

5.2.2 Pastoral modification

The second vegetation gradient (Axis 2) was strongly correlated with decreasing percentage of native species (78.8% of the variation), and we interpret it to represent an increase in pastoral modification due to grazing, fire and the invasion of exotic species (Fig. 3B). Exotic species richness increased along this gradient, while total and native species richness and native dominance scores decreased significantly (all $P < 0.01$ by simple regression).

Less-modified intermontane valleys and basins were indicated by the presence of native species which had low scores on Axis 2 (Fig. 3A). These included *Aciphylla aurea*, *Brachyglottis bellidioides*, *Celmisia gracilentia*, *Chionochloa rigida*, *Craspedia uniflora*, *Deyeuxia quadriseta*, *Epilobium brunnescens*, *Gaultheria depressa*, *G. macrostigma*, *Gentiana corymbifera*, *G. grisebachii*, *Geranium microphyllum*, *Leptinella dioica*, *Leucopogon colensoi*, *Lycopodium fastigiatum*, *Ozothamnus leptophyllus*, *Pentachondra pumila*, *Pimelea oreophila*, *Pratia angulata*, *Raoulia subsericea*, *Rytidosperma gracile*, *Stackhousia minima* and *Viola cunninghamii*. The exotic herb *Hieracium lepidulum* also had a low Axis 2 score, which suggests that it readily invades less-modified grasslands. The highest degree of pastoral modification was indicated by the presence of species with high scores on Axis 2, including the native short tussock *Poa cita*, and the exotic species *Aira caryophyllea*, *Rumex acetosella*, *Trifolium arvense* and *T. dubium* on well-drained landforms (i.e. samples with low scores on the principal vegetation gradient); *Festuca rubra*, *Poa pratensis*, *Crepis capillaris*, *T. repens* and *T. pratense* at sampling sites with intermediate Axis 1 scores; and *Dactylis glomerata*, *Carex ovalis*, *Cirsium arvense* on more moist, low-lying landforms. The four prominent exotic species *Hieracium pilosella*, *Agrostis capillaris*, *Anthoxanthum odoratum* and *Holcus lanatus* had similar, high scores on the modification gradient, and formed a sequence from left to right along the soil hydrology/landform gradient (Fig. 3A).

Environmental factors made a small contribution to the vegetation variation on the modification gradient (Fig. 3B). Simple regressions indicate that the degree of modification was greatest where summer maximum temperatures and soil pH were high, and rainfall:potential evapotranspiration ratios and soil organic matter content were low (the latter is possibly due either to recent soil genesis or to soil organic matter reduction as a consequence of pastoral use).

Waterloo and Kiwi Burn valleys in Southland, the Caples Valley in Otago, and the North and South Hurunui, Hope and Clyde valleys in Canterbury had the lowest average sample scores on the modification gradient (Fig. 4A). Those from the Acheron, Severn, Coldwater, Rainbow and Alma valleys (Nelson/Marlborough), the Rakaia and Twizel Outwash Plain catchments in Canterbury, and the Von and East Matukituki valleys in Otago were positioned towards the more modified end of the gradient.

5.3 ALLUVIAL VEGETATION TYPES

Eight alluvial vegetation types (plant communities A to H) were identified in the sample classification of 1096 plots (Fig. 5). The percentage of sampling sites within public conservation lands, and the average environmental and vegetation characteristics of each community, are summarised in Table 5. Occurrences of the most frequently recorded vascular plant species in each community are summarised in Table 6. The eight vegetation types can be aggregated into three plant community categories.

Category 1. Communities of well-drained soils and/or continental climates (i.e. a low ratio of rainfall to potential evapotranspiration, usually in combination with cold winters and hot summers) which are dominated by *Festuca novae-zelandiae* and *Poa colensoi* (Communities A, B and C), but which may contain *Chionochloa rigida* or *Chionochloa rubra* tall tussocks. These samples are positioned towards the left of the first ordination axis (Fig. 5A).

Category 2. Communities of moderately well- to well-drained landscape positions, in valleys with moderate to high rainfall and cool temperatures all year round, dominated by *Festuca matthewsii* and *Poa colensoi* (Communities D, E and F) and positioned to the left of centre of Axis 1 (Fig. 5B).

Category 3. Communities of poorly drained substrates and/or mild, high-rainfall catchments that are dominated by *Chionochloa rubra* (Communities G and H). These samples occur towards the right of ordination Axis 1 (Fig. 5C).

Each of the three categories comprised less- and more-modified plant communities, which we interpret as representing different degrees of native dominance, pastoral modification and invasion of exotic plant species. Plant communities were named according to community characteristics and the most frequent physiognomically dominant species, but these species were not necessarily present at all of the sampling sites included in that plant community.

Category 1. *Festuca novae-zelandiae* grasslands

Community A: Native-species-rich *Festuca novae-zelandiae* grasslands
Native-species-rich *F. novae-zelandiae* grasslands were recorded on elevated terrace, fan and glacial moraine surfaces in catchments which experienced relatively low rainfall, cool summers, and frosty winters (Table 5). Soil organic content was relatively high at most of the sampled sites, and soil pH was low, suggesting that soil cation leaching had occurred and that landforms were relatively old. This community was recorded in less than half of the sampled catchments, and was most characteristic of the Coldwater Valley in Marlborough, the Guyon catchment and the Nigger and Esk valleys in Canterbury, the Kiwi Burn catchment in Southland, and the adjacent Oreti and Mararoa valleys (Table 7).

Samples had relatively low scores on both environment (Axis 1) and pastoral modification (Axis 2) gradients (Fig. 5). Average exotic species richness was the lowest of any community; approximately three-quarters of species in any quadrat were native, and native dominance scores were high (Table 5). *Poa colensoi* and *F. novae-zelandiae* were the most frequently recorded native

Figure 5. Positions of the 1096 survey samples on the Axis 1 and 2 of the sample ordination. The three figures show three categories of plant community defined by the classification: **A**, *Festuca novae-zelandiae* communities A, B and C; **B**, *F. matthewsii* communities D, E and F; and **C**, *Chionochloa rubra* communities G and H.

