Post-pastoral succession in intermontane valleys and basins of eastern South Island, New Zealand

SCIENCE FOR CONSERVATION 227

S. Walker, W.G. Lee, G.M. Rogers

Published by
Department of Conservation
PO Box 10-420
Wellington, New Zealand

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
Individual copies are printed, and are also available from the departmental website in pdf form. Titles are listed in the DOC Science Publishing catalogue on the website, refer http://www.doc.govt.nz under Publications, then Science and Research.

ISSN 1173-2946
ISBN 0-478-22472-9

In the interest of forest conservation, DOC Science Publishing supports paperless electronic publishing. When printing, recycled paper is used wherever possible.

This report was prepared for publication by DOC Science Publishing, Science & Research Unit; editing by Lynette Clelland and layout by Ruth Munro. Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

CONTENTS

Post-pastoral succession in intermontane valleys and basins of eastern South Island, New Zealand

S. Walker[1], W.G. Lee[1], G.M. Rogers[2]

[1]Landcare Research, Private Bag 1930, Dunedin, New Zealand
[2]Department of Conservation, PO Box 5244, Dunedin, New Zealand

ABSTRACT

Alluvial ecosystems of eastern South Island, New Zealand, have been modified by the clearance of vegetation by fire since c. 800 yr BP, and used for extensive pastoralism for c. 150 years. Much of the former area of non-forest vegetation on alluvial substrates in the eastern South Island has been developed for agriculture and other uses, although native species still dominate these substrates in western intermontane valleys and basins that are remote from human settlement. Since the arrival of humans, late successional tall tussock and shrubland vegetation has been reduced, the area of short tussock grasslands has expanded, and there has been widespread invasion by exotic species. We describe the vegetation patterns in eastern South Island intermontane valleys and basins in relation to environment and pastoral modification, using data from 1096 vegetation sampling sites in 56 catchments and 4 conservancies in eastern South Island, New Zealand. Present vegetation patterns are poorly related to environmental factors, but are determined by the unique combination of landform characteristics within each catchment, and by the degree of modification that has occurred over pastoral since human settlement. Data collected at 17 fenceline and exclosure sites are used to describe the effects of grazing and grazing removal, and to predict the consequences of post-pastoral management. Decreases in native species richness and structural dominance are continuing in the vegetation of many intermontane valleys and basins as a consequence of current pastoral practices and grazing regimes. Post-pastoral changes will probably be determined by vegetation type, by the stature and density of the native physiognomic dominants at the time that grazing is removed, by environmental factors, and by the competitive abilities of the exotic species present. An appropriate conservation goal for these intermontane valleys and basins would be to increase the biomass and stature of native vegetation; in particular, the abundance of shrubs and tall tussocks on older, more stable landforms; and the density of tall and short tussocks on more frequently naturally disturbed landforms. Continued pastoral use is unlikely to be compatible with this conservation goal.

Keywords: alluvium, grassland, secondary succession, management, vegetation trends, grazing, exclosure

Walker, S.; Lee, W.G.; Rogers, G.M. 2003: Post-pastoral succession in intermontane valleys and basins of eastern South Island, New Zealand. *Science for Conservation 227*. 75 p.

1. Introduction

The alluvial land systems of intermontane valleys and basins in eastern South Island, New Zealand, are a product of Miocene to Pleistocene tectonic uplift, ice ages, and glacial retreat (Lee 1998). They are subject to a variety of periodic disturbances by frost, seasonal waterlogging, flooding, depositional processes and drought. They were probably among the relatively few ecosystems that included extensive areas of non-forest vegetation below treeline immediately before human settlement.

In their prehuman state, alluvial valley floors in New Zealand would have supported a diversity of plant communities associated with landforms of different ages and types, which were at various stages of recovery from disturbance. Little is known of past compositions and vegetation patterns in alluvial vegetation. It is likely, however, that many woody species (*Discaria,*[1] *Carmichaelia, Coprosma, Hebe, Melicytus, Olearia*, *Halocarpus* and *Phyllocladus* spp.) would have occupied stable, older alluvial surfaces under moist mid-Holocene climates (c. 7000–5000 yr BP; Wardle 1991). In the eastern catchments that are further from the Southern Alps, shorter, shrub–grassland vegetation types may have developed as the climate became drier in the late Holocene (McGlone & Moar 1998), although precipitation may have increased in the higher-elevation, western reaches of the intermontane valleys within the same period. There were probably more abrupt vegetation changes at the time of large-scale deforestation of eastern South Island catchments following the arrival of Polynesian people around 750 yr BP. At this time, the direct effects of fire were to remove seral valley-floor woodlands and shrublands, and to remove forest from the adjacent hillslopes (McGlone & Basher 1995). This is likely to have had indirect effects on vegetation by altering the catchment hydrological characteristics, i.e. changing flood frequencies, increasing runoff, exacerbating natural erosion, and increasing siltation. The simultaneous arrival of mammalian herbivores and exotic plant species with European pastoralists after c. 1850 led to even more profound vegetation changes. Early accounts suggest that accessible terrain, which had been partly or largely cleared of woody vegetation by Polynesian settlers, and the moderate to high fertility of alluvial soils, encouraged an early concentration of pastoral development and use in eastern South Island intermontane valleys and basins, which continues to the present day (O'Connor 1982).

The present-day vegetation of intermontane valleys and basins of eastern South Island comprises grassland with a variable, but usually minor, woody component, and a significant number of naturalised plant species (Wardle 1985; Walker & Lee 2000). Worldwide, riparian areas are among the most invaded of habitats (Rejmánek 1999; Planty-Tabbacchi et al. 1996). This is because recent alluvial landforms are intermittently reshaped by natural disturbances, creating gaps for the establishment of pioneer species and communities. Soils of

---

[1] Nomenclature follows Allan (1961), Moore & Edgar (1970), Connor & Edgar (1987), and Edgar & Connor (2000) for native species, and Webb et al. (1988) and Stace (1991) for exotic species.

floodplains and fans are younger, less leached, less acidic and more nutrient-enriched than those on adjacent, older alluvial terrace landforms and non-alluvial hillslopes, which encourages rapid growth rates and high fecundity in introduced species (Means et al. 1996; Peres 1997). In New Zealand intermontane valleys and basins, these younger landforms may be particularly vulnerable to invasion by introduced species that are adapted to exploiting regularly disturbed and nutrient-enriched soils because the native flora contains few species that are both frost-tolerant and able to rapidly and aggressively invade primary successional sites (Dansereau 1964). However, on older, more leached and more elevated alluvial landforms, periodic frosts may be the principal natural disturbance. Here, the vigour of exotic plants may be lower, and native tall tussocks and woody plants may be capable of holding their own against most invading species.

Intermontane valleys and basins are distinctive ecosystems in terms of physiography, climate and vegetation. They are among the few natural non-forest ecosystems that exist below treeline in New Zealand and contain several threatened woody species (e.g. *Hebe armstrongii, H. cupressioides*, *Helichrysum dimorphum* and *Olearia hectorii*). Efforts are now being directed towards gaining a more complete representation of the biodiversity of distinctive lowland rainshadow ecosystems such as these within public conservation lands. However, intermontane valleys and basins present problems for conservation management because of their high economic value, and the advanced state of vegetation modification within them. They are preferred sites for pastoral use because of their gentle terrain and the naturally moderate or elevated soil fertility of their more recent landforms. Grazing commenced in most intermontane valleys at an early stage of pastoral exploitation, and so the native vegetation of most intermontane valleys and basins has been substantially modified. They are also perceived to be particularly vulnerable to invasion by weeds, and there is concern that their remaining natural values will be extinguished by the proliferation of exotic grasses if grazing animals are removed (McKendry & O'Connor 1990; Widyatmoko & Norton 1997). Therefore, conservation management of intermontane valleys and basins has been a low priority over the last century, and stock grazing continues in most of these, including those bordered by forested public conservation lands.

