Montane outcrop vegetation of Banks Peninsula, South Island, New Zealand

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Abstract: Species composition patterns and vegetation–environment relationships were quantified for montane volcanic outcrops on Banks Peninsula. The flora of these habitat islands comprises 346 vascular plant species including 82 exotic species and 52 species that are nationally rare, regionally rare, or regional endemics. Both Multidimensional scaling (MDS) ordination analysis and TWINSPAN results illustrated the high compositional and environmental heterogeneity across the outcrops. MDS revealed that primary environmental factors related to community composition comprise both regional-scale gradients of altitude and outcrop-scale gradients of slope steepness, soil pH, area available to plants, maximum vegetation height, and the percentage of the surrounding vegetation that is forest. Accordingly, TWINSPAN separated four outcrop communities that occur on steeper slopes, have less fertile soils and tend not to face north from three outcrop communities that have shallower slopes, more fertile soils and tend to face north. Types in the first group are more likely to be bordered by forest or taller shrublands, whereas those in the second group occur on outcrops primarily bordered by grasslands and support more exotic species. Within these broader groups, communities differ in their altitude and the size, soil depth and shading of the outcrops on which they occur. We describe the vegetation of the seven communities; this ranges from predominance of stunted trees and taller statured species such as *Podocarpus hallii* and *Phormium cookianum* to vegetation of shrubby species such as *Heliohebe lavaudiana* and *Hebe strictissima*, to short vegetation of native woodland and grassland species such as *Polystichum vestitum* and *Rytidosperma corinum*, to exotic pasture-like vegetation of clovers and exotic grasses. The percentage of species on an outcrop face that are exotic is well modelled by site factors, with exotics increasing as the surrounding matrix becomes more disturbed, slopes become more gentle, the percentage of shade on the outcrop decreases, and soil fertility increases. In contrast, nearby disturbance has little influence on the percentage or number of species that are rare on an outcrop face; rather rare species richness is more strongly related to outcrop area and lack of shade, echoing patterns observed for rare outcrop species elsewhere in the world. These results highlight the importance of considering the high compositional heterogeneity among outcrops and the influence of disturbance to surrounding ecosystems in guiding conservation planning.

Keywords: basaltic outcrops; conservation; exotic plants; habitat islands; landscape context; Multi-dimensional scaling; rare plants; TWINSPAN, vegetation–environment relationships

Introduction

Worldwide, there has been a long-standing interest in the plant communities that occur on rock outcrops. Because of their extreme environments (shallow soils, exposed bedrock on the surface) they often harbour endemic species (see reviews by Baskin & Baskin 1988; Anderson et al. 1999; Seine et al. 2000), and provide refuges from grazing animals, human disturbance and fire. They therefore often support species that are rare in the landscape (Wardle J. 1971; Wardle P. 1991; Burke et al. 2003; Hunter 2003; Wiser & Buxton 2008) and in some areas they support ancient forests (Kelly et al. 1992). New Zealand has numerous resistant rock outcrops associated with diverse rock types. Outcrops have been recognised as providing highly important habitats for rare and threatened plants (Wardle 1991; Rogers & Walker 2002; de Lange et al. 2004) and invertebrates (e.g. Jamieson et al. 2000). Despite this interest, and a wealth of qualitative descriptions of outcrop vegetation (e.g. Cockayne 1928; Bell 1973; Wardle 1991), there have been few quantitative studies on outcrop vegetation in New Zealand and those that have been conducted have been either primarily focused on them as a minor component of the prevailing vegetation (e.g. Wardle 1971) or have concerned coastal cliffs exclusively (e.g. Atkinson 1972; Wilson & Cullen 1986). As a consequence, there is little understanding of whether New Zealand outcrop vegetation is fairly uniform or highly heterogeneous (which has important conservation implications), the importance of the environmental gradients known to be important determinants of outcrop composition elsewhere in the world such as elevation, slope, aspect, shading, soil chemistry, and soil depth (e.g. Winterringer & Vestal 1956; Ashton & Webb 1977; Baskin & Baskin 1988; Fuls et al. 1992; Wiser et al. 1996) or the importance of regional versus outcrop-scale environmental gradients (Wiser et al. 1996).

Banks Peninsula's montane volcanic outcrops represent islands of less disturbed vegetation amidst a diverse mosaic of original forest, regenerating forest and shrublands, tussocklands, and grasslands dominated by exotic species. These outcrops contribute significantly to regional plant biodiversity; although they comprise less than 5% of the total area, they contain over 33% of the region's plant species, 50% of the regional endemics, and 26% of the region's species considered nationally or regionally rare. They also provide a refuge for species that are vulnerable to fire and grazing by introduced ungulates (Wiser 2001). Nevertheless, removal of the once-intact forest matrix has had a profound impact on composition of these sites (Wiser & Buxton 2008), but how this influences distributions of different exotic and rare species is not well understood.

In order to better understand the vegetation of these outcrops we ask: (1) Are plant communities across Banks Peninsula's montane outcrops uniform or do they vary? (2) Do regional climatic and geographic gradients override the importance of within-outcrop -scale environmental gradients (e.g. slope, aspect, soil depth) to outcrop communities? (3) Are exotic species more important on outcrops surrounded by disturbed vegetation and conversely are rare species more important where the surrounding vegetation is intact? In recent years there has been increased interest by the local community in preserving the biota of these systems (Landcare Trust 2007) and answers to these questions have the added importance of informing conservation and management decisions.