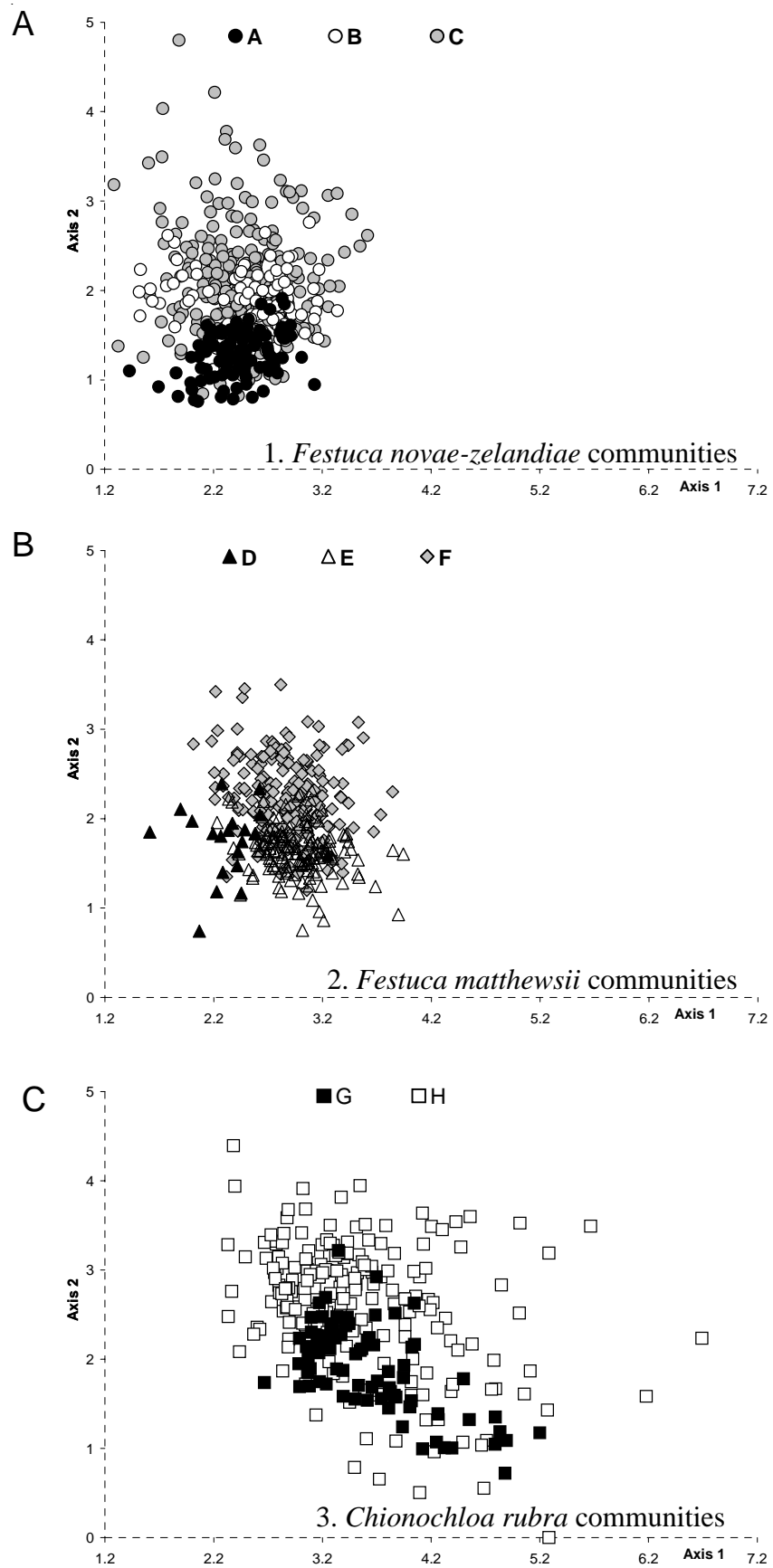


TABLE 5. CLIMATE, VEGETATION AND SUBSTRATE CHARACTERISTICS OF VEGETATION TYPES (A TO H) OF THE SAMPLE CLASSIFICATION.

VEGETATION CATEGORY AND TYPE	CLIMATE				VEGETATION					SUBSTRATE		
	% PCL	MAX. TEMP. (°C)	MIN. TEMP. (°C)	LOWEST R:PET ¹	EXOTIC RICHNESS	NATIVE RICHNESS	SPECIES RICHNESS	% NATIVE RICHNESS	NATIVE DOM. SCORE ²	% ORGANIC	OLSEN P	pH
1. <i>Festuca novae-zelandiae</i>												
A Native-species-rich <i>F. nov.</i>	12.6	19.7 ^c	-2.4 ^b	1.1 ^b	4.0 ^b	12.8 ^a	16.8 ^b	76.0 ^a	4.00 ^a	13.8 ^c	12.2 ^a	5.06 ^a
B Sweet vernal <i>F. nov.</i>	29.2	20.1 ^{ab}	-1.9 ^a	1.3 ^b	5.5 ^a	11.0 ^{bc}	16.5 ^b	66.3 ^b	3.42 ^{ab}	13.0 ^{bc}	10.1 ^a	5.08 ^a
C Species-poor <i>F. nov.</i>	26.9	20.3 ^a	-2.5 ^b	1.2 ^b	4.1 ^b	5.9 ^c	10.0 ^d	55.2 ^c	1.92 ^c	11.6 ^{ab}	13.5 ^a	5.06 ^a
2. <i>Festuca matthewsii</i>												
D Blue & snow tussock <i>F. mat.</i>	25.0	19.0 ^d	-2.7 ^c	2.5 ^c	5.3 ^{ab}	12.8 ^{ab}	18.0 ^{ab}	70.5 ^{ab}	4.55 ^a	8.5 ^a	11.0 ^a	5.40 ^b
E Moist blue tussock <i>F. mat.</i>	57.1	20.0 ^{abc}	-1.9 ^a	1.6 ^a	5.4 ^a	14.0 ^a	19.4 ^a	72.0 ^{ab}	3.26 ^{bc}	13.0 ^{bc}	12.2 ^a	5.00 ^a
F <i>F. mat.</i> or <i>F. nov.</i>	29.6	19.9 ^{bc}	-2.5 ^b	1.6 ^a	6.4 ^a	7.4 ^d	13.8 ^c	53.3 ^c	2.66 ^{cd}	11.9 ^{ab}	13.1 ^a	5.30 ^a
3. <i>Chionochloa rubra</i>												
G Modified <i>C. rubra</i>	26.9	20.0 ^{abc}	-1.8 ^a	1.6 ^a	6.9 ^a	9.8 ^c	16.7 ^b	57.7 ^c	2.40 ^{de}	13.6 ^{bc}	10.3 ^a	5.32 ^b
H Native-species-poor browntop	17.8	20.0 ^{abc}	-2.4 ^b	1.2 ^b	5.3 ^a	3.2 ^f	8.6 ^c	36.9 ^d	2.39 ^{de}	13.7 ^{bc}	12.3 ^a	5.24 ^b

¹ Rainfall to potential evapotranspiration ratio.² Native dom. score = native species dominance score.

TABLE 7. PERCENTAGE OF SAMPLING SITES IN VEGETATION TYPES (A-H) FROM THE SAMPLE CLASSIFICATION, WITHIN CATCHMENT ARRANGED ACCORDING TO GROUPS I TO VIII OF THE CATCHMENT CLASSIFICATION. The length (left-right) of the dendrogram arms to the left of the table represents the magnitude of the differences in composition between catchment groups.

Gp.	Catchment	Conservancy	A	B	C	D	E	F	G	H
I	Acheron	Marlborough			81					19
	Severn	"	9		36			5		50
	Alma	"	8		31					62
	Wairau	"	15		25			35		25
	Coldwater	"	33				33	33		
	Edwards	Canterbury	17		42			17		25
	Nigger	"	38		6		6	19	6	25
	Esk	"	41				5	36		18
	Clyde	"		50	25		25			
	Guyon	"	50				25	25		
	Twizel	"	29		57					14
	Cox	"	8		15		8	38		31
	Hooker-Tasman	"		21	58		4	17		
	Harper-Avoca	"		14	71			14		
	Rakaia	"			75			25		
	Mackenzie Outwash	"	18		64				9	9
	Rees	Otago		20	20		40		20	
	East Matukituki	"								100
	Kiwi Burn	Southland		100						
	II	Rainbow	Marlborough	14		29			36	
Ada		Canterbury		9			9	36		45
Henry		"	6	6	13		6	44		25
Waiau		"	13	4	8		13	46	17	
Doubtful		"		13			38	38	13	
Hopkins		"		5	5		45	23	18	5
Hope		"					64	36		
Kiwi Stream		"		8			33	17	25	17
North Hurunui		"					77	15	8	
South Hurunui		"					76	18		6
Dart		Otago		8	8		38	38		8
Hunter		"		17			8	42	17	17
West Matukituki		"					17	83		
Siberia		"			13		7	80		
III	Ahuriri	Canterbury	8		11		47	17	6	11
	Dobson	"		8	3		33	15	28	15
	Hawdon	"		36	18		27	9		9
	Poulter	"		43	13		17	7	17	3
	Waimakariri	"		16	72		2	4		7
	Acheron Stream	"	29		29					43
	Lake Stream	"	2	50	12			21		14
	Cass	"	18	32	14			32		5
	Lawrence	"		33	7		20	27		13
	Godley	"		7				20		7
	Macaulay	"	7		13	67		7		7
	Mararoa	Southland	24	13	20		19	15	4	6
	IV	Caples	Otago	20				60		10
Greenstone		"		20	27		40	7	7	
Von		"	19							81
Eglinton		Southland		17	21				25	38
Oreti		"	42	4	8			8		38
Weydon Burn		"	17					17		67
V	Dunstan Creek	Otago	13	22	19			31		16
	Upper Manuherikia	"	19	4	15		4	38	12	8
VI	Clarence	Canterbury	11	3	20			23	3	41
VII	Nevis	Otago	8		55		3	4	10	21
VIII	Waterloo	Southland					13	3	61	23

grasses, although *Deyeuxia quadriseta*, *D. avenoides*, *Rytidosperma gracile* and *R. thomsonii* were common, and *Festuca matthewsii* was recorded occasionally (Table 6). The presence of *Chionochloa rigida* and/or *C. rubra* at many sampling sites indicates tall tussock origins. Native intertussock species typically included the subshrub *Pimelea oreophila* and the forbs *Luzula rufa*, *Raoulia subsericea*, *Leucopogon fraseri*, *Celmisia gracilentia*, *Oreomyrrhis colensoi*, *Brachyglottis bellidioides*, *Viola cunninghamii*, *Gentiana corymbifera*, *Leptinella dioica* and *Stackbousia minima*. Prominent exotic species included *Agrostis capillaris*, *Anthoxanthum odoratum*, *Hypochaeris radicata* and *Hieracium pilosella*.