A more thorough understanding of the present vegetation and likely successional changes is required as a basis for gaining a more complete representation of eastern South Island intermontane valleys and basins in conservation lands. Most previous studies of seral non-forest vegetation in eastern South Island has focused on tussock grasslands in non-alluvial hill country (e.g. McKendry & O'Connor 1990; Treskonova 1991; Mark 1992; Rose et al. 1995; Duncan et al. 2001; Meurk et al. 2002). Vegetation types and patterns in intermontane valleys and basins in New Zealand have not been formally described until recently (Walker & Lee 2000, 2002). There has been little information available on the extent of introduced species invasions, so that the vegetation changes that might result from retirement from pastoral use cannot be predicted with any certainty. This study describes patterns of present-day vegetation in 56 alluvial catchments east of the Southern Alps within four South Island conservancies. We investigated outcomes of grazing-retirement within existing exclosure plots in intermontane valleys and basins, and described vegetation changes under pastoral management by measuring and interpreting vegetation contrasts across fencelines.

2. Objectives

To determine the rates and directions of change in the vegetation of intermontane valleys and basins in the Eastern South Island after the removal of grazing, and to relate these to environmental factors and vegetation patterns.

3. Study area

Grasslands were studied in 56 alluvial systems (hereafter 'catchments') comprising intermontane valleys and basins in 40 ecological districts (EDs) (Fig. 1). We use four conservancy boundaries to group the sampled catchments. These are:

1. Nelson/Marlborough (6 catchments). We sampled the Coldwater, Rainbow, Severn, Alma, Wairau and Acheron valleys, and two sites at the head of the Awatere Valley, which we include in the Acheron catchment in this report (Bounds, Travers, Sedgemere, Balaclava, Dillon and Miromiro EDs).
2. Canterbury (32 catchments). This conservancy contains the Clarence Valley (30 of the 66 Clarence sampling sites are within Nelson/Marlborough Conservancy, but are included in Canterbury), as well as the Waiau, Ada, Henry, and Edwards valleys, and moraine surfaces upstream of Lake Guyon (Ella and Lewis EDs), the Doubtful, Hope, North Hurunui, South Hurunui, and Kiwi Stream catchments (Lewis and Hope EDs), the Poulter, Esk, Nigger, Cox, Waimakariri, and Hawdon valleys (Minchin, Poulter, Cass, Arthur's Pass, Craigieburn, Coleridge, and Torlesse EDs), the Harper and Avoca valleys (Craigieburn and Coleridge EDs), the upper Rakaia Valley (Mt Hutt ED), the Acheron Valley downstream of Lake Lyndon (Torlesse ED), the Clyde, Lawrence, and Lake Stream valleys (Armoury, Hakatere and Arrowsmith EDs), the Macaulay, Godley, Cass, Hooker and Tasman, Dobson, and Hopkins valleys (Godley, Mt Cook and Dobson ED), the Ahuriri Valley (Huxley and Ahuriri EDs), and the Twizel River and Mackenzie Outwash Plain near Twizel Airport (Pukaki ED).
3. Otago (12 catchments). In Otago, we sampled the Hunter and Siberia valleys, and the east and west branches of the Matukituki River (Huxley, Okuru and Arawata EDs), Dunstan Creek, the Upper Manuherikia Valley (St Bathans, Lindis and Dunstan EDs), the Rees, Dart, Caples, and Greenstone valleys (Dart and Livingstone EDs), the Nevis Valley (Remarkables and Old Man EDs), and the Von Valley (Eyre ED).

4. Southland (6 catchments). We sampled the Eglinton, Mararoa, Kiwi Burn, Oreti (Dart, Livingstone, Darran, Eyre and Upukeroa EDs) and Waterloo valleys and the Weydon Burn (Taringatura and Takitimu EDs).

Vegetation patterns in 12 of these catchments in southern New Zealand (Walker & Lee 2000), and 35 catchments in Marlborough and Canterbury (Walker & Lee 2002) have been described in detail. We combined the Mackenzie alluvial system of Walker & Lee (2000) and the Twizel Outwash Plain alluvial system of Walker & Lee (2002) into a single 'catchment' (i.e. Mackenzie Outwash) in this report. The remaining ten catchments have not been previously described using data from this survey. Catchments retaining negligible native grassland vegetation were excluded from the survey (e.g. the Wilkin and Makarora valleys in Otago).

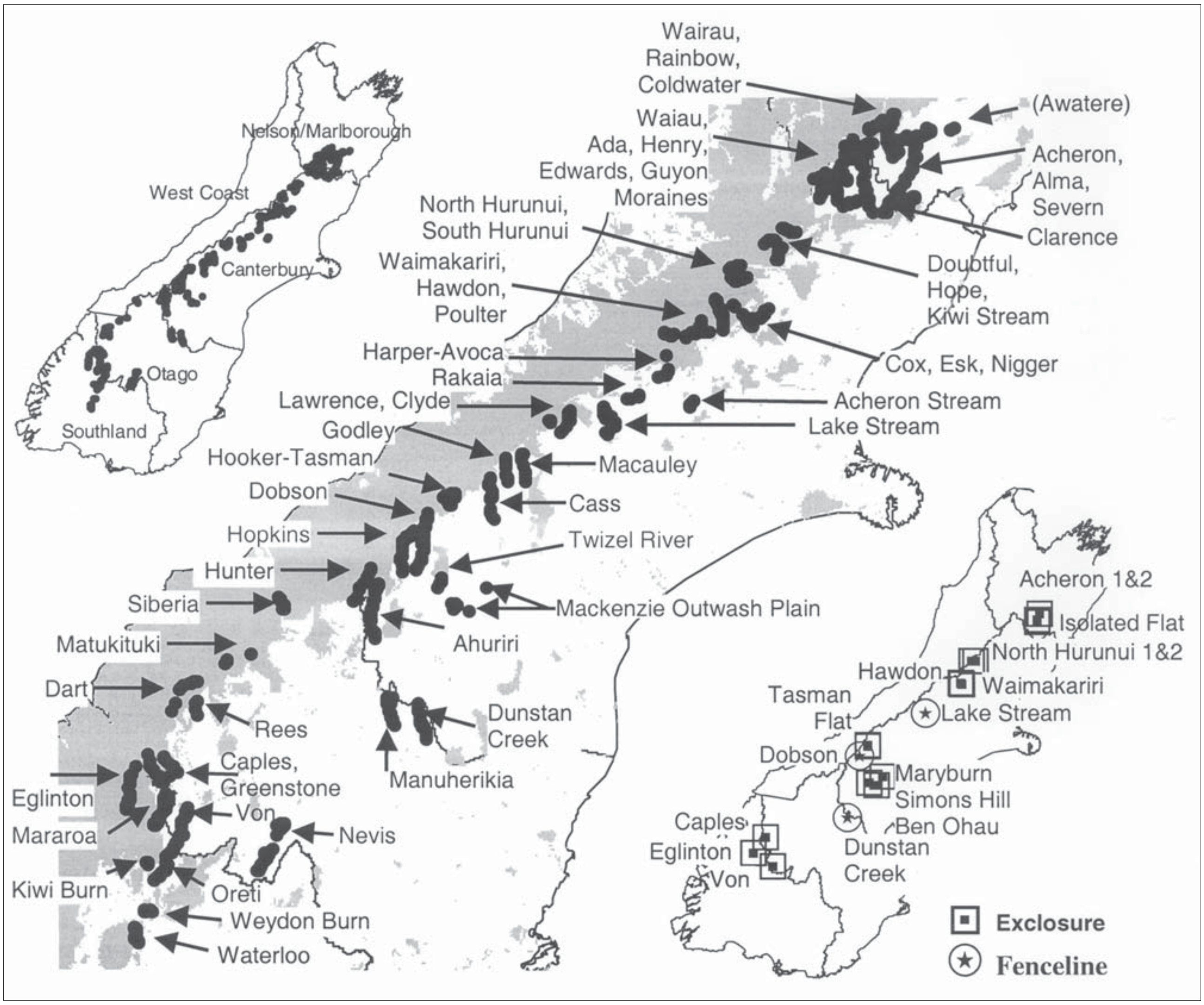


Figure 1. Map of the South Island, New Zealand, showing the locations of the studied catchments in the four conservancies (outlines in upper inset), and their relationship to public conservation lands (shaded). Positions of exclosures or retirement fences (squares) and fenceline effects (circled stars) are shown in the lower inset.