Methods

Study area

We studied rock outcrop vegetation on Banks Peninsula, South Island, New Zealand. Banks Peninsula is c. 1000 km^2 and was formed from Miocene volcanic eruptions, creating a geology of basaltic to trachytic volcanics (Weaver et al. 1985). Numerous outcrops are the remains of the hardest rocks that cooled slowly from their molten condition because they never breached the surface. The highest point is Mount Herbert at 920 m. Soils are derived from bedrock and loess and are moderately to very fertile (Dorsey 1988). Annual rainfall ranges from 600 mm at the driest (low altitude) locations to 2000 mm at some of the highest tops, with a winter maximum (NIWA 2003). Before humans arrived c. 700 years ago, the landscape was almost completely forested (Wilson 2008). Above 600 m most of this forest was dominated by *Podocarpus hallii*, *Griselinia littoralis* and *Pseudowintera colorata* (nomenclature follows Allan Herbarium 2000), except where beech was dominant in the south-east corner of the peninsula (Wilson 1998). Polynesians removed about a third of the forest before Europeans arrived in the mid-1800s; by 1920, less than 1% of the original forest remained (Wilson 1998). With subsequent regeneration, about 10% of the area is now forested, with a further 5% in open treeland and native scrub less than 6 m tall (Wilson 1998). The vegetation of much of Banks Peninsula is modified tussock grassland (*Chionochloa rigida, Festuca* spp., *Poa* spp. and exotic pasture grasses); before human settlement tussockland was largely restricted to higher altitude outcrops and steep coastal banks and cliffs.

Data collection

Sampling was restricted to outcrops occurring at altitudes greater than 500 m. This cut-off excluded frost-free environments and salt-spray-influenced coastal outcrops, and corresponds to a recognised altitudinal boundary in vegetation composition separating the upper cool-temperate zone from the lower cool-temperate zone (Wilson 2008). Outcrops were sampled across gradients of rainfall, geology, and altitude, and the range of variation in aspect, steepness and surrounding vegetation types. In total, 153 rock faces across 39 outcrop systems were sampled.

Within an outcrop, variation in composition and environmental conditions was sampled. Rock surfaces greater than 20 m^2 in surface area that differed in aspect by >40°, or in slope by >30°, or in whether they were shaded by nearby vegetation, were sampled as separate faces; 1–12 faces were defined within each of the outcrops sampled. As boundaries were defined topographically, sample areas were irregular in shape and size (cf. Ashton & Webb 1977; Porembski et al. 1995). On each face, cover of each vascular plant species was recorded with a relevé, using a modified Braun-Blanquet cover-abundance scale (1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%; Allen 1992). Maximum vegetation height was estimated to the nearest decimetre for heights under 3 m, 0.5 m for heights > 3 m and < 10 m, and to the nearest 1 m for vegetation ≥ 10 m tall. For each face, site variables measured were area, altitude, slope and aspect (corrected for magnetic declination). The amount of the face that was exposed rock was estimated to the nearest 5%. We calculated habitable area as face area × (100 − % exposed rock). Presence or absence of deep shading by nearby vegetation (> 75% cover) was recorded. A composite soil sample was collected from across the vegetated areas of the face. Soils were air dried, sieved, and analysed for pH, percent organic matter (loss on ignition), total N and available K, Ca, Mg, and P, and the minor nutrient Fe, which has been shown to have a significant relationship to outcrop vegetation that is independent of pH and major nutrients (Wiser et al. 1996). Analysis was done by Brookside Laboratory Association, New Knoxville, Ohio, USA, using Mehlich 3 extractant. Values for Ca, K, and P were square-root transformed before analysis to improve normality. C:N was calculated as a measure of soil N availability. Soil depth was measured across the vegetated areas using a graduated steel pin and the maximum soil depth was recorded. The structure of the matrix vegetation within 50 m of the outcrop was recorded based on visual estimates of the percentage cover (to the nearest 5%) of the following vegetation types: grassland, short shrubland (<1 m tall), tall shrubland (1–2 m tall) and forest.

Easting and northing of the geographic centre of each outcrop was determined from New Zealand metric series 260 topographic maps. For each outcrop location, values for annual rainfall were estimated from thin-plate splines (Hutchinson & Gessler 1994) fitted to annual rainfall data collected at local meteorological stations (Leathwick & Stephens 1998, unpublished). The mapped geological formation (one of six formations) of each outcrop was recorded (Sewell et al. 1992).

For each species observed we assigned biostatus (e.g. exotic vs native) based on the New Zealand Plant Names database (http://nzflora.landcareresearch.co.nz). We determined regional rarity following Wilson (1992) and national rarity following de Lange et al. (2004).

Data analysis

We used multi-dimensional scaling(MDS) to examine relationships between measured environmental factors and community composition on the 153 faces. We used TWINSPAN to classify the vegetation from 153 rock faces across 39 outcrop systems into seven community types. Classification and ordination analyses were done using PC-Ord (McCune & Mefford 1999). Community naming followed Atkinson (1985). Names derive from the three most frequent species having an average cover of >5% or the two species having the highest cover and frequency. More species were listed if required to distinguish that type.

To understand the importance of disturbance to the surrounding matrix vegetation versus other site variables in influencing why exotic and rare species are more common in some community types than others, we modelled the percentage of the species on each outcrop face that were exotic and the percentage and number of species that were rare, from the range of site variables we collected. We used a nested hierarchical model (Singer 1998) with 'site' included as a random variable, using PROC MIXED in SAS (SAS Institute Inc. 2001). This accounts for outcrop faces being nested within an outcrop site, and thus not being independent. Percentages were arc-sin square-root transformed before analysis. Variable selection was by backward elimination. In the final model only variables with $P < 0.01$ were retained.

Results

The native woody species *Griselinia littoralis* and *Melicytus alpinus* (sensu lato), the native fern *Asplenium appendiculatum*, the exotic grasses *Anthoxanthum odoratum*, *Holcus lanatus* and *Dactylis glomerata*, and the exotic flatweed *Hypochaeris radicata* have high frequency across all outcrops studied and occur in every community type we recognised (Table 1). Two Banks Peninsula endemics, *Heliohebe lavaudiana* and *Hebe strictissima*, occur across most recognised community types as well.