Community B: Sweet vernal—*Festuca novae-zelandiae* grasslands

This short-tussock grassland community, with somewhat higher exotic species richness and lower native species richness than Community A, predominated on stable fans and terraces in valleys where annual rainfall exceeded 1000 mm, but summer temperatures, and hence evapotranspiration, were relatively high (Table 5). They were recorded in less than half of the sampled catchments, and were most prominent in the Hawdon, Poulter, Clyde, Lawrence, Lake Stream, and Cass catchments in Canterbury (Table 7).

Approximately two-thirds of species per quadrat were native, and native species dominance scores were relatively high (Table 5). *Festuca novae-zelandiae* and *Poa colensoi* were the most commonly recorded native grasses (Table 6). Intertussock species such as *Leucopogon fraseri*, *Wahlenbergia albomarginata* and *Luzula rufa* and subshrubs of *Hebe pimeleoides*, *Gaultheria macrostigma* and *Pentachondra pumila* were common, while on more recent, well-drained floodplain surfaces the community included *Carex breviculmis*, *Luzula ulophylla* and *Raoulia australis*. Tall tussock origins were indicated by occasional records of *Chionochloa rigida* and *C. rubra*, but *Poa cita* and *Festuca matthewsii* were very rarely present. Sweet vernal (*Anthoxanthum odoratum*) was an almost constant exotic element, but *Agrostis capillaris* was less ubiquitous than at drier sampling sites. Other exotic forbs such as *Hieracium pilosella*, *Hypochaeris radicata*, *Crepis capillaris*, *Sagina procumbens* and *Plantago lanceolata* occurred frequently.

Community C: Species-poor *Festuca novae-zelandiae* grassland

This widespread community was recorded in two-thirds of sampled eastern South Island alluvial catchments (Table 7). It was most characteristic of the older alluvial surfaces of warmer, drier, greywacke-derived alluvial systems (Table 5), especially the Acheron, Severn and Edwards valleys in Marlborough, and the Clarence, Harper-Avooca, Rakaia, Hooker-Tasman and Twizel valleys, and on the Mackenzie Outwash Plain in Canterbury. It was also recorded on the floors of the Waimakariri (Canterbury), Mararoa (Southland), and Nevis (Otago) valleys.

Native species richness and native richness percentages were low, and native dominance scores were lower than in any other community (Table 5).

There were no constant species. The most frequently recorded native grasses were *F. novae-zelandiae*, *Poa colensoi* and *Rytidosperma thomsonii*, and intertussock species included *Leucopogon fraseri*, *Wahlenbergia albomarginata* and *Luzula rufa* (Table 6). The sedge *Carex muellerii*, the mat-forming

Raoulia parkii, and the exotic grass *Festuca ovina* were uncommon but distinctive species that we recorded in few other grassland types. *Antboxanthum odoratum*, *Agrostis capillaris*, *Hypochaeris radicata*, and *Rumex acetosella* were the most frequently recorded exotic species.

Category 2. *Festuca matthewsii* grasslands

Community D: Shrubby blue tussock—snow tussock—*Festuca matthewsii* grasslands

This vegetation type was recorded on well-drained recent greywacke floodplains and moraines in the high-rainfall heads of the Godley and Macaulay valleys in Canterbury, which experience low winter temperatures and high rainfall due to their proximity to the Main Divide.

Native species richness (12.8 species per quadrat), richness percentages (70.5%), and dominance scores were high (Table 5).

Festuca matthewsii was the most abundant native grass species (85% of quadrats; Table 6). The community frequently contained native grasses such as blue tussock (*Poa colensoi*), snow tussock (*Chionochloa rigida*), *Elymus solandri*, *Rytidosperma setifolium* and *Rytidosperma buchananii*, but *F. novae-zelandiae* was not recorded here. The most common native forbs were *Hydrocotyle microphylla*, *Wahlenbergia albomarginata*, *Luzula rufa* and *Leucopogon fraseri*. *Raoulia tenuicaulis* and *Scleranthus uniflorus* were present on more recent surfaces, while *Craspedia uniflora* and *Aciphylla aurea* were common on older terraces. Woody species were prominent, and included *Discaria toumatou*, *Dracophyllum uniflorum* and *Ozotamnus leptophyllus* and the subshrubs *Leucopogon colensoi*, *Muehlenbeckia axillaris* and *Coprosma petriei*. *Agrostis capillaris* was the most common exotic grass (70% of sampling sites), the exotic forbs *Hypericum perforatum* and *Hieracium pilosella* were almost constant, and *Rumex acetosella* was common. However, *Antboxanthum odoratum* and *Hypochaeris radicata* were recorded less frequently than in most other vegetation types.

Community E: Moist blue tussock—*Festuca matthewsii* grasslands

This community is most characteristic of the upper reaches of the less-modified, wetter western valleys, where soil pH is relatively low (Table 5). It was recorded in just over half of South Island alluvial systems (Table 7), most notably in the North and South Hurunui, Doubtful, Hope, Poulter, Ahuriri, Dobson, and Hopkins valleys in Canterbury, the Rees, Dart, Caples, and Greenstone valleys in Otago, and the Mararoa Valley in Southland.

Native species richness was higher than in any other community type, and native species dominance scores were also relatively high (Table 5).

Poa colensoi and *F. matthewsii* were the most frequently recorded native grasses, although *F. novae-zelandiae* and *Chionochloa rubra* were also present at many sampling sites (Table 6). Native forbs such as *Wahlenbergia albomarginata*, *Luzula rufa*, *Leucopogon fraseri*, *Celmisia gracilentia*, *Ranunculus multiscapus*, *Helicbrysum filicaule*, *Anisotome aromatica*, *Gonocarpus micranthus*, *Hydrocotyle microphylla* and *Leptinella squallida*, and the subshrub *Muehlenbeckia axillaris* were frequent components. Other characteristic native species included the forbs *Acaena inermis*, *Carex*

colensoi, *Epilobium brunnescens*, *Euchiton traversii*, *Galium perpusillum*, *Geranium sessiliflorum*, *Mazus radicans*, *Microtis oliganthus*, *M. unifolia* and *Schizeilema nitens* and the subshrubs *Coprosma atropurpurea* and *Gaultheria nubicola*. Relatively large numbers of introduced species were present, including the grasses *Anthoxanthum odoratum*, *Agrostis capillaris* and *Holcus lanatus* and the forbs *Cerastium fontanum*, *Hypochaeris radicata* and *Trifolium repens*.

Community F: Modified *Festuca matthewsii* or *F. novae-zelandiae* grasslands

This grassland type was widespread on floodplains, low terraces and fans in the mid-to-upper reaches of higher-rainfall alluvial systems. Average soil organic content was relatively low, and soil pH relatively high, suggesting a tendency for this vegetation to occupy more recent or regularly disturbed landforms (Table 5). It was recorded in a third or more of the sampled sites in the Wairau, Rainbow, and Coldwater valleys in Marlborough, in the Ada, Henry, Waiau, Doubtful, Hope, Esk, Cox, and Cass valleys in Canterbury, and in the Hunter, Siberia, West Matukituki, Dart, and Upper Manuherikia valleys in Otago (Table 7).