4. Methods

4.1 DATA COLLECTION

4.1.1 Species composition

Within each catchment, sampling quadrats were placed in herbaceous vegetation along the alluvial floor, using restricted randomisation (Greig-Smith 1983) to cover the range of altitudes, landforms and communities present (i.e. floodplains, fans, and terraces, and variations within these, such as old river channels, seepages, hollows, and backswamps). Forest vegetation, and non-grass communities on peat substrates, were not sampled. We positioned the lower elevation limit of sampling within each catchment where vegetation had been converted to pasture comprising negligible native content (e.g. by oversowing, topdressing and/or ploughing). In total, we selected 1062 quadrat sampling sites, representing different altitudes, landforms and plant communities within the sampled catchments. Within each site, a circular sampling quadrat (diameter 1 m) was placed at random. All vascular plant species within a quadrat were recorded in rank order of abundance (visually estimated), and exotic and native species richness, total species richness and percentage native species (vegetation characteristics) were calculated. A native species dominance score (maximum value 6) was calculated for each sampling site from abundance ranks, by adding allocated scores of 3, 2 and 1, if native species were ranked 1st, 2nd and 3rd, respectively.

4.1.2 Environment

At each site, the landform was categorised as floodplain, recent low terrace, upper older terrace, or fan (upper, middle and lower thirds). Alluvium parent material was determined from geological maps. Soil samples were collected at 819 (75%) of the quadrats and analysed for pH (with dilution in deionised water; pH decreases with leaching, and is related to soil age and rainfall), organic content (% dry weight by ignition for 2 h at 500°C; this is also related to soil age and disturbance history) and available phosphate content (Olsen P; a measure of fertility). Map coordinates (to nearest 100 m) and elevation (to nearest 10 m a.s.l.) were used to obtain estimates of climate factors for each sampling site point. These climate factors were estimated on a 100-m grid, using thin-plate-spline spatial interpolation of data from irregularly distributed New Zealand meteorological stations (Leathwick & Stephens 1998). The data included monthly estimates of rainfall; (rainfall:potential evapotranspiration (i.e. PET) ratio; minimum, maximum and mean temperature; and solar radiation and humidity (Leathwick et al. 1998).

4.1.3 Temporal change

To examine effects of cessation of grazing and of different management histories on vegetation, plant community data were collected inside and outside exclosures, and on either side of fencelines showing management-induced vegetation contrasts, using a modified height-frequency method (Scott 1965;

Dickinson et al. 1992; Fig. 1). Thirteen exclosures or grazing-retirement fencelines were located and sampled in four provinces.

1. Marlborough: three exclosures (6 height-frequency samples) in the Acheron Valley (Isolated Flat, Acheron 1 and Acheron 2).
2. Canterbury: two exclosures (4 samples) in the North Hurunui Valley, two grazing-retirement fencelines (in the Hawdon Valley and at the Mt Cook airfield in the Tasman Valley (4 samples), and three exclosures (6 samples) on outwash plains in the Mackenzie Basin (Simons Hill, Ben Ohau and Maryburn: Meurk et al. 2002).
3. Otago: one exclosure each in the Caples and Von valleys (4 samples).
4. Southland: one exclosure in the Eglinton Valley (2 samples).

To examine effects of different management histories on intermontane valleys and basins we sampled on both sides of four fencelines in Canterbury and Otago (Fig. 1).

1. Canterbury: three fenceline contrasts in the Waimakariri Valley, the Lake Stream catchment, and the Dobson Valley (6 height-frequency samples).
2. Otago: one fenceline contrast in Dunstan Creek (2 samples).

In addition, height-frequency data collected in 1981 in grazed vegetation adjacent to the exclosure in the Eglinton Valley in Southland Conservancy (Lee 1981) were compared with those collected in 1997, to show vegetation change under continuous grazing by stock over 26 years (cf. Walker & Lee 2000).

The full dataset for the classification and ordination data analyses below comprises the presence and absence of species within the 1062 quadrats and 34 height-frequency samples (1096 presence/absence samples in total).

4.2 DATA ANALYSIS

4.2.1 Statistical methods

The programs Teddybear (Wilson 1975) and S-PLUS (MathSoft Inc. 1999) were used for univariate statistical analyses. Multivariate analyses (ordinations and classifications) were performed using the program Golliwog (Wilson 1975). The geographic information system ArcView GIS (Environmental Systems Research Institute 2000) was used to measure the occurrence of sampling sites within public conservation lands.

4.2.2 Environmental classification and ordination of catchments

In order to summarise the environmental variation of the 56 different catchments, we used cluster analysis (city-block distance measure) to classify catchments in terms of environment alone. This classification derived eight groups of catchments with similar environmental characteristics in terms of landform, climate, soils and geological parent material (hereafter environmental types I to VIII). To standardise factors for this analysis, we represented landform and geological parent materials with the categories –2 and +2, while values for each climate and soil factor were assigned to one of five levels (–2 to +2, where 0 = average and scores of –2 and +2 were assigned to values below or above one standard deviation from the average, respectively). We tabulated the average quadrat environmental and vegetation characteristics (i.e. exotic and native species richness, total species richness, percentage native species and native dominance score) for each environmental type, and compared these between types using Tukey's test. As a means of displaying the environmental variation, we used the first two components of a Principal Components Analysis ordination (PCA; Goodall 1954), which shows the positions of each catchment and environmental type in relation to the main sources of environmental variation.

4.2.3 Vegetation gradients (ordination)

Detrended Correspondence Analysis ordination (DCA; Hill & Gauch 1980) was used to summarise the compositional variation of the 1096 samples, extracting the first four vegetation axes (i.e. gradients). Each axis with Eigenvalue > 0.2 standard deviations (SD) was regarded as a significant vegetation gradient, and was interpreted by calculating simple and step-down predictive multiple regression equations of environmental and vegetation factors (independent variables) on axis ordination score (dependent variable), using the sampling sites as replicates (Snedecor & Cochran 1980). We used the following small set of independent environmental variables in the step-down predictive multiple regressions, because correlated variables are likely to obscure interpretation.

1. Quantitative variates: average minimum temperature of the coldest month, average maximum temperature of the warmest month, lowest monthly rainfall:potential evapotranspiration ratio, soil pH and organic content percentage.
2. Qualitative variates (i.e. comprising 0 or 1 scores for each variate): greywacke base rock (negatively related to schist) and terrace and fan landform categories (negatively related to the floodplain category).

Among the vegetation variables, native species richness, total species richness, percentage native species and native dominance score were positively related (i.e. non-independent, and therefore only one of these could be used in the step-down predictive multiple regressions). Of these, percentage native species, which has been used as a surrogate for pastoral modification (cf. Walker & Lee 2000, 2002), was best correlated with ordination axes in simple regressions. It was therefore used as the single composite vegetation variable in the analyses.

4.2.4 Vegetation types and catchment groups (classification)

Classification was used to group the 1096 quadrat and height-frequency samples into vegetation types (the sample classification), and also to group the 56 catchments in terms of their average species composition (the catchment classification). To distinguish community types and groups of ecologically similar species, we classified all quadrats individually (hereafter referred to as the sample classification). We used cluster analysis (Clifford & Stephenson 1975; flexible sorting system, city-block distance measure, $\beta = 0.25$), which was terminated at the arbitrary eight-group level for sampling sites (plant communities A to H) and species (groups of ecologically similar species i to viii).

