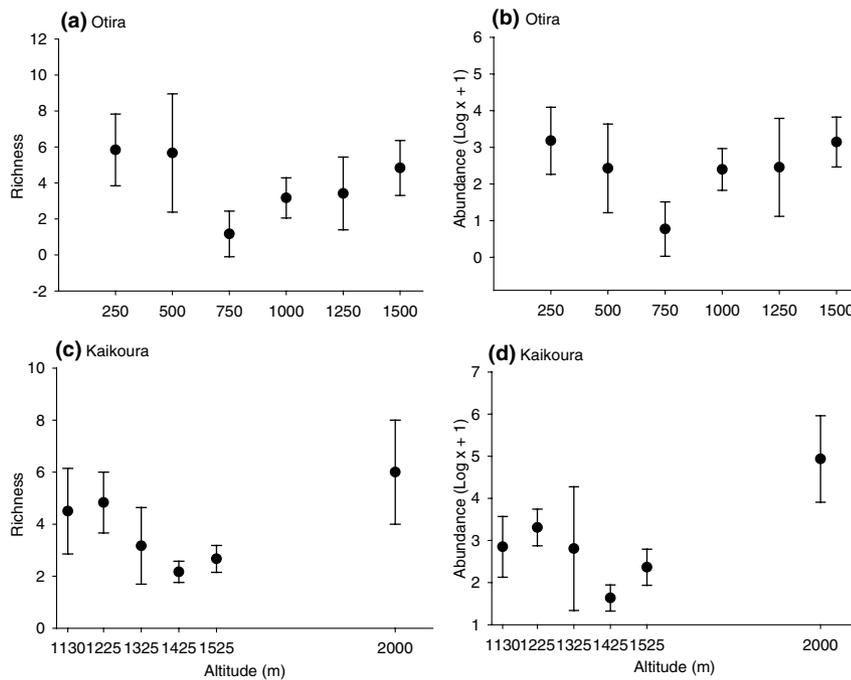


Figure 3 Invertebrate (a) taxa richness and (b) abundance [$\log(x + 1)$] from Otira along an altitudinal gradient ($n = 12$). Invertebrate (c) taxa richness and (d) abundance [$\log(x + 1)$] from Kaikoura along an altitudinal gradient ($n = 6$). Mean (\pm SD) are shown.

Invertebrate richness at Kaikoura also varied significantly along the altitudinal gradient (Fig. 3c. ANOVA $F_{5,30} = 5.85$, $P = 0.01$) peaking at K2000. The location K2000 differed significantly from K1325, K1425 and K1520 (Scheffe's *post hoc* test $P = 0.02$, $P < 0.01$ and $P = 0.01$, respectively). There was significant variation in invertebrate abundance

along the Kaikoura altitudinal gradient (Fig. 3d. ANOVA $F_{5,30} = 4.14$, $P = 0.01$), with K2000 (highest in abundance) significantly different from K1425 and K1520 (Scheffe's *post hoc* test, $P = 0.03$ and 0.04 , respectively).

The structure of invertebrate communities at Otira varied along the altitudinal gradient (Table 4; NPMANOVA

Table 4 Presence of invertebrate family and order extracted from bryophytes along an altitudinal gradient at Otira, New Zealand. Membership in one of four general groups (a–d) is included, based on presence/absence at different altitudes (see text for explanation). The numbers indicate the presence of a taxon from each location, noting that twelve samples were taken from each location