The MDS analysis revealed that the primary environmental factors that related to community composition are the regional-scale gradient of altitude and the outcrop-scale gradients of slope steepness, soil pH, area available to plants, maximum vegetation height, and the percentage of the surrounding vegetation that is forest (Fig. 1). The altitude and area gradients are illustrated by gradients of native species composition. For example, the liane *Metrosideros diffusa* and the epiphytic ferns *Pyrrosia eleagnifolia* and *Microsorum pustulatum* are most abundant on smaller outcrops and those at lower altitudes, whereas the grass *Hierochloe redolens,* shrubs *Brachyglottis lagopus, Dracophyllum acerosum* and large monocot *Phormium cookianum* are more abundant on larger and higher altitude outcrops. The complex gradient related to steeper slopes, taller outcrop vegetation, and outcrops more frequently surrounded by forest corresponds to the first TWINSPAN split (Fig. 2). The taller-statured species *Podocarpus hallii* and *Phormium cookianum* are more abundant on the steeper sites surrounded by forest, and the smaller, herbaceous *Trifolium repens*, *T. dubium*, and *Rytidosperma clavatum* become more prominent on shallow outcrops surrounded by grasslands (Fig. 3).

We recognised seven community types from the TWINSPAN analysis (Table 1, Fig. 2). These types encompass significant variation both among and within communities in both composition and site conditions. Slope, soil chemistry, and aspect distinguished four communities types occurring on steeper slopes, having less fertile soils, and tending not to face north (types 1–4) from three outcrop communities that have shallower slopes, more fertile soils, and tend to face north (Types 5–7; Fig. 2). Types 1–4 are more likely to be bordered by forest or taller shrublands, whereas types 5–7 occur on outcrops primarily bordered by grasslands and support more exotic species. Within these two major groups, communities vary in their altitude, annual rainfall, geographic position, the size of the outcrop faces on which they occur, soil fertility, and the height of their vegetation. In the descriptions that

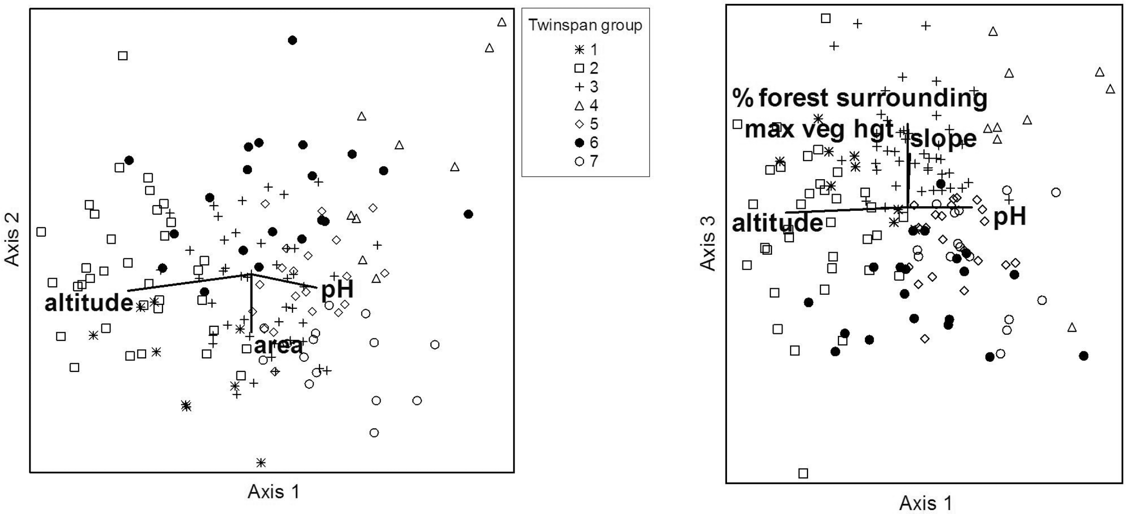

Figure 1. MDS ordination of 153 plots coded by the seven TWINSPAN plant communities on Banks Peninsula rock outcrops: (a) axes 1 vs 2, (b) axes 1 vs 3. Vectors represent site variables having an r^2 with either axis > 0.2. Positions of plot scores are coded by TWINSPAN group.

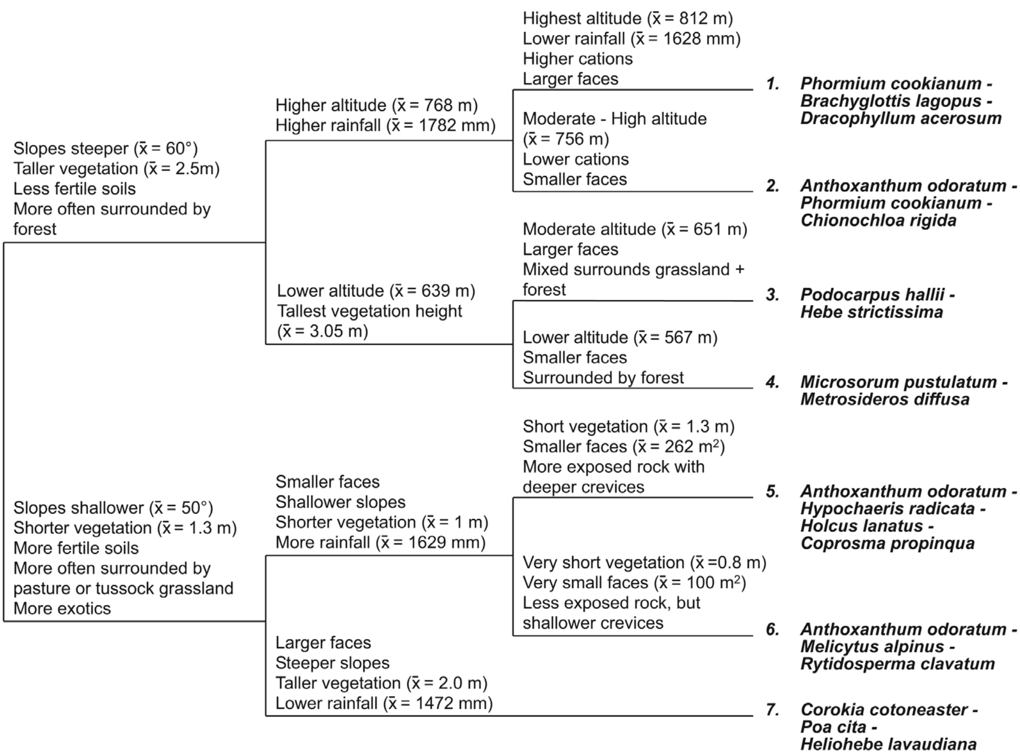

Figure 2. Hierarchical relationships of TWINSPAN plant communities on Banks Peninsula rock outcrops and associated environmental contrasts.