Native species accounted for just over half the species present, and native dominance scores were low (Table 5).

Short tussock grasses (*Festuca matthewsii* or *F. novae-zelandiae*) were the most common community physiognomic dominants (Table 6), and *Poa colensoi* and *P. cita* were recorded frequently. Other common native species included the forbs *Wahlenbergia albomarginata*, *Acaena inermis* and *Luzula rufa*, and the subshrub *Muehlenbeckia axillaris*. *Uncinia divaricata* and *Leptinella pectinata* were distinctive native intertussock species, which we recorded in few other vegetation types. The most frequent exotic grasses were *Anthoxanthum odoratum* and *Agrostis capillaris*. *Holcus lanatus* and *Poa pratensis* were also common, and exotic forbs included *Hieracium pilosella*, *Trifolium repens*, and *Hypochaeris radicata*.

Category 3. *Chionochloa rubra* grasslands

Community G: Modified *Chionochloa rubra* grasslands

Modified *C. rubra* grasslands were restricted to c. 30% of the sampled catchments, especially those characterised by low rainfall, mild winters, and relatively low evapotranspiration as a consequence of low summer temperatures (Table 5), i.e. the Waterloo and Eglinton valleys in Southland. However, they were also recorded in the Dobson Valley in Canterbury and the Nevis Valley in Otago, which experience extremely low winter temperature minima (Tables 2 and 7).

The species composition and the extent of modification of these grasslands varied widely. Native *C. rubra* tussocks were present in 38% of sampling sites, and *Poa cita* tussocks in 19% (Table 6). Native species richness ranged from high (14 species per quadrat in the Waterloo Valley) to very low (2 and 4 species per quadrat in the Nigger Valley in Canterbury and the Rees Valley in Otago, respectively). Average exotic species richness was higher than in any other community type, and native species dominance scores were relatively low (Table 5), which suggests a high degree of pastoral modification and/or susceptibility to plant invasion.

Chionochloa rubra grasslands were characteristic of sampling sites with impeded drainage, and a suite of moisture-demanding native herbs included *Acaena caestiglauca*, *Blechnum penna-marina*, *Bulbinella angustifolia*, *Carex coriacea*, *Carex gaudichaudiana*, *Celmisia gracilentia*, *Gentiana grisebachii*, *Geranium microphyllum*, *Gonocarpus micranthus*, *Hydrocotyle novae-zeelandiae*, *Juncus gregiflorus*, *Leptinella squallida*, *Oreomyrrhis ramosa*, *Pratia angulata* and *Uncinia rubra*. The exotic grasses *Festuca rubra* and *Holcus lanatus* were typically present, while *Anthoxanthum odoratum* and *Agrostis capillaris* occurred frequently, as they did in most other vegetation types. *Trifolium repens* and *Hypochaeris radicata* were the most commonly occurring exotic forbs, but *Hieracium praealtum*, *Prunella vulgaris*, *Stellaria alsine* and *Trifolium dubium* were also frequently recorded.

Community H: Native-species-poor browntop grasslands

This community was recorded on a variety of landforms in catchments which experience moderate to low rainfall and low winter temperatures, and where soil organic content and soil pH are relatively high (Table 5). It accounted for high proportions of sampling sites in the Severn and Alma valleys in Marlborough, in the Clarence and Ada valleys and in Acheron Stream in Canterbury, and in the lower East Matukituki and Von valleys in Otago and in the Eglinton, Oreti and Weydon Burn in Southland.

Native species richness, and percentage native species were lower in this community than in any other vegetation type, and native dominance was generally low (Table 5).

Remnant tussocks of *Chionochloa rubra* occurred in about one-third of sampling sites, and *Festuca novae-zeelandiae* and *Poa cita* were also occasionally present (Table 6). Browntop (*Agrostis capillaris*) occurred more frequently here than in any other vegetation type. Other common exotic species included the grasses *Anthoxanthum odoratum*, *Holcus lanatus*, *Festuca rubra*, *Poa pratensis*, *Dactylis glomerata*, and the forbs *Trifolium repens*, *Cerastium fontanum*, *Hypochaeris radicata* and *Rumex acetosella*. Distinctive elements included the native species *Schoenus pauciflorus* and *Stellaria gracilentia*, and the moisture-demanding exotic species *Carex ovalis*, *Cirsium arvense*, *Dactylis glomerata*, and *Trifolium pratense*. However, species such as *Celmisia gracilentia*, *Leucopogon fraseri*, *Luzula rufa*, *Poa colensoi* and *Wahlenbergia albomarginata* were rare, and the exotic species *Hieracium praealtum* and *H. pilosella* were seldom recorded in this vegetation type.

We suggest that this community was mainly derived from *Chionochloa rubra* grasslands and tussock-shrubland communities that were formerly widespread on relatively poorly drained substrates in these valleys. The modified grasslands of today are probably the consequence of reduction and/or elimination of *C. rubra* cover by fire, grazing or mechanical soil drainage.

5.4 CATCHMENT GROUPS

Eight catchment groups (I–VIII: Tables 7 and 8) were identified by the grouped classification. These catchment groups comprised alluvial systems that were most similar in the range and proportions of communities they contained. Nevertheless, considerable differences existed between the catchments within these groups.

The first catchment group (I) was represented by a large group of 19 catchments (Table 7) which contained comparatively few vegetation types. Native-species-poor vegetation types with low native dominance scores (i.e. C, F and H; Table 5) were the most common plant communities. A low proportion of the sampling sites (14%) fell within public conservation lands (Table 8). These included sampling sites in the Cox and Tasman valleys in Canterbury, the East Matukituki Valley in Otago, and the Kiwi Burn in Southland.

Catchment group II comprised catchments in Marlborough (1), Canterbury (9) and Otago (4), which contain both less-modified (Community E) and more-modified (Community F) *Festuca matthewsii* grasslands (Tables 7 and 8). The average percentage of native species was relatively high (c. 61%), but native dominance scores were generally low. About half of the intermontane valleys and basins sampled in this catchment group lay within conservation lands (i.e. much of the Dart, North and South Hurunui, West Matukituki, Siberia and Hopkins catchments; Table 8).

The third catchment group (III) comprised 11 Canterbury catchments and the Mararoa Valley in Southland (Table 7), and included *Festuca novae-zelandiae*, *F. matthewsii* and *Chionochloa rubra* grasslands (in particular Communities C, D, F and H). Average native-species-richness was higher than in catchment group II, but the percentage of native species (i.e. the degree of pastoral modification) was similar (c. 61%; Table 8). However, native dominance scores were significantly higher than most other catchment groups. Public conservation lands covered c. 37% of the sampled extent of this catchment

TABLE 8. PERCENTAGE OF SAMPLING SITES REPRESENTED IN PUBLIC CONSERVATION LANDS, AND AVERAGE VEGETATION CHARACTERISTICS OF QUADRATS IN THE EIGHT CATCHMENT GROUPS FROM THE CATCHMENT CLASSIFICATION (I TO VIII).

Numbers in parentheses indicate the number of catchments and quadrats, 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).

CATCHMENT GROUP	% PUBLIC CONSERVATION LANDS	AVERAGE EXOTIC RICHNESS	AVERAGE NATIVE RICHNESS	AVERAGE SPECIES RICHNESS	PERCENTAGE NATIVE RICHNESS	NATIVE DOMINANCE SCORE
I (19; 215)	14.4	4.7 ^b	6.0 ^d	10.7 ^e	51.8 ^c	2.47 ^{bc}
II (14; 190)	49.5	5.3 ^{ab}	8.8 ^{bc}	14.0 ^{bc}	60.8 ^{ab}	2.60 ^{bc}
III (12; 332)	36.9	5.4 ^{ab}	9.4 ^b	14.8 ^{bc}	61.0 ^{ab}	3.16 ^a
IV (6; 91)	57.7	5.5 ^{ab}	7.6 ^c	13.1 ^{cd}	51.0 ^c	1.93 ^c
V (2; 66)	0.0	6.3 ^a	9.7 ^b	16.0 ^{ab}	57.9 ^{abc}	2.74 ^{abc}
VI (Clarence: 1; 56)	0.0	4.7 ^b	5.5 ^d	10.2 ^e	48.6 ^c	2.95 ^{ab}
VII (Nevis: 1; 77)	0.0	4.7 ^b	7.2 ^{cd}	11.9 ^{de}	56.1 ^{bc}	2.25 ^{bc}
VIII (Waterloo: 1; 31)	0.0	5.9 ^{ab}	12.9 ^a	18.8 ^a	69.7 ^a	3.97 ^a

group. Plant communities from this group in the Hawdon, Poulter and Waimakariri valleys and in Acheron Stream fell within National Parks or Conservation Areas, but catchments to the south of the Waimakariri River (e.g. the Lake Stream, Lawrence, Godley, Dobson and Ahuriri valleys) were less well represented in conservation lands.