Family	Order	Otira					
		O250	O500	O750	O1000	O1250	O1500
Entomobryidae	Collembola	4	7	3	2	9	4
Taxa 1	Aranae	3	4	2	3	2	
Oppiidae	Acari	7	1	1		2	10
Oribatulidae	Acari	5	3		2	2	
Phthiraceridae	Acari	3	1		1	3	
Oribatelidae	Acari	7	1		5	3	
Taxa 2	Coleoptera	3	4		1	1	
Brachystomellidae	Collembola		7	1	4		2
Eutieiidae	Acari	3	4			1	
Isotomidae	Collembola		8		2		8
Sminthuridae	Collembola		1	1			1
Ceratopogonid	Diptera		1		6	6	
Taxa 3	Lepidoptera		1		1	1	
Onchyiuridae	Collembola		1		2		
Taxa 4	Symphyla		1				1
Chironomidae	Diptera	2	6				
Taxa 5	Diplura	2	1				
Aphididae	Hemiptera	1	1				
Epilohmanniidae	Acari				1	2	6
Staphylinidae	Coleoptera				1	3	1
Oribotritidae	Acari	1					
Nanhermanniidae	Acari	3					
Pedrocortesellidae	Acari	2					
Cecidomyiidae	Diptera	1					
Thripidae	Thysanoptera	1					
Taxa 6	Isopoda	1					
Taxa 7	Pseudoscorpion	1					
Neanuridae	Collembola	2					
Taxa 8	Polydesmida	4					
Forficulidae	Dermoptera	1					
Taxa 9	Hymenoptera	1					
Tomoceridae	Collembola		1				
Taxa 10	Geophila		1				
Taxa 11	Spirobolida		1				
Curculionidae	Coleoptera		1				
Taxa 12	Hemiptera		1				
Microzetidae	Acari			1			
Formicinae	Hymenoptera			1			
Taxa 13	Diptera				1		
Coccoidea	Hemiptera					1	
Tectochepeide	Acari						10
Taxa 14	Protura						2
Invertebrate taxa/ altitude		22	23	7	14	13	10
Total invertebrate taxa				42			

$F_{5,66} = 6.28$, $P < 0.01$). Of the forty-two families collected from invertebrates at Otira, fifteen taxa were cosmopolitan along the altitudinal gradient (Table 4, group A). Chironomidae, Diplura and Aphididae were found only at the two lowest altitudes (group B), whilst Epilohmanniidae and Staphylinidae were only found at the three highest altitudes (group C). Twenty-two families were only collected from bryophytes at one altitude each (group D): eleven families at O250, five at O500, two at both O750 and O1500 and one taxa at both O1000 and O1250.

Invertebrates collected from Kaikoura bryophytes also showed differences in community structure along the altitudinal gradient (Table 5; NPMANOVA $F_{5,30} = 7.55$, $P < 0.01$). Twenty-two invertebrate families were collected from all Kaikoura sites, twelve of which were cosmopolitan across all sites (Table 5, group A). Two taxa were found only at lower altitudes (group B), Sminthuridae and Aphididae were only collected at K1130, Coccoidea only at K1225, Protura at K1520, and Neanuridae, Crotonidae, Thripidae, and Cicadellidae at K2000 (group C).

Table 5 Presence of invertebrate family and order extracted from bryophytes along an altitudinal gradient, Kaikoura, New Zealand. Membership in one of three general groups (a–c) is included, based on presence/absence at different altitudes (see text for explanation). The numbers indicate the presence of a taxon from each location, noting that six samples were taken from each location

Family	Order	Kaikoura							
		K1130	K1225	K1325	K1425	K1520	K2000		
Brachystomellidae	Collembola	6	6	6	6	1	3	Group A	
Entomobryidae	Collembola	6	3	3		4	6		
Oribatellidae	Acari	4	5	1		6	1		
Staphylinidae	Coleoptera	1	1			1	4		
Chironomidae	Diptera	3		1	1		3		
Ceratopogonid	Diptera		3	2	5		4		
Taxa 1	Aranae	2	1				1		
Oribatulidae	Acari		4	1			5		
Taxa 2	Lepidoptera			1	1		3		
Isotomidae	Collembola	1				1			
Taxa 3	Hemiptera		1			1			
Taxa 4	Coleoptera			1		1			
Taxa 5	Diptera	1	3	2					Group B
Opipiidae	Acari		1	1					
Sminthuridae	Collembola	2						Group C	
Aphididae	Hemiptera	1							
Coccoidea	Hemiptera		1						
Taxa 6	Protura					1			
Neanuridae	Collembola						2		
Crotonidae	Acari						3		
Thripidae	Thysanoptera						1		
Cicadellidae	Hemiptera						1		
Invertebrate taxa/ altitude		10	11	10	4	8	13		
Total invertebrate taxa		22							

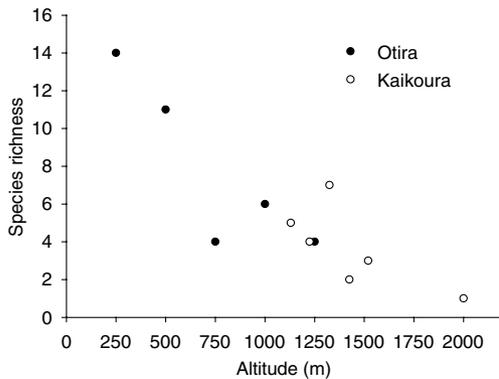


Figure 4 Total bryophyte species richness from Otira (closed symbols) and Kaikoura (open symbols) from each location along an altitudinal gradient.