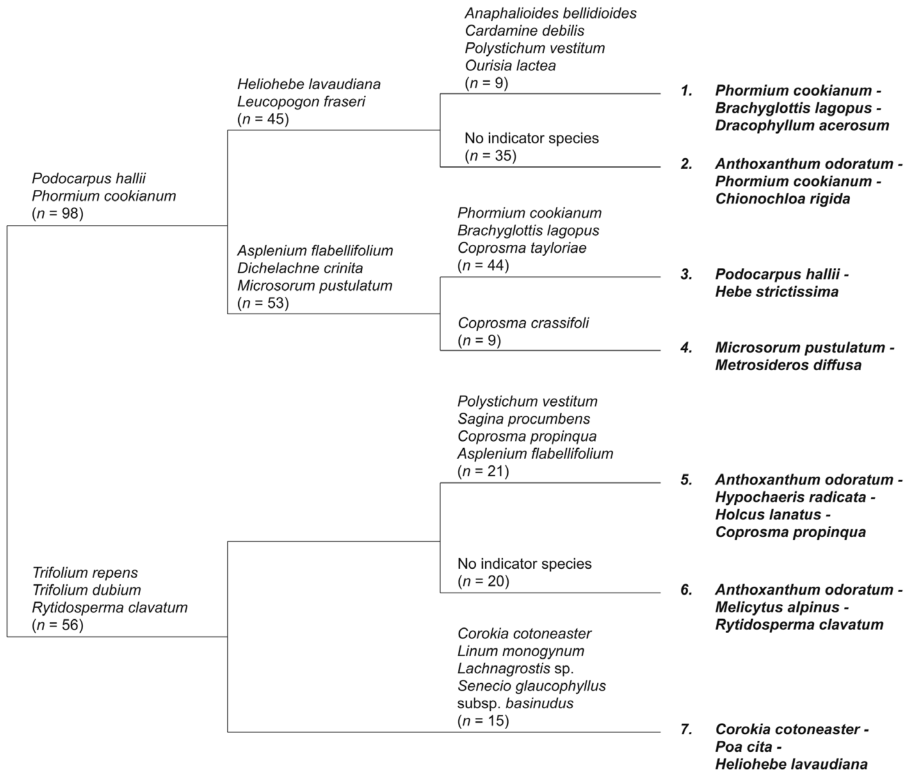

Figure 3. Indicator species in Banks Peninsula rock outcrop communities associated with the divisive splits in TWINSPAN.

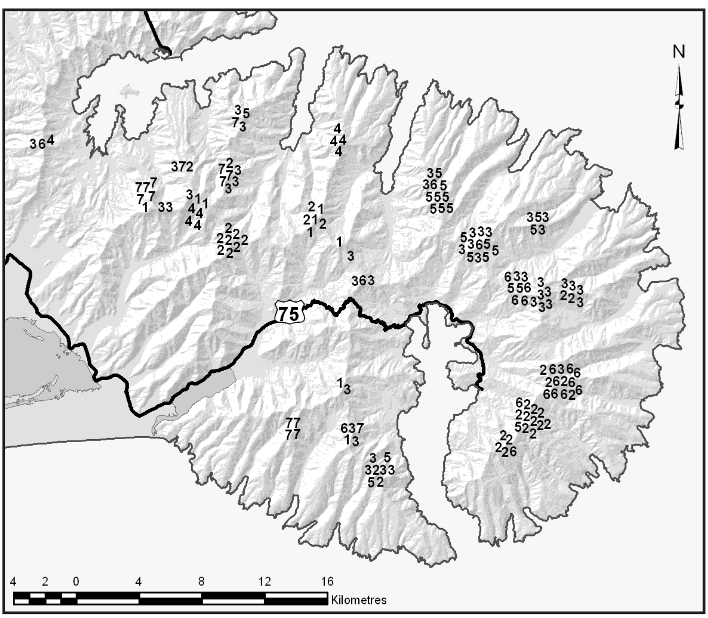

Figure 4. Map of Banks Peninsula, New Zealand, study area indicating approximate rock outcrop sampling positions and designated plant community types according to TWINSPAN. Sampling positions have been adjusted to improve readability.

Table 1. Classification of rock outcrop communities on Banks Peninsula, New Zealand, provided by TWINSPAN. The mean cover class for plots where the species is present in the community is followed by the constancy (percent of plots in the community where the species was present) within each community. + = present in community, but in less than one-third of the plots, * = exotic species. Species appearing in community names are in bold. Indicator species for individual community types are shown in italics. Species are grouped (indicated by shading) according the community type in which they have the highest constancy; species with constancy > 80% across most groups are shown in a band at the top of the table.