The fourth catchment group (IV) comprised six alluvial systems in north-western Southland and south-western Otago (Table 7). Native-species-poor browntop grasslands (Community H) and native-species-rich *Festuca novae-zelandiae* short tussock grasslands (Community A) predominated, and native dominance was low. With the exception of the two most eastern catchments (the Von and Oreti valleys), most of the sampled extent of these alluvial catchments was included in public conservation lands (Table 8).

A fifth catchment group (V) comprised two inland Otago catchments (Dunstan Creek and the Upper Manuherikia) which contained no public conservation lands (Tables 7 and 8). *Festuca novae-zelandiae* grasslands (Communities A, B and C), and modified *F. novae-zelandiae* tussock grasslands (Community F) were the most common vegetation types, although relicts of *Chionochloa rubra* grasslands (Communities G and H) were also present. Exotic species richness was higher here than in any other catchment group, but the plant communities also contained numerous native species (average 9.7 species per quadrat).

The Clarence, Nevis and Waterloo valleys were distinguished as separate catchment groups (Tables 7 and 8). All contained remnants of *Chionochloa rubra* grasslands (Communities G and H). The Clarence Valley (catchment group VI) included modified *Festuca matthewsii* and *F. novae-zelandiae* grassland types (A, C and F; Table 7), while in the Nevis Valley, species-poor *F. novae-zelandiae* short tussock grasslands (Community C) predominated. The Waterloo Valley was distinguished by a high proportion of *C. rubra* grasslands (Community G) and a high degree of native dominance (Table 8). None of the intermontane valleys and basins sampled in these three catchment groups were included in public conservation lands (Table 8).

5.5 CORRELATION BETWEEN VEGETATION AND ENVIRONMENTAL TYPES

Plant communities were widely distributed among environmental types: most plant communities (except shrubby blue tussock—snow tussock—*Festuca matthewsii* grasslands (Community D) which was restricted to the Godley and Macaulay valleys) were represented in all but the most restricted environmental types (i.e. V and VIII) (Table 9). There was also little correlation between catchment groups (based on the overall similarity in present vegetation between catchments) and environmental types (based on similarities between catchments in terms of environment). The Clarence, Nevis and Waterloo valleys, which were distinguished as separate catchment groups in terms of vegetation (Tables 7 and 8), are not unique in terms of environment, and valleys that are grouped into catchment types on the basis of similar vegetation are typically drawn from a range of different environmental types. These results

emphasise the fact that the relationship between the present vegetation of intermontane valleys and basins and environmental factors is weak.

5.6 PROTECTION IN PUBLIC CONSERVATION LANDS

Twenty-eight percent of all intermontane valley and basin sampling sites fall within public conservation lands, but there are significant differences between conservancies (Table 3). Southland Conservancy has the highest percentage of sampled sites in public conservation land (average c. 35%), while Nelson/Marlborough Conservancy has the lowest (1.5%, i.e. two sampling sites in the upper Rainbow catchment).

Certain environmental types of intermontane valleys and basins are well represented in public conservation lands (Table 4). In particular, high proportions of environmental types VII and VIII, in the high-rainfall southwestern part of the study area fall within National Parks and other conservation lands. However, dry, subcontinental rainshadow environmental types A (greywacke-derived substrates) and VI (schist-derived substrates) are very poorly represented in public conservation lands.

Intermontane valley and basin plant communities and catchment types identified in the present study are also unequally represented within public conservation lands (Tables 5 and 8). Certain native-species-rich and native-

TABLE 9. PERCENTAGE OF SAMPLING SITES IN EACH PLANT COMMUNITY (A TO H) AND EACH CATCHMENT GROUP (I TO VIII) THAT FALL WITHIN EACH OF THE EIGHT ENVIRONMENTAL TYPES.

ENVIRONMENTAL TYPE	I	II	III	IV	V	VI	VII	VIII
Plant community (<i>n</i>)	(7)	(7)	(7)	(8)	(5)	(7)	(7)	(5)
1. <i>Festuca novae-zelandiae</i>								
A Native-species-rich <i>F. nov.</i>	13	11	6	10	6	9	2	11
B Sweet vernal - <i>F. nov.</i>	2	19	6	7	14	5	6	15
C Species-poor <i>F. nov.</i>	48	24	6	15	6	36	6	19
2. <i>Festuca matthewsii</i>								
D Blue & snow tussock— <i>F. mat.</i>				5				
E Moist blue tussock— <i>F. mat.</i>	2	12	26	14	6	13	16	
F <i>F. mat.</i> or <i>F. nov.</i>	19	15	3	22	14	13	45	
3. <i>Chionochloa rubra</i>								
G Modified <i>C. rubra</i>	3	4	26	6		7	6	22
H Native-species-poor browntop	15	14	26	3		17	18	33
Catchment group (<i>n</i>)	(3)	(4)	(4)	(4)	(1)	(3)	(3)	(2)
I	56	2	5	19	100		16	11
II	15	15	5	23			74	
III		56		41		25		
IV		10	51				10	89
V	29					23		
VI				17				
VII						53		
VIII			39					

dominated vegetation types (e.g. Community A—native-species-rich *F. novae-zelandiae* grassland) and catchment types that are distinctive in terms of the range and types of communities they contain (e.g. catchment groups V, VI, VII and VIII) are particularly poorly represented.

Finally, few of the catchments that contain a wide diversity of present-day vegetation types relative to their sampled extents (represented by the range of scores on the principal ordination axis, Fig. 4B) are protected in conservation lands. These include the Acheron, Alma, Wairau and Severn valleys in Nelson/Marlborough Conservancy, the Greenstone and Nevis valleys in Otago, the Ada, Cass, Clarence, Edwards, Esk, Henry, Lawrence and Nigger valleys in Canterbury and the Oreti Valley in Southland.

5.7 TEMPORAL TRENDS IN THE VEGETATION OF INTERMONTANE VALLEYS AND BASINS

5.7.1 Effects of grazing exclosure

Existing exclosures in intermontane valleys and basins were located in five of the eight plant communities identified by the sample classification (Tables 10 and 11). No exclosures were located within communities D (shrubby blue tussock—snow tussock—*F. matthewsii* grassland) or E (moist blue tussock—*F. matthewsii* grassland), and only one exclosure sample (from grazed vegetation at Simons Hill) was classified within Community A (native-species-rich *F. novae-zelandiae* grassland). Community H (native-species-poor browntop grasslands) was eliminated by the exclusion of recently established exclosures in the North Hurunui Valley (established 1999) and the Hawdon Valley retirement fence (established 1998 but temporarily breached after floods in 1999). Only two of the eight catchment groups contained exclosures (i.e. catchment groups I and IV: Table 11).

We report the direction of differences in native richness and native biomass proportions in grazed and ungrazed vegetation at each exclosure site (because exclosures were not replicated at any site, the differences in vegetation characteristics could not be tested for significance).