Bryophyte species richness showed a general decrease on both mountains as altitude decreased. At Otira, species composition changed along the altitudinal gradient (NPMA-NOVA $F_{5,66} = 14.34, P < 0.01$). Otira bryophyte richness generally decreased from O250 (fourteen species) to four species at O750m and O1250 (Fig. 4). Six bryophytes were

found at more than one altitude (Table 6, group A), however, twenty-five species were unique to one altitude only (group B). Twelve bryophyte species were unique to O250, seven unique to O500, two unique species at O1000 and O250, and O750 and O1500 each had one unique species. Similarly, bryophyte communities along the Kaikoura gradient varied significantly (MANOVA $F_{5,30} = 12.42, P < 0.01$). On the Kaikoura gradient, seven species were found at the lower end of the gradient decreasing to only one species at K2000m. Of the eleven species collected from Kaikoura, four bryophyte species were found at more than one altitude (Table 7, group A). Three species were unique to K1325, and each of K1225, K1425, K1520 and K2000 had one unique species (group B). Overall, the changes in community structure were similar along the altitudinal gradients of both mountains. In both Tasmania and New Zealand, a much higher proportion of bryophyte families were found only on one of the two mountains, compared with invertebrate families.

DISCUSSION

This study has shown that there were significant changes in richness and abundance with altitude, although the trends were not consistent between different mountains, or between

Table 6 Presence of bryophyte species, families and bryophyte type (moss or liverwort) along an altitudinal gradient from Otira, New Zealand. Membership in one of two general groups (a, b) is included, based on presence/absence at different altitudes (see text for explanation). The numbers indicate the presence of a species within samples from each location, noting that twelve samples were taken from each location

Species	Family	Type	Otira						
			O250	O500	O750	O1000	O1250		O1500
<i>Breutelia pendula</i> (Sm.) Mitt.	Bartramiaceae	Moss			9	10	2	9	Group A
<i>Campylopus clavatus</i> (R. Br.) Wils.	Dicranaceae	Moss			3	1	7	2	
<i>Racomitrium crispulum</i> (Hook. F. & Wils.) Hook. F. & Wils.	Grimmiaceae	Moss				1	5		
<i>Wijkia extenuata</i> (Brid.) Crum	Sematophyllaceae	Moss	2	1				12	
<i>Dicranoloma billardierei</i> (Brid. ex anon.)	Dicranaceae	Moss	2					8	
<i>Rhacocarpus purpurascens</i> (Brid.) Par.	Hedwigiaceae	Moss					7	1	
<i>Gakstroemia weindorferi</i> (Herzog) Grolle	Lepidolaenaceae	Liverwort			2				Group B
<i>Lepidolaena palpebrifolia</i>	Lepidolaenaceae	Liverwort			6				
<i>Geocalyx caledonicus</i> Stephani	Geocalycaceae	Liverwort			2				
<i>Chiloscyphus spiniferus</i>	Geocalycaceae	Liverwort			1				
<i>Chiloscyphus bicillatus</i>	Geocalycaceae	Liverwort			4				
<i>Lepidozoea concinna</i>	Lepidoziaceae	Liverwort			1				
<i>Lepidozoea leavifolia</i> (Hook.f. & Taylor) Taylor ex Gottsche et al.	Lepidoziaceae	Liverwort			5				
<i>Schistochila ciliata</i> (Mitten) Stephani	Schistochilaceae	Liverwort			3				
<i>Bazzania involuta</i> Mont.) Trev.	Raduleaceae	Liverwort			1				
<i>Lophoedeia sonterea</i>	Raduleaceae	Liverwort			1				
<i>Ptychomnion aciculare</i> (Brid.) Mitt.	Ptychomniaceae	Moss			3				
<i>Distichophyllum pulchellum</i> (Hampe ex C. Muell.) Mitt.	Hookeriaceae	Moss			2				
<i>Brachythecium salebrosum</i> (Web. & Mohr) B. S. G.	Brachytheciaceae	Moss				4			
<i>Thuidium sparsum</i> (Hook. F. & Wils.) Jaeg.	Thuidiaceae	Moss				4			
<i>Weymouthia cochlearifolia</i> (Schwaegr.) Dix.	Meteoriaceae	Moss				1			
<i>Sematophyllum contigium</i> (Mitt.) Mitt.	Sematophyllaceae	Moss				2			
<i>Metsgeria</i> sp.	Metzgeriaceae	Liverwort				1			
<i>Radula</i> sp.	Raduleaceae	Liverwort				2			
<i>Bartramia mossmaniana</i> C. Muell.	Bartramiaceae	Moss				2			
<i>Brachythecium paradoxum</i> (Hook. F. & Wils.) Jaeg.	Brachytheciaceae	Moss				5			
<i>Isotachis lyallii</i>	Balantiopsaeae	Liverwort					6		
<i>Campylopodium medium</i> (Duby) Giese & Frahm	Dicranaceae	Moss					2		
<i>Bryum laevigatum</i> Hook. F. & Wils.	Bryaceae	Moss						2	
<i>Isotachis montana</i> Colenso	Balantiopsaceae	Liverwort						1	
<i>Hypnum cupressiforme</i> Hedw. var. <i>cupressiforme</i>	Hypnaceae	Moss						2	
Bryophyte species/altitude			14	11	4	6	4	4	
Total bryophyte species					31				