Species name	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7	
***Hypochaeris radicata**	2	100	2	94	2	98	1	89	**2**	**100**	2	100	2	100
***Anthoxanthum odoratum**	2	100	**3**	**91**	2	98	2	100	**3**	**100**	**3**	**100**	2	100
Melicytus alpinus	2	78	2	80	1	77	1	78	2	90	**2**	**80**	2	100
Asplenium appendiculatum	2	100	1	60	2	100	2	44	1	100	2	60	1	80
***Holcus lanatus**	1	100	1	60	1	89	+	22	**2**	**100**	1	90	2	100
Griselinia littoralis	2	100	2	69	2	95	2	89	2	67	2	35	2	87
*Dactylis glomerata	1	89	2	54	2	86	2	56	2	95	2	80	2	100
Grammitis poeppigiana	1	56	+	11	+	16								
Uncinia rubra	1	56	+	3	+	7								
Ourisia lactea	*2*	*78*	+	3	+	5								
Gaultheria depressa var. novaezelandiae	2	56	+	29	+	5			+	5				
Rytidosperma gracile	2	56	+	17	+	11			+	14				
Hymenophyllum multifidum	3	78	+	11	2	41			+	14				
Aciphylla aurea	1	78	1	34	1	77	2	56	2	48	+	10		
Raoulia glabra	1	56	+	11	+	23			1	52	+	25		
Anaphalioides bellidioides	*2*	*100*	+	11	1	48			1	52	+	5	+	13
Phormium cookianum	**3**	**100**	**3**	**77**	*2*	*86*			2	38	+	5	2	47
Deyeuxia avenoides	2	100	2	77	2	93	2	44	1	81	2	75	1	53
Hierochloe redolens	2	100	2	54	2	55			+	24	+	5	2	67
Brachyglottis lagopus	**3**	**100**	2	89	*2*	*80*			2	71	2	75	2	73
Polystichum vestitum	*1*	*89*	+	29	1	68	+	33	*1*	*71*	+	5	1	40
Dracophyllum acerosum	**3**	**89**	**3**	**57**	+	27					+	25	2	53
Chionochloa conspicua	3	78	+	9	+	16					+	5	+	7
Anisotome aromatica	3	78	2	34	2	50			+	14	1	45	+	33
Cardamine debilis	*1*	*78*	+	3	1	45	1	67	1	52			1	40
Rubus cissoides	2	78	1	40	1	75	2	44	+	29	+	10	1	47
*Hieracium pilosella	2	78	2	34	1	50			1	62	1	40	1	47
Gaultheria antipoda	1	67	2	60	1	50			+	10			+	27
Blechnum montanum	2	56	+	11	+	7			+	5			+	13
Stellaria decipiens	1	56	+	23	1	48	+	11	+	10			+	13
Asplenium hookerianum	1	56	+	17	1	39	+	11	+	29			+	20
Muehlenbeckia complexa	1	56	+	26	1	34			2	52	2	50	1	53
Festuca novae-zelandiae	2	56	+	14	+	14			+	14	+	10	+	33
Chionochloa rigida	+	33	**3**	**57**	+	30			+	24	3	40	+	33
Pseudowintera colorata	+	11	+	11	1	52			+	19				
Coprosma tayloriae	2	89	2	66	*2*	*89*	+	11	2	86	+	25	+	33
Podocarpus hallii	2	78	2	74	**2**	**91**	2	44	2	43	+	10	+	33
Pseudopanax colensoi	2	78	2	46	2	86	3	44	2	52	+	15	+	33
Hebe salicifolia	1	67	+	14	1	68	+	22	+	24	+	5	+	7
Myrsine divaricata	2	44	1	40	1	50	+	11	+	29			+	13
Epilobium pubens	1	44	+	3	1	52	+	11	1	43			+	33
Coprosma rhamnoides	1	44	1	57	1	91	2	44	1	81	1	40	1	60
Huperzia varia	+	33	+	9	1	59	+	33	+	10	+	5	+	13
Hebe strictissima	+	33	3	51	**2**	**93**	2	89	2	86	*3*	*70*	2	67

Species name	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7	
Fuchsia excorticata	+	22	+	9	2	59	+	22	+	33	+	5	1	47
Ctenopteris heterophylla	+	11	2	46	1	64	+	11	1	38	+	5	1	40
Astelia fragrans			+	20	1	52							+	7
Pteridium esculentum			+	17	2	55			+	19	+	5	+	33
Microsorum pustulatum	+	33	+	29	2	86	**3**	**89**	2	71	2	60	2	47
Coprosma linariifolia	+	22	+	26	1	45	1	67	+	14	+	20	1	53
Olearia paniculata	+	11	+	3	+	16	2	78	+	5	+	10	+	7
Helichrysum lanceolatum	+	11			+	20	2	56	+	24	+	5	+	33
Coprosma crassifolia	+	11					1	67	+	10			1	47
Metrosideros diffusa					2	41	3	67	+	5				
Melicytus ramiflorus			+	3	2	34	2	56					+	20
Pyrrosia eleagnifolia			+	3	+	20	2	78	+	14	2	35	+	20
Myrsine australis					1	36	2	56					+	33
Pittosporum tenuifolium			+	3	+	23	2	56	+	10	+	5	+	33
Coprosma lucida			+	17	+	30	2	89					+	33
Asplenium flabellifolium	+	11	+	29	1	77	2	89	*1*	*86*	+	25	1	93
*Rumex acetosella	1	78	1	51	1	59			1	90	2	85	1	60
*Cerastium fontanum	1	67	1	46	1	77	1	44	1	100	1	80	1	93
*Aira caryophyllea	1	56	2	49	1	77	1	56	1	100	2	80	1	80
*Cynosurus cristatus	2	44	+	3	+	25			1	76	+	30	2	60
*Trifolium repens	1	44	+	29	+	14			1	81	1	60	1	73
*Crepis capillaris	1	44	1	40	1	43	+	33	1	90	1	40	1	87
**Sagina procumbens*	+	33	+	6	+	20			1	81	+	5	1	60
Helichrysum filicaule	+	22	+	31	1	55	+	11	1	71	1	55	+	20
Geranium sessiliflorum	+	22	+	17	+	11			1	57	1	35	+	20
*Lolium perenne			+	3	+	20			1	62	+	25	1	40
Thelymitra sp.			+	20	+	27			+	24	1	50		
Rytidosperma clavatum	+	11	+	23	+	14	+	11	2	57	**2**	**80**	2	73
Heliohebe lavaudiana	2	89	2	80	+	27			2	38	2	60	**2**	**93**
Coprosma propinqua	1	78	+	31	1	41	+	33	***2***	***71***	+	5	1	80
Luzula banksiana var. orina	1	78	+	31	1	73	+	33	1	62	2	45	1	87
Leucopogon fraseri	2	78	2	66	+	16	+	11	+	14	3	40	2	87
Poa cita	1	78	1	43	2	50	2	78	2	48	2	60	**2**	**93**
*Agrostis capillaris	2	67	2	46	2	43			+	29	1	50	1	73
Rytidosperma buchananii	2	56	+	6	+	5			+	24	1	35	2	60
Rytidosperma unarede	1	44	2	37	2	59	2	56	2	71	2	50	2	80
*Trifolium dubium	1	44	+	14	+	30			1	76	2	60	1	87
Elymus sp.	1	44	+	11	+	14	1	67	1	43	1	35	1	93
Rytidosperma corinum	+	33	2	69	2	39			+	19	+	20	2	47
Thelymitra longifolia	+	33	+	26	1	43			1	52	+	15	1	67
Celmisia gracilenta	+	33	2	49	+	20	+	22	1	38	+	15	2	73
*Cirsium vulgare	+	33	+	3	+	14			+	10			1	80
Crassula colligata	+	33	+	14	1	61	1	67	1	81	1	60	1	100
Wahlenbergia gracilis	+	22	+	14	+	25	+	22	+	19	+	30	1	60
Poa colensoi	+	22	+	11	+	18			+	5	+	5	1	73
Corokia cotoneaster	+	22	3	40	+	27	+	22	+	5			***2***	***93***
Dichelachne crinita	+	22	+	20	1	66	2	89	1	67	2	70	1	93
*Linum catharticum	+	11			+	2							1	53
*Digitalis purpurea	+	11	+	9	1	41	+	33	1	48	+	5	1	53