Percentage native richness was higher in ungrazed exclosures than in adjacent grazed vegetation at four of the ten sites (Fig. 6A; Table 11): in the three exclosures in the Acheron Valley, i.e. at Isolated Flat, Acheron 1 and Acheron 2 in Marlborough, and in the Caples Valley in Otago. It was lower in ungrazed exclosures than in adjacent grazed vegetation at the remaining six sites: i.e. Tasman Flat in the Hooker-Tasman catchment, Simons Hill, Ben Ohau and Maryburn in the Mackenzie Outwash system in Canterbury, in the Von Valley in Otago, and in the Eglinton Valley in Southland.

Native species accounted for higher percentages of vegetation biomass (summed height-frequency) within exclosures than in the adjacent grazed vegetation, at five sites (Fig. 6B; Table 11): Isolated Flat and the Acheron 1 site in Marlborough, at Tasman Flat and Maryburn in Canterbury, and in the Caples Valley in Otago. The remaining exclosures contained smaller proportions of native species than adjacent grazed vegetation: i.e. the Acheron 2 site in

TABLE 10. ENCLOSURE AND FENCELINE (F) SITES SAMPLED TO EXAMINE TEMPORAL CHANGES IN INTERMONTANE VALLEYS AND BASINS, ARRANGED BY PLANT COMMUNITIES (A-H) OF THE SAMPLE CLASSIFICATION (COLUMNS) AND BY CONSERVANCY AND CATCHMENT (ROWS).

NZMS Sheet No. and six-figure grid references are shown. Indents indicate site names where these numbered >1 per catchment. * = recently fenced site, not included in temporal change analyses. Numbers in parentheses represent the number of height-frequency (h-f) plots at each site.

Community	A	B	C	D	E	F	G	H
NELSON/MARLBOROUGH								
Acheron								
Acheron 1 N30 164908			Grazed & ungrazed (2)					
Acheron 2 N31 164877			Grazed & ungrazed (2)					
Isolated Flat N30 198999						Grazed & ungrazed (2)		
CANTERBURY								
North Hurunui								
North Hurunui 1 L32 243324								Grazed & ungrazed (2)
North Hurunui 2 L32 284337								Grazed & ungrazed (2)
Waimakariri (F) K33 096006			More modified (1)				Less modified (1)	
Lake Stream (F) J35 587600		More & less modified (2)						
Hawdon K33 084018								Grazed & ungrazed (2)
Hooker-Tasman H36 785137							Grazed & ungrazed (2)	
Dobson (F) H37 666997								More & less modified (2)
Mackenzie Outwash								
Simons Hill H38 890580	Grazed (1)					Ungrazed (1)		
Maryburn I38 980700		Grazed & ungrazed (2)						
Ben Ohau H38 803617			Grazed & ungrazed (2)					
OTAGO								
Dunstan Creek (F) G40 480120					More modified (1)		Less modified (1)	
Von E42 440430		Grazed (1)				Ungrazed (1)		
Caples E41 340840		Grazed & ungrazed (2)						
SOUTHLAND								
Eglinton D41 170610			Grazed & ungrazed (2)					
Total h-f plots	1	7	9	0	1	4	4	8

TABLE 11. VEGETATION DIFFERENCES AT EXCLOSURE AND FENCELINE SITES INDICATING TEMPORAL CHANGES IN INTERMONTANE VALLEYS AND BASINS, SHOWING PLANT COMMUNITIES (A TO H) OF THE SAMPLE CLASSIFICATION, CATCHMENT GROUPS (I TO VIII) OF THE CATCHMENT CLASSIFICATION, AND CONSERVANCIES.

Differences (+ = higher, - = lower) refer to ungrazed compared with grazed vegetation (exclosure sites), and to less-modified vegetation compared with more-modified vegetation (fenceline sites).

	COMMUNITY	CATCHMENT GROUP	CONSERVANCY	NATIVE RICHNESS	NATIVE BIOMASS	NATIVE GRASS BIOMASS
Exclosure site						
Maryburn	B	I	Canterbury	-	+	+
Caples	B	IV	Otago	+	+	+
Acheron 1	C	I	Nelson/Marlborough	+	+	+
Acheron 2	C	I	Nelson/Marlborough	+	-	-
Ben Ohau	C	I	Canterbury	-	-	-
Eglinton	C	IV	Southland	-	-	-
Isolated Flat	F	I	Nelson/Marlborough	+	+	+
Simons Hill	F/A	I	Canterbury	-	-	-
Von	F/B	IV	Otago	-	-	-
Hooker-Tasman	G	I	Canterbury	-	+	-
Fenceline site						
Waimakariri	G/C	III	Canterbury	-	+	+
Lake Stream	B/B	III	Canterbury	+	+	+
Dobson	H/H	III	Canterbury	+	+	+
Dunstan Creek	G/E	V	Otago	+	+	+
Eglinton*	-/C	IV	Southland	-	-	no change

* Less-modified vegetation (1981; not included in the plant community classification) compared with more-modified vegetation at the same site, which was resampled after 26 years (1997; included in the plant community classification).

Marlborough, at Simons Hill and Ben Ohau in Canterbury, and in the Von Valley in Otago.

The biomass (summed height-frequency) of native grasses was higher within exclosures than in the adjacent grazed vegetation at the Isolated Flat and Acheron 1 sites in Marlborough, at Maryburn in the Mackenzie Basin (Canterbury) and in the Caples Valley in Otago (Fig. 6C; Table 11).

We found no relationship between ungrazed versus grazed differences in native species richness and biomass proportions (dependent variates) and most examined vegetation and climate variables (independent variates). The positive relationship between native species richness in grazed vegetation and increased percentage native species biomass with grazing removal, in four exclosures in southern alluvial systems (Walker & Lee 2000), was not consistent in the ten-exclosure dataset presented here. Higher native biomass percentages were recorded in exclosures where native species accounted for the smallest fraction of the total richness in the grazed vegetation outside exclosures (i.e. at Isolated Flat and at Site 1 in the Acheron Valley in Marlborough, and in the Caples Valley in Otago; $R^2 = 0.43$, $P < 0.05$ by linear regression; Fig. 6B, D). This relationship is probably spurious, and reflects the loss of native species in grazed vegetation, and their survival inside exclosures, since the time that the exclosures were established in the Caples and Acheron valleys.

Figure 6. Effects of enclosure at 10 sites in intermontane valleys and basins: percentage A, native richness (species number); B, summed height-frequency all native species (native abundance); C, summed height-frequency native grasses (per sampling point; Scott 1965; Dickinson et al. 1992) in grazed vegetation and adjacent ungrazed vegetation in enclosures, showing year of enclosure where known. D, relationship between difference in ungrazed and grazed vegetation in % native abundance, and % native richness in grazed vegetation, showing the least squares linear regression line ($P < 0.05$).