For the catchment classification, we used identical classification methods but averaged vegetation composition over the sampling sites within that catchment: two sampling sites from the Awatere Valley were included in the nearby Acheron catchment for this analysis, and both quadrats and exclosure plot samples from the Mackenzie Basin were grouped within the Mackenzie Outwash Plains 'catchment'. Again, classification was terminated at the eight-group level, distinguishing eight catchment groups (I to VIII).

We calculated the percentage of sampling sites within each catchment and each catchment group that were classified within each of the eight plant communities. The average quadrat vegetation characteristics (exotic and native species richness, total species richness, percentage native species and native dominance score) were compared between plant communities, catchment groups and conservancies using Tukey's test. Data from the 34 height-frequency samples were omitted from these tests. Climate factors for each site (average minimum temperature of the coldest month, average maximum temperature of the warmest month, and lowest monthly rainfall:potential evapotranspiration ratio) and soil factors (% organic content, pH and Olsen P) for 819 sampling sites were also compared between plant communities, catchment groups and conservancies using Tukey's test.

4.2.5 Protection in public conservation lands

The percentage of sampling sites within public conservation lands was calculated for each environmental type, vegetation type and catchment group from the three classifications. These data were used to comment on priorities for the protection of intermontane valley and basin environments and vegetation and catchment types within public conservation lands.

4.2.6 Temporal changes

The retirement fenceline in the Hawdon Valley (established in 1998 but temporarily breached after floods in 1999) and the two exclosures in the North Hurunui Valley (established in 1999) were established too recently for height-frequency samples to show meaningful differences in vegetation. We therefore excluded these samples from analyses of temporal change.

Because the dates of establishment and the initial compositions of most exclosures are unknown, we calculated the differences between vegetation inside and outside exclosures, and on either side of fencelines. Differences (D_x) in exotic and native biomass and richness, and in native richness and biomass percentages, were calculated as $D_x = x_e - x_g$, where x_e and x_g are vegetation characteristics inside and outside the exclosure, or the less- and more-modified sides of fencelines, respectively. Rank correlation coefficients were calculated between difference indices (D_x) and climate and vegetation characteristics of the continually grazed vegetation (temperature and rainfall from interpolated surfaces, native and exotic richness, biomass, and native grass abundance), using the exclosure sampling sites as replicates.

5. Results

5.1 CHARACTERISTICS OF INTERMONTANE VALLEYS AND BASINS

5.1.1 Flora

A total of 336 vascular plant species (255 native and 81 exotic species) were recorded in the 1096 vegetation samples. Non-composite dicotyledon herbs were the largest group of native species (34%), followed by sedges, rushes and allied plants (17%; Table 1). Woody plants (gymnosperm and dicotyledon trees, shrubs and subshrubs) accounted for 17%, composite dicotyledon herbs for 16%, and grasses made up 11% of the native flora. Of the exotic species, the largest group (44%) was also non-composite dicotyledon herbs, whereas grasses accounted for 25% and composite dicotyledon herbs for 21% (Table 1). Sedges, rushes and allied plants accounted for only 6% of the exotic flora and woody plants for 4%. A list of vascular plant species recorded within sampling sites in the four DOC conservancies is appended (Appendix 1).

All 56 catchments and all but eight quadrats contained exotic species, and 17 quadrats contained no native species (Table 2). Most (769 quadrats, i.e. 70%) of all quadrats contained $\geq$ 50% native species. Average native species richness

TABLE 1. NUMBERS OF SPECIES IN NATIVE AND EXOTIC PLANT LIFE-FORM GROUPS RECORDED WITHIN SAMPLING SITES IN THE FOUR CONSERVANCIES.

CONSERVANCY (NO. QUADRATS + HEIGHT-FREQUENCY SAMPLES)	NELSON/ MARLBOROUGH (*112+6*)	CANTERBURY (*584+20*)	OTAGO (*224+6*)	SOUTHLAND (*142+2*)	TOTAL (%) (*1062+34*)
NATIVE SPECIES					
Ferns and fern allies	**1**	**4**	**4**	**3**	**5**
Gymnosperms		**2**		**1**	**2**
All monocotyledons	**27**	**66**	**49**	**45**	**78**
Orchids	1	5	3	5	6 (2)
Grasses	13	26	21	17	28 (11)
Other: sedges, rushes and allied plants	13	35	25	23	44 (17)
All dicotyledons	**44**	**131**	**95**	**90**	**170**
Dicotyledon herbs-composites	11	35	20	20	42 (16)
Dicotyledon herbs-other	21	59	59	56	87 (34)
Dicotyledon trees and shrubs	3	18	7	6	21 (8)
Dicotyledon subshrubs	9	19	9	8	20 (8)
EXOTIC SPECIES					
All monocotyledons	**8**	**20**	**15**	**14**	**25**
Grasses	7	15	12	12	20 (25)
Other: sedges, rushes and allied plants	1	5	3	2	5 (6)
All dicotyledons	**23**	**46**	**32**	**30**	**56**
Dicotyledon herbs-composites	8	15	13	9	17 (21)
Dicotyledon herbs-other	14	28	18	20	36 (44)
Trees and shrubs	1	3	1	1	3 (4)

ranged from c. 15 species per quadrat in the North Hurunui Valley to 1 species per quadrat in the East Matukituki Valley, and average exotic richness ranged from 3 species per quadrat in the Clyde Valley in Canterbury to 7 species per quadrat in the Poulter Valley (Table 2). Exotic and native species richness were not related at the level of quadrats, or across the 56 catchments, i.e. there was no tendency for sampling sites or catchments with higher native species richness to contain either higher or lower numbers of exotic plant species.

At the level of the four conservancies, native and exotic species richness were correlated: i.e. quadrats in Nelson/Marlborough Conservancy comprised fewer native species and fewer exotic species on average than the other three regions, while both average native and exotic species richness per quadrat were highest in Southland Conservancy (Table 3). Intermontane valleys and basins in the Nelson/Marlborough Conservancy had a lower percentage of native species and lower native dominance than the other three conservancies (Table 3).

5.1.2 Environment

Eight environmental types of catchment (I to VIII) were defined by the environmental classification of the 56 catchments (Tables 2 and 4; Fig. 2A–C). This classification separated catchments primarily on the basis of alluvial parent material: catchments derived from greywacke, which are predominantly located in Canterbury and Marlborough and which tend to experience high summer temperature maxima and low summer rainfall:potential evapotranspiration ratios (environmental types I to V), are distinguished from Otago and Southland catchments with schist (i.e. environmental types VI and VII) or igneous intrusive substrates (environmental type VIII). The eight environmental types differed significantly in native dominance score, but showed no significant differences in other vegetation characteristics.

Environmental types I to V are separated according to substrate, severity of winter temperature minima and summer maxima.

Type I (comprising the Acheron and Rainbow valleys in Marlborough, the Edwards and Twizel valleys in Canterbury and the Upper Manuherikia Valley in Otago; Fig. 2B–C) is distinguished by subcontinental climates characterised by particularly low rainfall, high summer temperature maxima and low winter temperature minima. Only 2% of sampling sites in this environmental type were within public conservation lands. Broad, relatively stable terrace landforms, some of which may be of glacial origin, predominate in these catchments.

Type II includes 12 Canterbury valleys, the Coldwater Valley in Marlborough and the Oreti Valley in Southland, which contain a variety of landforms dominated by terraces and fans, and have intermediate climatic and soil characteristics (Table 4; Fig. 2B–C).