Table 7 Presence of bryophyte species, family and bryophyte type (moss or liverwort) along an altitudinal gradient from Kaikoura, New Zealand. Membership in one of two general groups (a, b) is included, based on presence/absence at different altitudes (see text for explanation). The numbers indicate the presence of a species within samples from each location, noting that six samples were taken from each location

Species	Family	Type	Kaikoura							
			K1130	K1225	K1325	K1425	K1520	K2000		
<i>Philonotis tenuis</i> Tayl.) Reichdt	Bartramiaceae	Moss	3	3	1	6	5		Group A	
<i>Breutelia pendula</i> (Sm.) Mitt.	Bartramiaceae	Moss	5	2	1					
<i>Bartramia papillata</i> Hook.f. & Wils.	Bartramiaceae	Moss		3	1					
<i>Racomitrium crispulum</i> (Hook.f. & Wils.) Hook.f. & Wils.	Grimmiaceae	Moss			1		6			
<i>Brachythecium salebrosum</i> (Web. & Mohr) B. S. G.	Brachytheciaceae	Moss	1						Group B	
<i>Brachythecium paradoxum</i> (Hook.f. & Wils.) Jaeg.	Brachytheciaceae	Moss	5							
<i>Hypnum cupressiforme</i> v <i>cupressiforme</i>	Hypnaceae	Moss	1							
<i>Bryum laevigatum</i> Hook.f. & Wils.	Bryaceae	Moss		4						
<i>Schistidium apocarpa</i> (Hedw.) B. S. G.	Grimmiaceae	Moss			1					
<i>Ceratodon purpureus</i> (Hedw.) Brid.	Grimmiaceae	Moss			3					
<i>Philonotis pyriformis</i> (R. Br. Ter.) Wijk & Marg.	Bartramiaceae	Moss			1					
<i>Thuidium sparsum</i> (Hook.f. & Wils.) Jaeg.	Thuidiaceae	Moss				1				
<i>Gakstroemia weindorferi</i> (Herzog) Grolle	Lepidolaenaceae	Liverwort					1			
<i>Leptodontium interruptum</i> (Mitt.) Broth	Pottiaceae	Moss						8		
Bryophyte species/altitude			5	4	7	2	3	1		
Total bryophyte species					14					