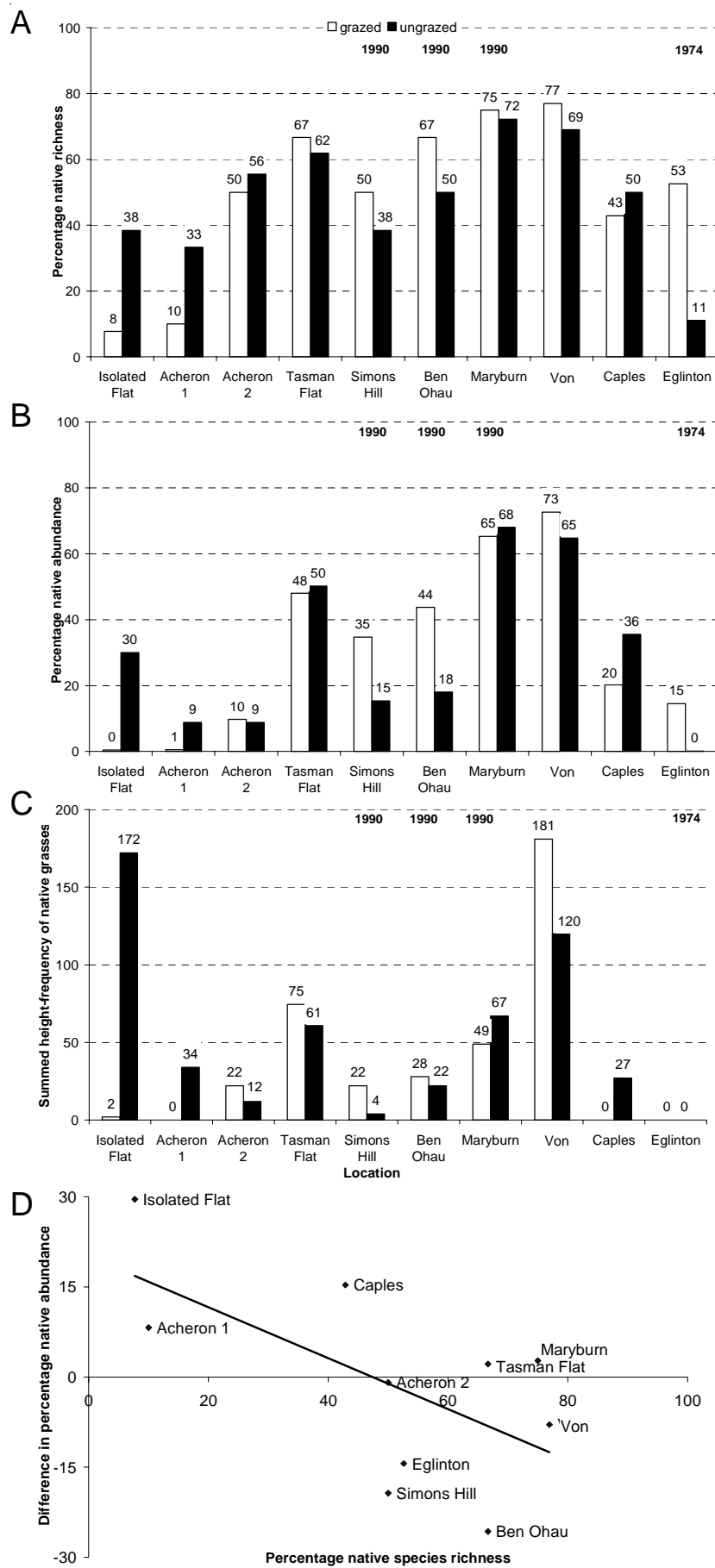
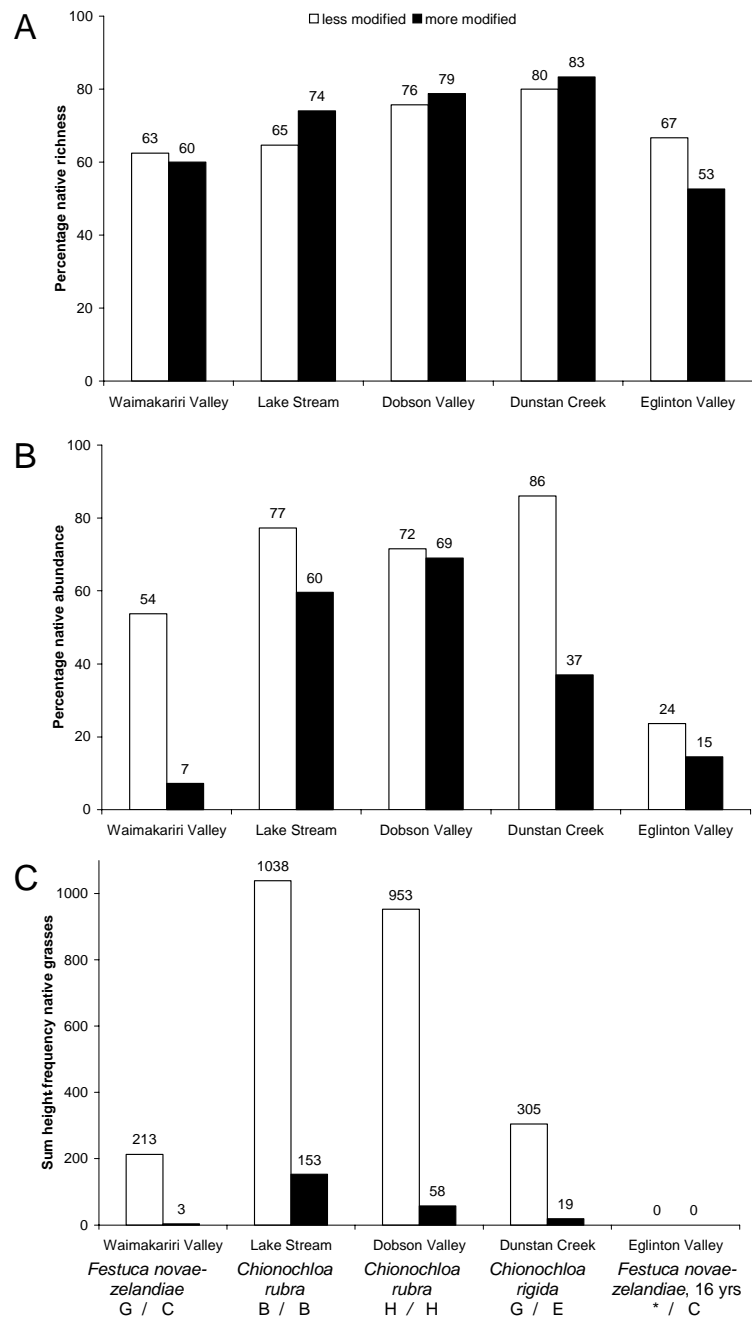


Figure 7. Effects of grazing in intermontane valleys and basins: percentage A, native richness; B, native abundance; and C, summed height-frequency native grasses in grazed vegetation. Measurements were taken in more- and less-modified vegetation on either side of fencelines at four sites, and over a 26-year sampling interval at the Eglinton Valley site. X-axis labels show dominant native tussock species and assigned plant communities (A-H) from the overall classification (* sample excluded from the classification).



5.7.2 Effects of grazing

We used four fenceline contrasts (Waimakariri, Lake Stream, Dobson and Dunstan Creek) and sequential records from one grazed sample adjacent to the enclosure in the Eglinton Valley as evidence for temporal changes with pastoral management. Since we collected quantitative height-frequency data at these fencelines, we were able to define modification in terms of relative native species biomass or abundance (i.e. percentage height-frequency score per sampling point), and successional stage of native vegetation (assuming the modification sequence is from shrub-tussockland to tall tussock to short tussock to exotic grasses and forbs; Treskonova 1991).

The height-frequency samples included five of the eight intermontane valley and basin plant communities (B, C, E, G and H: Tables 10 and 11) and covered

three of the eight catchment groups (III, IV and V; Table 11). The classification defined more- and less-modified grasslands beside fencelines in the Waimakariri and Dunstan Creek catchments as different communities, but identified communities on either side of fencelines within the same community, despite substantial physiognomic differences, in the Lake Stream and Dobson catchments (Table 10).

Native richness percentage was higher in more-modified vegetation in the Lake Stream catchment, but also higher in less-modified vegetation in the Eglinton Valley (Fig. 7A, Table 10). Native species richness percentages were very similar on both sides of the three remaining fencelines (Waimakariri, Dobson and Dunstan Creek). As might be expected, native biomass proportions and native grass biomass totals were higher in less-modified grasslands at all fencelines (Fig. 7B-C; Table 11).

6. Discussion and conclusions

6.1 PRESENT VEGETATION PATTERNS AND RELATIONSHIPS WITH ENVIRONMENTAL FACTORS

The intermontane valleys and basins of eastern South Island are diverse environments that span steep climatic gradients and encompass a variety of soils, parent materials and landform types. However, present vegetation patterns cannot be readily predicted from environmental factors: vegetation gradients were weakly correlated with climate, soil, parent material and landform, and vegetation types and catchment groups were distributed across the different environmental types identified in the environmental classification. We suggest that the weak relationship between current vegetation and environment is due to extensive changes in vegetation since the arrival of humans. The vegetation appears not to have reached a new equilibrium with the environment since that time. General relationships between present patterns of vegetation and the environment are probably also obscured by differences between the studied catchments in the type, timing and extent of the anthropogenic disturbances that have occurred, which have resulted in a complex array of seral states. Furthermore, the fact that most plant communities occur in many different types of environment suggests that there has been some homogenisation of the flora and vegetation. This homogenisation is probably a consequence of the elimination of late successional, fire- and grazing-sensitive species from these ecosystems, and the ingress of generalist exotic species.