Type III comprises six native and exotic species-rich greywacke catchments (the Clyde and Hopkins valleys in Canterbury, the schist Von, Greenstone and Caples valleys in Otago and the Waterloo in Southland) that share cool summers and comparatively mild winter temperatures, and organic-rich soils with relatively high pH but low Olsen P (Table 4; Fig. 2B–C). These catchments have extensive floodplains but relatively few fans. More than a third of sampling sites in both environmental types II and III were within public conservation lands.

TABLE 2. AVERAGE CLIMATE, VEGETATION, AND SOIL CHARACTERISTICS ACROSS ALL SAMPLING QUADRATS (*n*) IN THE 56 STUDIED ALLUVIAL SYSTEMS. Shown: environmental group to which the catchment is assigned, the percentage of sampling sites in the public conservation lands (% PCL), the range of sampling elevation (m. a.s.l.), maximum temperature of the warmest month, minimum daily temperature of the coldest month, total annual rainfall; number (richness) of exotic and native species, % native species and native dominance score (max = 6); and soil % organic content, Olsen P, pH and parent material (Gw = greywacke, Sch = schist, Ms = mudstone, In = igneous intrusives).

				CLIMATE			VEGETATION				SUBSTRATE			
CATCHMENT (ENVIRON. GP.)	*n*	PCL (%)	ELEVATION RANGE (m)	MAX. TEMP. (°C)	MIN. TEMP. (°C)	RAINFALL (mm)	EXOTIC RICH.	NATIVE RICH.	% NATIVE RICH.	NATIVE DOM. SCORE	% ORGANIC CONTENT	OLSEN P	pH	PARENT MATERIAL
Nelson/Marlborough														
Coldwater (II)	13	0	930–1120	19.4	–3.7	1648	6.2	4.7	40	2.08	10.1	7.8	5.4	Gw
Rainbow (I)	14	14	830–940	20.2	–3.3	1764	6.2	6.3	49	1.36	10.7	7.6	5.4	Gw
Severn (IV)	22	0	870–1060	20.1	–3.6	1163	5.2	3.4	35	2.32	11.3	16.2	5.1	Gw
Wairau (IV)	20	0	950–1210	18.8	–3.8	1753	4.9	6.7	55	4.05	13.4	7.8	5.0	Gw
Alma (IV)	13	0	980–1030	19.7	–3.6	1290	4.5	4.2	46	3.46	13.7	12.1	4.9	Gw
Acheron (I)	36	0	710–990	20.8	–3.2	1025	4.5	3.3	41	1.14	10.2	25.5	5.2	Gw
Canterbury														
Clarence (IV)	66	0	660–1250	19.7	–3.2	1591	4.7	5.5	49	2.95	16.9	11.2	5.1	Gw
Waiau (IV)	24	0	690–910	20.5	–2.9	1861	6.5	8.4	55	1.46	13.2	9.8	5.3	Gw
Ada (IV)	11	9	770–1000	19.8	–3.0	2314	6.1	5.6	49	2.27	19.7	13.0	4.9	Gw
Guyon (V)	4	0	830–900	20.2	–3.0	1681	5.0	10.0	66	2.25	23.2	10.2	4.7	Gw
Henry (IV)	16	0	750–1040	19.8	–3.0	1951	5.3	7.6	59	3.06	23.6	17.2	5.1	Gw
Edwards (I)	12	0	680–790	20.9	–2.6	1236	4.8	6.8	57	3.08	14.8	11.0	5.1	Gw
Doubtful (II)	8	38	530–660	21.1	–1.9	2044	6.8	8.3	51	1.00	21.8	12.2	4.9	Gw
Hope (IV)	11	27	670–750	20.4	–2.0	2259	5.0	10.2	66	1.18	22.0	11.5	4.6	Gw
Kiwi Stream (II)	12	17	590–670	20.8	–1.9	1651	5.6	7.6	57	0.83	17.5	7.3	5.0	Gw
North Hurunui (II)	13	100	650–710	20.2	–1.6	3089	5.2	15.0	75	3.38	13.4	10.7	5.3	Gw
South Hurunui (IV)	17	100	750–930	19.5	–2.1	2543	4.4	13.6	76	4.65	10.2	7.5	5.4	Gw
Cox (IV)	3	100	670–680	20.4	–1.5	1584	5.0	11.7	70	3.33	10.4	5.6	5.3	Gw
Poulter (II)	30	73	480–640	20.8	–1.1	1752	7.0	9.6	54	2.30	13.7	10.2	4.9	Gw
Esk (II)	22	0	750–950	19.8	–1.9	1247	4.3	9.1	65	3.36	13.6	11.4	5.3	Gw
Nigger (II)	16	0	680–790	20.3	–1.7	1184	5.1	7.9	59	3.31	12.0	14.9	5.3	Gw
Hawdon (II)	11	100	560–640	20.6	–1.1	2016	6.1	10.2	60	1.45	14.2	8.5	5.0	Gw
Waimakariri (II)	57	77	500–700	20.6	–1.1	2001	4.3	6.3	56	1.89	15.1	8.7	4.8	Gw
Harper-Avoca (II)	7	14	540–640	20.7	–1.3	1305	3.9	6.4	63	1.71	10.8	6.0	4.9	Gw
Rakaia (II)	4	0	440–490	21.0	–1.2	1214	5.0	3.8	43	1.25	6.9	4.7	5.3	Gw
Acheron Stream (II)	7	100	760–860	20.3	–1.6	1326	4.6	9.7	65	4.00	14.9	11.0	4.8	Gw
Lake Stream (II)	42	0	630–780	20.0	–1.8	1155	6.0	9.5	59	3.48	11.6	8.1	5.1	Gw
Lawrence (IV)	15	40	690–910	19.4	–2.2	2065	3.9	10.3	72	4.73	9.7	9.3	5.5	Gw
Clyde (III)	4	25	830–870	19.2	–2.3	4298	3.0	9.5	75	5.25	8.6	11.2	5.5	Gw
Macaulay (IV)	15	0	835–1120	18.7	–2.6	2826	4.5	12.1	71	4.40	8.4	10.9	5.4	Gw
Godley (IV)	15	40	780–907	19.8	–2.7	2708	6.4	10.0	61	3.40	8.6	11.2	5.4	Gw
Cass (IV)	22	0	800–1140	19.3	–2.7	1925	4.5	8.6	64	4.55	10.7	9.6	5.3	Gw
Hooker-Tasman (V)	24	92	640–740	20.6	–4.1	3396	5.1	6.0	53	1.38	7.0	7.4	4.9	Gw
Dobson (IV)	40	38	560–900	20.7	–2.9	2506	6.5	10.7	59	3.48	7.5	9.1	5.0	Gw
Hopkins (III)	22	68	560–840	20.5	–2.7	2419	5.5	10.7	64	1.82	10.1	15.6	4.9	Gw
Ahuriri (VI)	36	14	740–960	20.3	–2.7	1717	5.4	11.2	63	3.17	9.0	12.7	4.9	Sch/Gw
Twizel (I)	7	0	680–780	21.4	–2.7	806	3.3	8.3	71	2.57	10.5	9.8	5.1	Gw
Mackenzie Outwash (V)	11	0	440–555	22.6	–3.5	637	5.4	7.0	49	1.91	4.7	8.2	5.5	Gw
Otago														
Hunter (VII)	12	50	390–550	21.1	–1.6	2991	4.8	7.5	62	3.75	11.1	15.4	5.3	Sch
Siberia (VII)	15	100	600–650	19.3	–0.7	4363	4.3	6.7	61	3.33	11.3	20.1	5.5	Sch
East Matukituki (VII)	3	100	390–390	20.4	0.1	2454	5.0	1.0	17	0.67	8.2	10.2	5.5	Sch
West Matukituki (VII)	6	100	510–560	19.5	–0.4	2739	4.3	8.2	66	4.17	8.4	17.5	5.3	Sch
Dunstan Creek (VI)	32	0	740–1000	20.1	–3.7	1008	6.5	9.9	58	2.97	9.2	16.7	5.5	Sch
Upper Manuherikia (I)	26	0	600–1000	21.0	–3.7	779	6.2	9.5	59	2.46	11.7	21.9	5.5	Gw
Dart (VII)	13	100	400–650	18.9	–0.4	3437	3.5	7.8	63	4.77	11.9	19.2	4.8	Sch
Rees (VII)	5	0	470–530	19.5	–0.5	2040	6.0	9.0	58	3.00	7.8	11.2	5.3	Sch
Caples (III)	10	100	350–450	19.9	–0.3	1410	5.7	13.6	69	3.60	21.8	1.9	5.4	Gw
Greenstone (III)	15	67	350–630	19.2	–0.7	1823	5.9	12.0	65	2.07	15.5	8.2	5.4	Gw
Von (III)	16	0	370–690	20.2	–1.0	1018	6.4	3.4	24	1.31	8.1	8.6	5.5	Gw/Sch
Nevis (VI)	77	0	680–910	19.3	–3.3	881	4.7	7.2	56	2.25	8.7	16.7	5.1	Sch/Ms
Southland														
Mararoa (IV)	54	20	610–730	18.8	–1.6	1190	5.2	10.1	65	3.33	13.8	12.3	4.8	Gw
Eglinton (VIII)	24	100	330–480	19.6	–0.1	2107	5.1	5.2	48	0.63	17.1	7.3	5.4	In
Oreti (II)	26	31	490–710	19.5	–1.3	1227	5.2	8.5	57	2.54	14.2	13.4	5.1	Gw
Kiwi Burn (VIII)	3	100	530–560	19.6	–1.0	1252	3.3	14.0	81	3.33	26.5	13.1	5.5	Gw/In
Weydon Burn (VII)	6	67	400–440	20.1	–0.7	1096	5.5	6.5	43	3.00	20.6	12.5	5.2	Gw
Waterloo (III)	31	0	450–580	19.3	–0.7	1150	5.9	12.9	70	3.97	22.6	4.3	5.4	Gw