Species name	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7	
Koeleria novozelandica	+	11	+	17	+	7			+	29	+	25	1	60
Microtis unifolia	+	11	+	23	1	36	+	11	+	33	1	35	1	73
Lachnagrostis sp.	+	11	+	11	+	27			+	10			*1*	*80*
*Vicia sativa	+	11	+	20	1	57			1	62	1	40	1	87
Linum monogynum	+	11	+	11	+	18			+	5			*1*	*87*
Carex breviculmis			+	26	+	7			+	24	+	25	1	53
*Arenaria serpyllifolia			+	6	+	2	+	22	1	38	+	10	2	53
Oxalis exilis					+	7			+	14			1	53
Haloragis erecta					+	7	+	11					1	60
Polystichum neozelandicum			+	6	+	9			+	10			1	67
Vittadinia australis			+	3	+	5					+	5	1	67
*Sonchus oleraceus					+	7			+	19	+	10	1	67
*Silene gallica			+	3	+	9			+	29	+	15	1	73
Senecio glaucophyllus subsp. basinudus			+	6	+	18	+	22	+	33	+	15	*1*	*100*

follow we use the term 'rare' broadly to include species that are either nationally rare (de Lange et al. 2004), regionally rare, or endemic to the region (Wilson 1992).

Type 1. *Phormium cookianum – Brachyglottis lagopus – Dracophyllum acerosum*

This community was observed on nine large ($\bar{x}$ = 800 m^2) outcrop faces at higher altitude sites (ranging from 750 to 850 m) on the western side of Banks Peninsula (Fig. 4). All faces have steep slopes ($\bar{x}$ = 67°) and either face east or south. Other species with high frequency include the native herb *Anaphalioides bellidioides,* and native grasses *Deyeuxia avenoides* and *Hierochloe redolens* (Table 1). This community harbours 17 rare species. Three of these, *Deschampsia tenella, Dolichoglottis lyallii,* and *Schoenus pauciflorus,* occur only in this community type. These faces have high species richness ($\bar{x}$ = 58 species per face), which may be a consequence of their larger size. On average, 20% of the species on each face are exotic, with the flat weed *Hieracium pilosella* reaching its highest frequency in this community.

Type 2. *Anthoxanthum odoratum – Phormium cookianum – Chionochloa rigida*

This community type was observed on 35 small ($\bar{x}$ area = 240 m^2) faces on summit bluff systems, or immediately below them, at moderate to high altitudes ($\bar{x}$ altitude = 756 m). They are dispersed across Banks Peninsula (Fig. 4) and may face in any direction. *Chionochloa rigida* is the only species that reaches its highest frequency in this community, but *Brachyglottis lagopus* is also highly frequent (Table 1). This community harbours 18 rare species. Three of these, *Hymenophyllum atrovirens, Myrsine nummularia*, and *Poa kirkii*, only occur in this community type. On average, 21% of the species on each face are exotic.

Type 3. *Podocarpus hallii – Hebe strictissima*

This community type was observed on 44 large ($\bar{x}$ = 960 m^2) faces at moderate altitudes ($\bar{x}$ altitude = 651 m). They occur throughout the study area (Fig. 4) and face all directions except north. The woody species *Coprosma tayloriae, Pseudopanax colensoi,* and *Coprosma rhamnoides* occurred on over 80% of the faces and reached their highest frequency in this community type (Table 1). The fern *Microsorum pustulatum* is also highly frequent. Thirty rare species occur in this community type; this is the highest number of rare species in a single community. Five of these – *Carmichaelia kirkii, Grammitis ciliata, Hymenophyllum rarum, Neomyrtus pedunculata,* and *Oxalis magellanica* – occurred only in this community type. Like community type 1, these faces are relatively species rich ($\bar{x}$ = 57 species per face), which is likely a consequence of their large size. On average, 21% of the species on each face are exotic.

Type 4. *Microsorum pustulatum – Metrosideros diffusa*

This community type was observed on nine small ($\bar{x}$ area = 180 m^2) faces at lower altitudes ranging from 510 to 612 m. All faces occur in the north-western part of Banks Peninsula (Fig. 4) and may face any direction. All faces are predominantly bordered by forest and occur on or near summit bluff systems. The woody species *Coprosma lucida* and *Olearia paniculata* and the fern *Pyrrosia eleagnifolia* occurred on over 75% of the faces and reach their highest frequency in this community type (Table 1). This community harbours six rare species, with *Earina mucronata* and *Carex goyenii* occurring only in this type. On average 17% of the species on each face are exotic.