Table 8 Summary of trends along altitudinal gradients found in this study

General trends along altitudinal gradient	
Tasmania	
Invertebrate richness	Significant decrease with altitude over most of the gradient
Invertebrate abundance	No significant trend. Does not appear to follow invertebrate richness
Bryophyte spp./family richness	Significant change, but different patterns on different mountains. No overall pattern
New Zealand	
Invertebrate richness	Significant change, but no clear general pattern. Not an overall decrease with altitude
Invertebrate abundance	One mountain significant change. Similar trends to invertebrate richness
Bryophyte spp./family richness	Significant decrease in richness with altitude across both mountains

the invertebrate and bryophyte communities (Table 8). There were some instances of decreasing richness and abundance along the altitudinal gradient, but this trend was certainly not consistent between mountains. It was also clear that in some instances, invertebrate richness and abundance had similar patterns, but in other circumstances they did not. Both invertebrates and bryophytes showed significant changes in richness and abundance with altitude, but there was no consistent trend across the four mountains.

Evidence of variation in the diversity and community composition of bryophytes and their associated invertebrates along an altitudinal gradient was found. We used a robust experimental design incorporating four independent altitudinal gradients (four mountains in two countries) with replication within and between sites on each mountain, and sampled all sites on all four mountains within a short period of time to reduce the effects of temporal variation. If this study had no mountain replication, or pseudo-replication within a mountain system (e.g. Loiselle & Blake, 1991; Wolf, 1994; Pendry & Proctor, 1997; Rakotondrainibe & Raharimalala, 1998; Rautio, 1998), trends along an altitudinal gradient could have been detected. Similarly, if sampling were carried out at only small or large spatial scales, variation would not have been detected at other important spatial scales (e.g. Haslett, 1997).

Why has this study not found more consistent relationships with altitude, when so many previous studies have found trends with diversity along altitudinal gradients? It is possible that some studies have not been robust enough to assess variation at different scales, hence they have confounded site scale variation with altitude. However, it is also possible that altitudinal gradients do exist for some taxa and some mountains, as many studies, assessing a variety of organisms, have found consistent trends along altitudinal gradients (e.g. Kikkawa & Williams, 1971; Hunter & Yonzon, 1993; Wolf, 1994; Pendry & Proctor, 1997; Rakotondrainibe & Raharimalala, 1998; Rautio, 1998; Lobo & Halffter, 2000). There could also be a bias in the literature towards publishing only positive results (Gurevitch & Hedges, 1999), because studies that have found negative or inconclusive results are sometimes rejected from peer-reviewed journals, or not even submitted for publication (Moller & Jennions, 2001; Jennions & Moller, 2002).

Many previous studies have found bryophyte diversity frequently varying along altitudinal gradients, but in a

complex manner. In the Andes, bryophytes have been found to increase in cover and species richness along an altitudinal gradient from lowland to montane forest (van Reenan & Gradstein, 1983). On four Pacific Islands assessed by Vitt (1991), bryophyte species richness on two islands (tropical and sub-tropical) was found to monotonically increase as altitude increased, and the two other islands (cool temperate) both show low- and mid-altitude peaks in species richness. This study found that species diversity decreased as altitude increased in New Zealand, but a mid-altitudinal peak in diversity was found at Mt Field (Tasmania), and Mt Rufus generally had no change in diversity. However, there tends to be a change in species composition as altitude increased. Along an altitudinal gradient on the Chichibu mountains in central Japan (Nagano, 1969), bryophyte species composition was similar at low- and mid-altitudes, but changed completely at high altitudes. Ratkowsky & Ratkowsky (1982) found mosses to be highest in species richness at middle- and low-altitudes of Mt Wellington, Tasmania, but liverworts were more species rich in middle- and higher-altitudes, which is a similar finding to the Mt Field bryophyte trends in this study. At high altitudes in Tasmania, the bryophyte floras are very similar (Table 3), dominated by the mosses *Andreaea mutabilis* and *Grimmia pulvinata* which are known alpine inhabitants (Scott & Stone, 1976; Kantvilas & Jarman, 1991). The two most common species at low altitudes, *Wijkia extenuata* and *Campylopus clavatus*, and are generally found in a range of habitats (Scott & Stone, 1976; Kantvilas & Jarman, 1991). The majority of other bryophyte species found in Tasmania were unique to one location (Table 3), which is a common feature of bryophyte communities (Ratkowsky & Ratkowsky, 1982; Vitt, 1991; Wolf, 1993; Vitt & Belland, 1997). As most of the bryophyte species were found at only one location, other factors may be more important than altitude in determining composition. Such factors may include moisture and climate tolerance (Slack, 1977; Lee & La Roi, 1979; During, 1992; Wolf, 1994; Li & Vitt, 1995; Vitt & Belland, 1997; Gonzalez, 1998).