TABLE 3. PERCENTAGE OF SAMPLING SITES REPRESENTED IN PUBLIC CONSERVATION LANDS, AND AVERAGE VEGETATION CHARACTERISTICS OF QUADRATS IN THE FOUR CONSERVANCIES.

Numbers in parentheses indicate the number of catchments and sampling sites, respectively. Superscript letters in common indicate that data are not significantly different between regions or groups (i.e. $P > 0.05$ by Tukey's test).

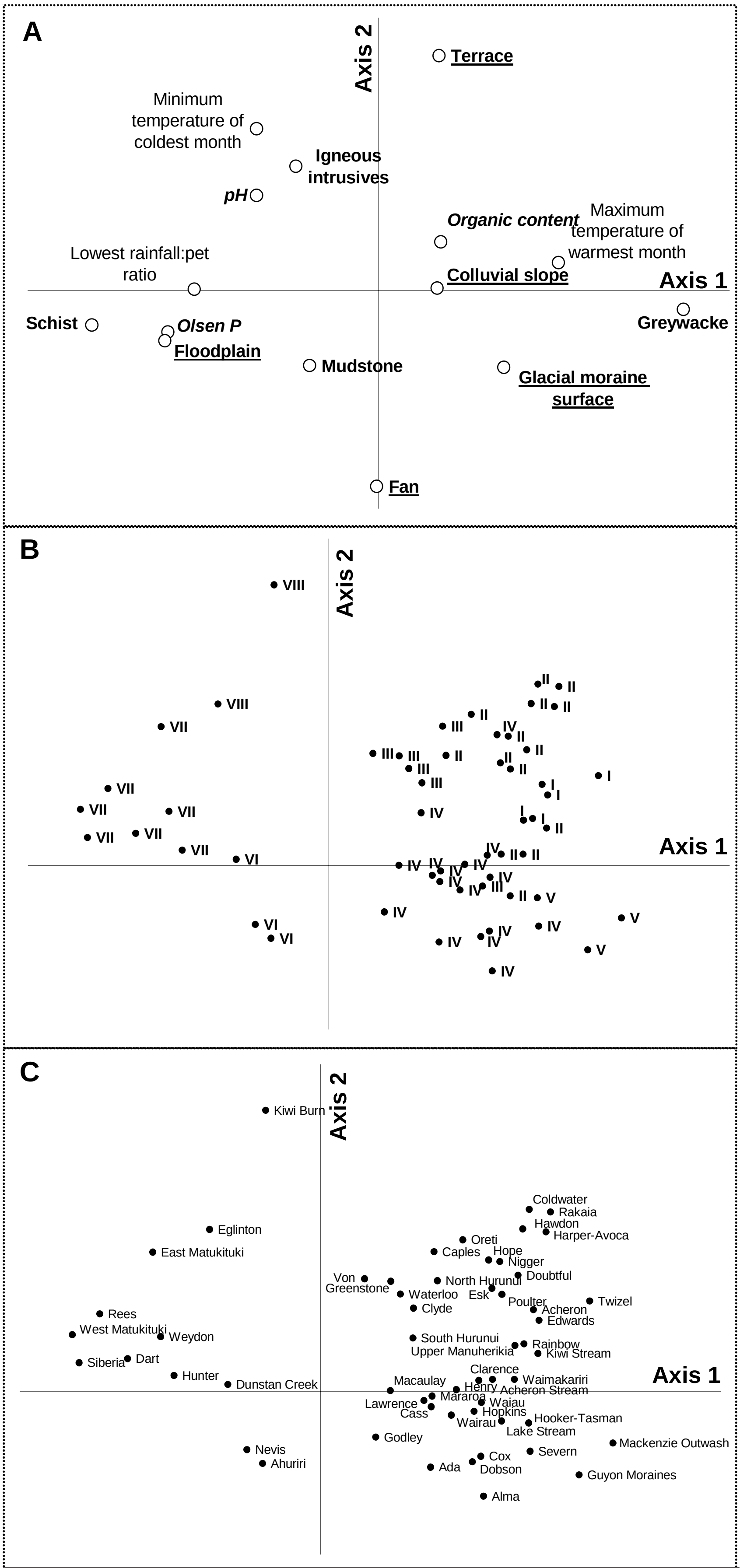
CONSERVANCY	% PUBLIC CONSERVATION LANDS	AVERAGE EXOTIC RICHNESS	AVERAGE NATIVE RICHNESS	AVERAGE SPECIES RICHNESS	PERCENTAGE NATIVE RICHNESS	NATIVE DOMINANCE SCORE
Nelson/Marlborough (*6; 112*)	1.5	5.0^{a}	4.5^{c}	9.5^{b}	44.2^{b}	2.17^{b}
Canterbury (*32; 584*)	33.4	5.2^{a}	8.5^{ab}	13.7^{a}	59.0^{a}	2.84^{a}
Otago (*12; 224*)	27.4	5.2^{a}	8.0^{b}	13.3^{a}	56.2^{a}	2.69^{ab}
Southland (*6; 142*)	34.7	5.3^{a}	9.6^{a}	14.9^{a}	61.7^{a}	2.86^{a}

TABLE 4. AVERAGE CLIMATE AND SOIL CHARACTERISTICS, PERCENTAGE OF SAMPLING SITES WITH DIFFERENT LANDFORM CHARACTERISTICS AND GEOLOGICAL PARENT MATERIALS, AND AVERAGE VEGETATION CHARACTERISTICS IN THE EIGHT ENVIRONMENTAL TYPES (I TO VIII).