Type 5. *Anthoxanthum odoratum – Hypochaeris radicata – Holcus lanatus – Coprosma propinqua*

This community type occurred on 21 outcrop faces at moderate altitudes (all but one face occur between 600 and 720 m), primarily to the east of Akaroa Harbour (Fig. 4). Slopes of these faces are highly variable, ranging from nearly horizontal to nearly vertical and have a range of aspects. Vegetation tends to be short in stature; the maximum vegetation height is typically less than 2 m. Faces typically border grassland or short shrubland. As indicated by the community name, the most abundant species on these faces are exotic herbs and grasses. The herbs *Rumex acetosella, Cerastium fontanum*, *Trifolium repens,* and *Crepis capillaris* and the grass *Aira caryophyllea* occur on over 80% of the faces and are more frequent in this community than in any other (Table 1). Overall 37% of the species on each face are exotic. Nine rare species occur in this community, but none are found exclusively there.

Type 6. *Anthoxanthum odoratum – Melicytus alpinus – Rytidosperma clavatum*

This community occurred on 20 outcrop faces across a wide range of altitudes (505–810 m), primarily to the east of Akaroa Harbour (Fig. 4). As with community type 5, slopes and aspects are highly variable. In contrast to type 5, however, faces are very small ($\bar{x}$ area = 100 m^2) and the vegetation is very short, typically being less than 1 m. The exotics *Rumex acetosella, Cerastium fontanum* and *Aira caryophyllea* occur on 80% or more of the faces (Table 1) and exotic species make up 37% of the total on each face, the same level as for community 5. Average species richness, however, is lower than that of community 5 ($\bar{x}$ species richness = 32 vs 51). Seven regionally rare species occur in this community, but none are found exclusively there.

Type 7. *Corokia cotoneaster – Poa cita – Heliohebe lavaudiana*

Fifteen faces supported this community type. They occur on large faces ($\bar{x}$ area = 1870 m^2) at moderate altitudes (610–710 m) and are confined to the western side of the Akaroa Harbour (Fig. 4). Most slopes are steep (greater than 45°, $\bar{x}$ slope = 65°) and aspect is variable. Other species with high frequency (>90%) include the herbs *Senecio glaucophyllus* subsp. *basinudus*, *Crassula colligata*, the grasses *Dichelachne crinita* and *Elymus* sp., the fern *Asplenium flabellifolium*, and the exotic herb *Cerastium fontanum* (Table 1). Fifteen rare species occur in this community, and four of these – *Anogramma leptophylla, Cystopteris tasmanica*, *Daucus glochidiatus and Hymenophyllum cupressiforme* – were observed only in this community. This community has the highest species richness of any type ($\bar{x}$ species per face = 78), which is likely a consequence of the large size of the faces. On average, 31% of the species on a given face are exotic.

The hierarchical regression showed that the percentage of exotic species increases as the percentage of the surrounding matrix occupied by forest decreases, but that other site variables are important as well. The percentage of exotics also increases as slopes become more gentle, the amount of shade on the outcrop decreases, and soil fertility increases (as indicated by soil K). The hierarchical regression model incorporating these four variables explained 76% of the variation in the data (Table 2).

The second hierarchical regression showed that the intactness of the surrounding matrix was a critical predictor of neither the percentage nor number of rare species on an outcrop face. The percentage of rare species was moderately well modelled by altitude; the model explained 57% of the variation and rare species increased with increasing altitude (Table 3). Both the area available to plants and the percentage shading were significant predictors of the numbers of rare species on an outcrop face, jointly explaining 75% of the variation. The number of rare species increased as the area available to plants increased and as the outcrop face became less shaded (Table 3).

Discussion

At the scale of Banks Peninsula, the regional-scale geographic gradient of altitude has the strongest relationship, of the measured parameters, to variation in composition across montane outcrops. Altitude incorporates the direct gradients of precipitation and windiness (which both increase with altitude) and temperature (which decreases with altitude). The importance of altitude corresponds with the primary drivers of compositional variation on the peninsula generally (Wilson 2008), with outcrops elsewhere in New Zealand (Wardle 1977), and the world in mountainous regions (e.g. Ashton & Webb 1977; Cabido et al. 1990; Maycock & Fahselt 1992; Wiser et al. 1996). The moderate to high altitude community types are dispersed across the peninsula, whereas the lower altitude communities studied are more geographically distinct, being confined either to the east (communities 5 and 6) or the west (communities 4 and 7). These geographic distinctions primarily reflect climate differences (rain-bearing winds are from the south and south-east, resulting in an overall decline in average rainfall from the south-east to the north-west that is more pronounced at lower altitudes; climates to the east are distinctly more oceanic than to the west; Wilson 2008) and secondarily may reflect orogeny (Akaroa volcanics are younger than those to the west).

Important secondary gradients reflected properties that vary both among outcrops and among individual outcrop faces. Of these the importance of outcrop size and area available to plants (Cabido et al. 1990; Porembski

Table 2. Hierarchical multiple regression model of the percentage of exotic plant species on Banks Peninsula rock outcrops at two spatial scales. Percentage variables were arc-sin square-root transformed before analysis. Variable selection was by backward elimination. In the final model only variables with $P < 0.01$ were retained.

Spatial scale	Fixed-effect	Estimate	SE	*F*	*P*
Entire outcrop	None				
Outcrop face	Slope	−0.0017	0.0003	34.2	<0.0001
	% forest surrounding	−0.0402	0.0079	26.1	<0.0001
	Ln(K)	0.1100	0.026	17.3	<0.0001
	% shading	−0.0010	0.0003	10.9	0.0013
	$r^2 = 0.76$				

Table 3. Hierarchical multiple regression model of the a) percentage of rare plant species and b) number of rare plant species on Banks Peninsula outcrops at two spatial scales. Percentage variables were arc-sin square-root transformed before analysis. Variable selection was by backward elimination. In the final model only variables with $P < 0.01$ were retained.