Altitudinal gradients may play some role in generating community structure and diversity, but this study and others (e.g. Whittaker & Niering, 1975; Loiselle & Blake, 1991; Vitt, 1991; Fleishman *et al.*, 2000) strongly suggest that factors operating at smaller scales (such as moisture, food and substrate), and larger scales (such as climate and

precipitation) are likely to be at least as important, especially for bryophytes and the invertebrates living in them. One of the main findings of this study was the high level of variation in richness and abundance between all scales, from local patches to biogeographical regions. This variation is not unexpected given the high degree of spatial patchiness in both bryophyte and invertebrate communities (Gerson, 1969; Joosse & Verhoef, 1974; Gerson, 1982; Smrz, 1992; Setälä *et al.*, 1995). Bryophytes have many attributes that can affect the spatial distribution and abundance of invertebrates (Gerson, 1982). They are able to rapidly absorb water, reduce evaporation of their substrate, as well as provide insulation against extreme environmental conditions, such as cold and wind (Gerson, 1982; Smrz, 1992). This modification of the habitat allows a variety of animals, such as Collembola and Diptera, to aggregate because they are otherwise unable to tolerate dry conditions (Joosse & Verhoef, 1974; Leinaas & Somme, 1984; Usher & Booth, 1984). Oribatid mites are known to aggregate where there is decaying plant material and where there is a high level of moisture, such as is found in bryophyte communities (Bonnet *et al.*, 1975; Seyd & Seaward, 1984). In general, most locations from all four mountains have unique bryophyte species communities, possibly because of differing micro-climates at each location (Usher, 1983). These different bryophyte communities in turn could support unique invertebrate communities.

Differing taxonomic resolution could be an issue in determining the patterns of diversity. The invertebrates collected in this study were identified only to family, whereas the bryophytes were identified to species level. There was variation in invertebrate diversity at all scales, with richness not varying with altitude any more than among sites. This is not a case for invertebrates where the number of families was reasonably constant between locations, and an altitudinal pattern may exist at a finer taxonomic resolution (e.g. species and genera). The identification of individual invertebrate species would have given an insight into individual preferences and possible behavioural changes along altitudinal gradients. However, because of the high turnover of families along the four altitudinal gradients (Tables 2, 4, 5), species-level identifications would have not given any further insight in the search for general patterns along altitudinal gradients.

This lack of a consistent pattern in the community structure of invertebrate/bryophyte communities along altitudinal gradients has important consequences for management regimes at broader regional scales both now and over the coming century. Altitudinal gradients have been used extensively as surrogates for future climate change (e.g. Whittaker & Tribe, 1996; Boggs & Murphy, 1997; Fielding *et al.*, 1999; Hodkinson *et al.*, 1999; Fleishman *et al.*, 2000), as changes in temperature occur over short distances. With changes in mean temperature and precipitation predicted to occur over the coming century (Houghton *et al.*, 2001), climatic zones along the altitudinal gradients are expected to shift. Increases in the frequency of extreme climatic events will also subject all organisms to stresses that they possibly

are not adapted to deal with (Houghton *et al.*, 2001). This study found no consistent trend for the bryophyte/invertebrate community on various mountains at one point in time, suggesting that it would be difficult to assess how these communities would respond to a changing climate based solely on the diversity and composition of taxa present at one point in time. It is quite likely that different bryophyte and invertebrate communities would behave differently based on their individual circumstances.

From a conservation point of view, it is quite clear that in order to retain the unique diversity of these bryophyte/invertebrate communities, habitat conservation needs to be aimed at a variety of spatial scales. A few representative sites at a few altitudes on one mountain are clearly not appropriate. Similarly, the ecological role that each species plays within this system is of vital importance. This information only comes from taxonomic verification and species-specific behavioural and ecological studies for both bryophytes- and moss-inhabiting-invertebrates.

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