ENVIRONMENTAL TYPE	I	II	III	IV	V	VI	VII	VIII
% sampling sites in conservation lands	2	42	36	18	63	3	76	100
Climate								
Max. temp. of warmest month (°C)	20.8	20.3	19.6	19.7	21.0	19.7	19.9	19.6
Min. temp. of coldest month	–3.2	–1.5	–0.8	–2.8	–3.9	–3.2	–0.8	–0.2
Lowest rainfall:PET ratio	0.8	1.2	1.6	1.4	2.3	1.0	2.6	1.9
Soil								
Organic content (%)	11.3	14.2	16.6	13.2	8.9	8.9	11.4	18.1
Olsen P	18.0	10.1	6.4	11.8	8.2	16.0	16.3	7.9
pH	5.3	5.0	5.4	5.1	5.0	5.2	5.2	5.4
Landform (% of sampling sites)								
Fan	9	33	8	35	9	41	29	11
Terrace	70	51	55	25	17	28	31	41
Floodplain	18	11	35	32	3	26	37	48
Glacial moraine surface	0	3	0	5	69	0	3	0
Colluvial slope	2	1	0	1	0	1	0	0
Geological parent material (% of sampling sites)								
Greywacke	100	100	94	100	100	3	3	0
Schist	0	0	6	0	0	83	97	0
Igneous intrusives	0	0	0	0	0	0	0	100
Mudstone	0	0	0	0	0	14	0	0
Vegetation characteristics (average across all sampling sites) *								
Exotic species richness	5.0	5.3	5.9	5.3	5.1	5.3	4.7	4.9
Native species richness	6.4	8.5	11.1	8.3	6.1	8.8	7.1	6.2
Total species richness	11.4	13.7	17.0	13.6	11.2	14.1	11.7	11.1
Percentage native species	53	59	60	57	53	58	57	52
Native dominance score	1.9	2.4	3.0	3.2	1.6	2.6	3.5	0.9

* These factors were not used for the environmental classification of catchments.

Figure 2. Environmental classification of the 56 studied catchments, displayed on the first two component axes of the principal components analysis (PCA) ordination. A, environmental factors influencing the principal components; B, distribution of environmental types (I–VIII); and C, positions of the 56 catchments, on the principal components.



The broad, braided greywacke valleys of environmental type IV are largely situated in Canterbury and Marlborough, although this environmental type includes the Mararoa Valley in Southland (Table 4; Fig. 2B–C). Winter temperatures and ratios of rainfall to evapotranspiration are low, indicating that the climate is relatively extreme, although less continental than in environmental type I. Relatively few sampling sites in this environmental type (c. 18%) fell within public conservation lands. Landforms in these valleys include fans, floodplains and terrace in similar proportions.

Glacial outwash and moraine surfaces are represented in environmental type V (Guyon Moraines, Hooker-Tasman and Mackenzie Outwash catchments in Canterbury). Although the rainfall:potential evapotranspiration ratios show a considerable range of values within this group, soils are generally characterised by low organic matter contents and Olsen P values.

Environmental type VI comprises the Ahuriri Valley in Canterbury, and Dunstan Creek and the Nevis Valley in Otago, which share cold winters and dry summers (i.e. low rainfall:potential evapotranspiration ratios). This environmental type is very poorly represented in public conservation lands (c. 3% of sampling sites).

The remaining two environmental types (VII and VIII) experience higher rainfall and higher winter temperatures, and are far better represented in public conservation lands (76% and 100% of sampling sites, respectively) than type VI. The Dart, East and West Matukituki, Hunter, Rees and Siberia valleys in western Otago and the Weydon Burn in Southland of environmental type VII are distinguished from the Eglinton Valley and the Kiwi Burn (environmental type VIII) largely on substrate factors: the latter is derived from igneous intrusive rocks, rather than schist, and soils have relatively high organic content but low Olsen P values.

5.2 VEGETATION GRADIENTS

The first two axes (vegetation gradients) identified by the ordination of all 1096 quadrat and height-frequency samples (the sample ordination) had Eigenvalues of > 0.30 SD. Subsequent gradients represent relatively minor vegetation gradients (Eigenvalues < 0.2 SD) and were not examined further.

5.2.1 Environment

The first axis of the sample ordination represents the principal vegetation gradient across the plant communities sampled in the study (Fig. 3A). There was a transition from communities comprising short native grasslands of *Rytidosperma* and *Deyeuxia* spp. with intertussock species such as *Carex breviculmis, Luzula ulophylla* and *Raoulia* spp. (low scores) to vegetation types dominated by *Chionochloa rubra* and sedges and rushes such as *Carex coriacea*, *C. gaudichaudiana*, *Juncus gregiflorus*, *Schoenus pauciflorus*, *Uncinia rubra* and the exotic sedge *Carex ovalis* (highest Axis 1 scores). *Festuca novae-zelandiae*, *Poa colensoi* and *Chionochloa rigida* had relatively low scores on this axis, the native grasses *Festuca matthewsii* and *Poa cita* and the exotic grasses *Anthoxanthum odoratum* and *Agrostis capillaris* had

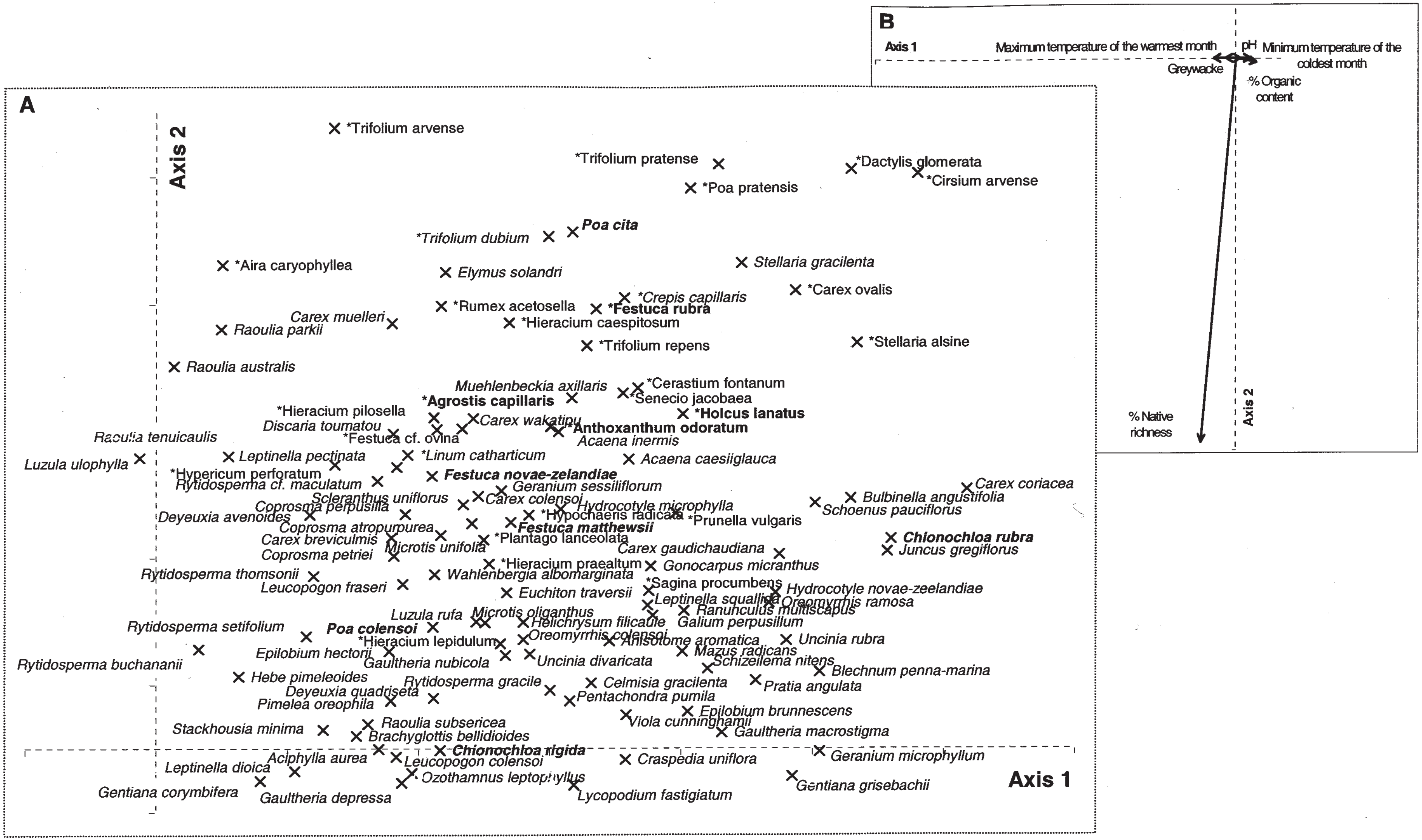


Figure 3. Relative positions on the first two axes of the all-samples ordination of: A, the 111 most common alluvial grassland species (native species in italic type, asterisks indicate exotic species, community dominants in bold); and B, vectors (arrows) indicating the direction of correlation and percentage variation explained by environmental and vegetation factors in step-down predictive multiple regression on sample ordination score.

intermediate scores, whereas the exotic grasses *Holcus lanatus* and *Dactylis glomerata* and the exotic forb *Cirsium arvense* had high scores.