Spatial scale	Fixed-effect	Estimate	SE	*F*	*P*
(a) Percentage of rare species					
Entire outcrop	None				
Outcrop face	altitude	0.0003	0.0001	8.17	0.0051
	$r^2 = 0.57$				
(b) Number of rare species					
Entire outcrop	None				
Outcrop face	In (area available to plants)	0.27	0.44	12.4	0.0006
	percentage shading	-0.010	0.004	8.06	0.0054
	$r^2 = 0.75$				

et al. 1996; Wesche et al. 2005), soil pH (Jarvis 1974; Wiser et al. 1996), slope steepness (Wiser et al. 1996), and maximum vegetation height (Parmentier et al. 2005) has been noted in other outcrop studies; whereas the importance of surrounding vegetation is only just beginning to be quantified (Wiser & Buxton 2008).

Exotic species are a significant component of all community types (comprising from 17 to 37% of the species), with the percentage of exotics being the highest in the low-statured community types (types 5 and 6), primarily confined to the eastern side of Akaroa Harbour (Fig. 4). The distribution of community type 6, in particular, corresponds to that part of the peninsula that has the mildest, most oceanic climate (Wilson 2008). These montane outcrops lack the succulent exotics characteristic of lower altitude, coastal volcanic cliffs of the eastern South Island (Healy 1959; Wardle 1991). Our models showing which outcrop faces support more exotics echo well-documented trends that exotics increase with disturbance (e.g. Allan 1936; Crawley 1987), here indicated by the loss of forest surrounding an outcrop, and increased soil fertility (e.g. Amor & Piggin 1977; Hobbs 1989), indicated by increased soil K. Additionally, the sites on outcrops that are the most similar to surrounding disturbed areas (i.e. have gentle slopes and little shade), and are likely to be more accessible to browsing animals, are the most prone to invasion. Earlier work showed that the exotic outcrop flora shares more species with the surrounding matrix than does the native flora (Wiser & Buxton 2008). Further, outcrops are less distinctive from one another in their exotic than in their native species, suggesting that exotic species are homogenising outcrop communities (Wiser & Buxton 2008). In addition to homogenising the vegetation, exotic weeds are known to threaten rare outcrop plants in New Zealand, lowering establishment and most likely reducing growth and survival of plants (e.g. de Lange 1998; Miller & Duncan 2004).

Of particular concern are invasions by three woody weeds – *Pinus radiata* (observed in communities 2, 3 and 7), *Ulex europaeus* (gorse; observed in all communities except community 1) and *Cytisus scoparius* (Scotch broom; observed only in community 2) – which usurp available habitats indefinitely. *Pinus radiata* is readily distributed to outcrops by windblown seed. Gorse and Scotch broom distribute to the outcrops less easily, reaching sites where seed can arrive downhill from a source upslope or is transported by animals (H. Wilson, pers. comm.). Whereas pine can be readily removed from outcrop sites, attempts to remove gorse and broom by spraying are more problematic as this can result in pronounced mortality of nearby native outcrop species.

Of the 52 regionally or nationally rare species observed, one-third (17) are restricted to a given community type; the others are typically spread across at least three community types. They do, however, vary in frequency and richness across community types and make up the highest percentage of the flora in those communities that occur at higher altitudes, echoing the importance of altitude to composition of the outcrop communities generally. The importance of the area of the outcrop face available to plants to the number of rare species reflects well-documented relationships between area and species richness. That richness of rare species increases as outcrop faces become less shaded reflects patterns of outcrop rarity that are well documented elsewhere in the world, where rare outcrop species are typically concentrated in open, sunny microhabitats with shallow soils (Baskin & Baskin 1988).

These results have specific conservation implications. Our results show that outcrop communities are not uniform, but rather are highly heterogeneous both in composition and environment. To adequately represent the compositional variation across outcrops, protected areas need to encompass the important regional gradient of altitude, and gradients of variation both within and between outcrops of slope steepness, soil chemistry, and outcrop area. Our models for numbers and proportions of rare species on outcrop faces emphasise that maintaining intact vegetation on the larger outcrops and those at higher elevations is especially important to retain these strongholds of rarity. The prevalence of exotic plants on outcrop faces suggests that reservation alone is not sufficient to ensure the long-term integrity of the outcrop communities. Our models showed that surrounding vegetation that is open and grazed by stock is likely to facilitate weed invasion, especially on outcrops having gentler slopes and more fertile soils. Gentle slopes and open surrounding vegetation also facilitate access to the outcrops by exotic grazing mammals, which in turn may enhance soil fertility. Planting exotic conifers adjacent to outcrops can increase their rate of spread onto the outcrops themselves.

Because few quantitative surveys have been conducted on cliffs and outcrops in New Zealand, more information is required if we are to understand why community composition, rare species presence, and exotic abundance vary across different outcrops. We know of high levels of endemism and rare taxa on outcrops of both limestone (e.g. Druce & Williams 1989) and ultramafic rock (Lee 1992), but only have a rudimentary understanding of how outcrops of other geologies compare. Exotic invasion varies widely on outcrops worldwide from 3% (Southern Appalachian outcrops > 1200 m; Wiser 1994) to 46% (granitic outcrops of the Seychelles; Biedinger & Fleischmann 2000), but we do not know how and why levels of invasion vary across New Zealand outcrops and which types of exotics pose the biggest threat (e.g. woody weeds vs turf-forming grasses). We have very limited understanding on how crucial intact vegetation in the surrounding matrix is to the integrity of outcrop vegetation or the degree to which outcrops serve as refuges for native species in otherwise denuded landscapes. More fundamentally, we lack basic information on species distributions, and autecology of dominant and rare outcrop species in New Zealand. Such understandings are crucial if we are to understand their importance to regional and national biodiversity and ensure that their integrity is maintained.

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