The first axis was relatively weakly related to the measured environmental factors (Fig. 3B). Increasing minimum temperature of the coldest month, rainfall:potential evapotranspiration ratio and soil organic content and soil pH, and decreasing maximum temperature of the warmest month, and a transition in alluvium parent material (from greywacke to schist) together accounted for 14% of the variation in the step-down predictive multiple regression equation. Percentage native species per quadrat decreased along the gradient (c. 8%). Simple regressions indicated a transition from elevated landforms such as terraces to low-lying landforms such as floodplains along this gradient ($P < 0.05$ and $P < 0.001$ respectively). The gradient was also correlated with latitude ($P < 0.05$ by simple regression), suggesting that the incidence of saturated soil conditions increases somewhat from north to south, as temperature maxima and evapotranspiration decrease.

These results suggest that the principal gradient of vegetation variation in intermontane valleys and basins was related to local soil hydrology, which is determined by the local landform features within a catchment. Plant communities of drought-prone, free-draining surfaces were recorded in sampling sites that have low Axis 1 scores, while communities characteristic of soils with impeded drainage had high scores on this gradient. The latter includes backswamps and old river channels on floodplains and low terraces, fan toe seepages and bogs, and cut-off meanders and oxbows, which are saturated for extended periods of the year, and may show some degree of peat development or have higher soil organic contents. Canterbury's broad braided river valleys of recent, free-draining greywacke-derived alluvium had the lowest average scores on the hydrology/landform gradient (e.g. the Mackenzie Outwash, Hooker-Tasman, Cass, Godley, Harper-Avoca and Rakaia catchments; Fig. 4A). They contain few permanently saturated landforms, and short tussock grassland types predominate. Catchments such as the Waterloo Valley in Southland, which contain moraine-impounded landforms with impeded drainage supporting *Chionochloa rubra* and associated species, including remnant woody plants such as *Halocarpus bidwillii*, tended to have the highest average Axis 1 scores (Fig. 4A).

The range of first-ordination-axis sample scores within a catchment reflects the amount of plant community variation, in terms of the principal vegetation gradient (Fig. 4B). We collected a larger number of samples from larger catchments, and these tended to cover a greater range of scores on the first axis, i.e. larger catchments contained a greater variety of communities. Nevertheless, in several catchments, plant community variation was large relative to their sampled extent. These include the Acheron, Alma, Wairau and Severn valleys in Nelson/Marlborough Conservancy, the Eglinton and Oreti valleys in Southland, the Greenstone and Nevis valleys in Otago, and the Ada, Cass, Clarence, Edwards, Esk, Henry, Lawrence, and Nigger valleys in Canterbury.

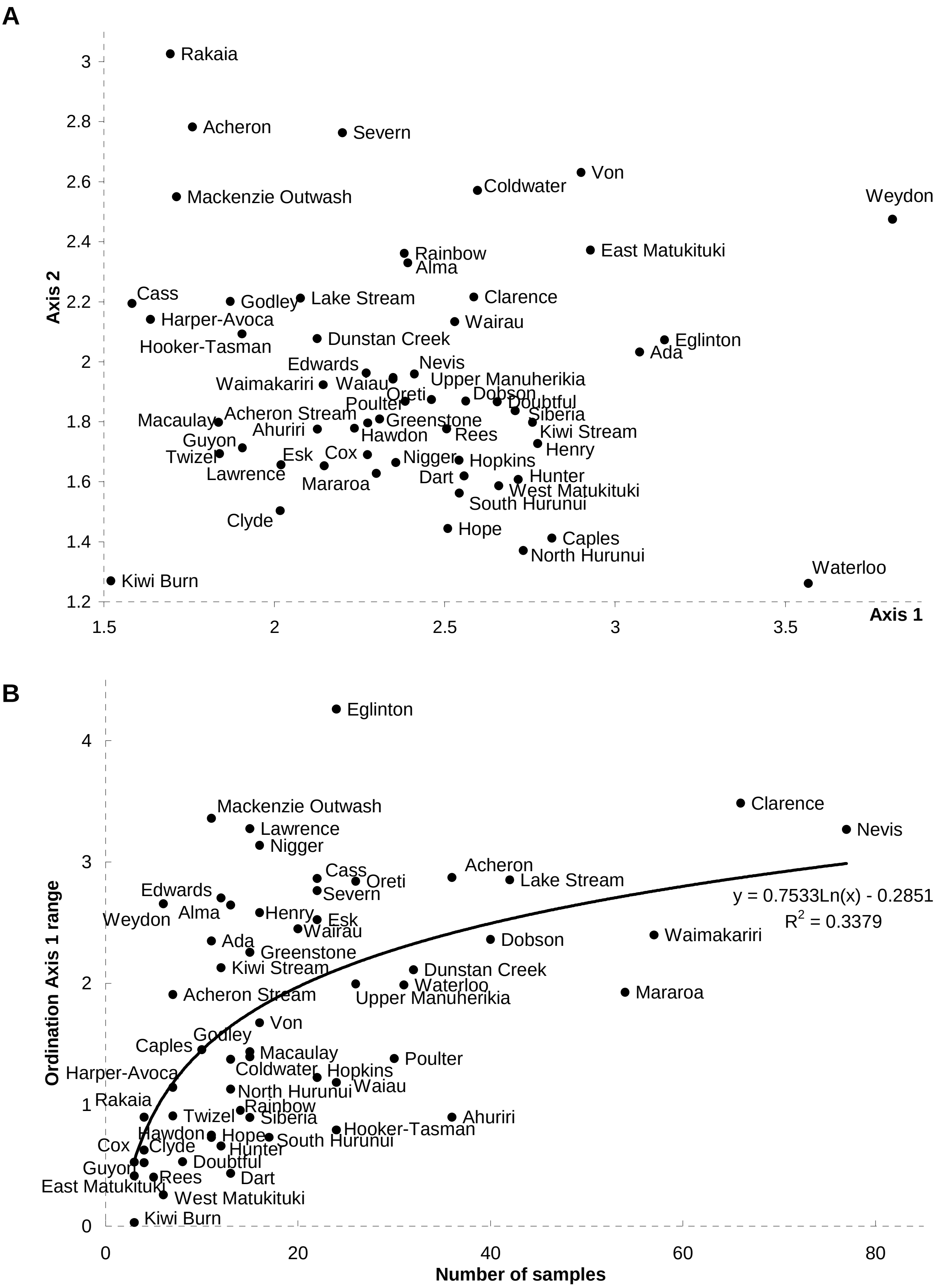


Figure 4. A, Average sample scores in each of the 56 catchments on the firsttwo azes of the all-samples ordination; and B, the relationship between the range of Axis 1 sample scores (i.e. total variation along the principal axis) relative to the number of samples in each catchment (i.e. its sampled extent).