Local soil hydrology and drainage was the best environmental predictor of present-day vegetation composition that we could identify. Native tussock species were sorted along this principal vegetation gradient in most of the surveyed intermontane valleys and basins. As a general rule, *Festuca novae-zelandiae* and *F. matthewsii* short tussock grasslands, and occasionally

Chionochloa rigida tall tussock grasslands, tended to dominate on better-drained landforms. *F. novae-zelandiae* was widely distributed, but tended to occur towards the lower, warmer and drier reaches of valleys, where it predominated on well-drained, older and less-fertile terraces. *F. matthewsii* short tussock grasslands were characteristic of both recent floodplains and older, more leached upper terraces in the moist upper reaches of intermontane valleys and basins, where frost inversions were most severe. The tall tussocks *Chionochloa rigida* (in Southland, Otago and southern Canterbury) and *Chionochloa flavescens* (in northern Canterbury and Marlborough) extended from adjacent hillslopes and colluvial landforms onto relatively stable terraces and fans near the heads of some catchments, but neither was common on alluvial landforms in intermontane valleys. However, grasslands dominated by the tall tussock *Chionochloa rubra* were widespread, and tended to dominate species-poor plant communities on poorly drained and low-lying landforms in the middle to lower reaches of intermontane valleys. The short tussock *Poa cita* occurred mainly on fertile, moderately well-drained recent landforms (e.g. floodplains and recent fans) in the lower reaches of valleys. It was often associated with highly-modified communities with high proportions of exotic grasses and forbs.

The second major vegetation gradient represents the extent of modification of the vegetation by pastoral use: native-species-rich plant communities that were physiognomically and numerically dominated by native plant species were replaced along this gradient by native-species-poor plant communities with a high proportion of exotic species. We suggest that modification has been caused by a combination of fire, grazing and browsing (especially by domestic sheep and cattle, and feral rabbits, hares, deer, goats and possums), and the invasion or deliberate introduction of exotic plants that are better adapted to mammalian grazing than New Zealand native species. Elevated soil fertility as a consequence of natural disturbances, topdressing with superphosphate fertilisers, and the redistribution of nutrients via animal dung and carcasses has probably favoured exotic species. Fire (and more recently, herbicides) has been used to clear successional shrublands and to reduce the density of tussock grasslands on alluvial valley floors to improve stock grazing access. Wetlands have been mechanically drained in many catchments, especially in the more accessible lower reaches of alluvial systems where the economic return on pasture development has been more favourable.

The vegetation in less accessible catchments showed a lower degree of pastoral modification and greater native species dominance, possibly because these experienced lower intensities of land use in the past. Many catchments may have been heavily grazed by sheep in the late 19th century only, although many subsequently carried high numbers of deer before control measures in the 1970s. The degree of pastoral modification was not strongly related to environment, which suggests that vegetation has been more-or-less equally susceptible to modification across the whole range of intermontane valley and basin environments sampled. Down-valley sampling sites experiencing higher summer maximum temperatures and lower rainfall:potential evapotranspiration ratios tended to be more modified and less native-dominated, but this may simply reflect the geographic proximity of the lower reaches of alluvial catchments to settlements and hence more intensive pastoral use. Accordingly,

down-valley gradients in modification were absent where stock were impounded over summer by steep surrounding topography, and grazing pressure was spread more-or-less evenly over the valley floor (e.g. the Siberia Valley in Otago).

The soil hydrology/landform and pastoral modification gradients closely resemble the climate/landform and pastoral modification gradients that were identified as principal or secondary sources of vegetation variation in southern New Zealand intermontane valleys and basins by Walker & Lee (2000), and in Canterbury and Marlborough intermontane valleys and basins by Walker & Lee (2002).

6.2 PREHUMAN VEGETATION PATTERNS, AND CHANGES FOLLOWING THE ARRIVAL OF HUMANS

Intermontane valleys and basins are one of the few non-forest ecosystems that existed below treeline in New Zealand in prehuman times, but all have been substantially modified by anthropogenic fire since Polynesian times, and by pastoral use in the last 150 years. Therefore, the conservation of indigenous biodiversity in intermontane valleys and basins must incorporate an understanding of the potential vegetation composition and pattern before modification so as to set appropriate goals for ecosystem recovery. We can predict these potential prehuman vegetation patterns in a broad sense, by considering natural ecological processes in intermontane valley and basin ecosystems, and by extrapolating from present species distributions and knowledge of their environmental tolerances and autecology.

Under prehuman disturbance regimes, intermontane valleys and basins would have supported vegetation at different stages of succession towards dominance by woody plants, which was controlled by the frequency of frosts, flooding, debris avalanches and other natural disturbances. Short tussock grasslands are likely to have been far less widespread than they are at present. We suggest that *Festuca matthewsii* would have been confined to areas of recent disturbance and younger landforms (e.g. floodplains) in the confined upper reaches of intermontane valleys, where rainfall is high, temperatures are relatively cool all year round, and frosts are most frequent and severe. Further down valley, as summer temperature maxima and evapotranspiration increased, short tussock grasslands of *Poa cita* probably replaced *F. matthewsii* as a dominant species on the most recent fertile floodplains and fans. The place of the more stress-tolerant *F. novae-zelandiae* in prehuman plant communities is more difficult to delineate. We suggest that it occurred locally in the warmer, drier, middle and lower reaches of intermontane valleys on recent gravel terraces and other landforms with thin, well-drained soils that were incapable of supporting taller woody vegetation.

More stable alluvial surfaces in intermontane valleys and basins would have previously supported later-successional communities in a sequence from tall tussock grasslands to tussock-shrubland mixtures, shrublands and finally low forest communities on the oldest, most elevated terraces and at forest margins. Evidence for these pre-existing communities in intermontane valleys and basins

is provided by isolated, and probably highly-modified stands of individual tall tussocks and shrubs in areas that are now almost exclusively occupied by short tussock grasslands. Remnant stands of gymnosperms such as *Halocarpus bidwillii* (bog pine), *Phyllocladus alpinus* (mountain toatoa) and *Podocarpus nivalis* in several catchments (e.g. in the Greenstone and Mararoa valleys of Otago and Southland, and in the Hope, Esk, Nigger, Poulter, Ahuriri and Mackenzie Outwash Plain catchments in Canterbury) are among the clearest indicators of the substantial physiognomic changes that have occurred. Elsewhere, evidence that short tussock grasslands are derived from taller plant communities is more sparse and cryptic (e.g. we counted four *C. rubra* tussocks in the Hunter Valley in Otago). We suggest that in cooler, higher-elevation valley-heads, *F. matthewsii* may have been replaced on landforms of increasing age by tall tussocks such as *Chionochloa flavescens* or *C. rigida*, and that frost-tolerant shrubs of *Brachyglottis*, *Coprosma*, *Dracophyllum*, *Gaultheria*, *Halocarpus*, *Hebe*, *Ozothamnus*, *Phyllocladus* and *Podocarpus* species increased in density and towards the lower limits of tall forest. Whipcord *Hebe* species (e.g. *H. armstrongii*, *H. bectorii*, *H. lycopodioides* and *H. propinqua*) may have been prominent in these woody communities. In the lower, drier reaches of valleys, the elevated terraces and fans that are occupied by *F. novae-zelandiae* grasslands today probably supported tall tussocks (*Chionochloa flavescens* or *C. rigida*), and woody species such as *Discaria toumatou* (matagouri), *Kunzea ericoides* (kānuka), *Leptospermum scoparium* (mānuka), *Aristotelia*, *Carmichaelia*, *Coprosma*, *Corokia*, *Halocarpus*, *Phyllocladus*, *Podocarpus*, *Hebe*, *Melicope*, *Melicytus*, *Myrsine*, *Olearia* and/or *Ozothamnus* species. Because many of these native woody species are both frost-tolerant and apparently capable of recolonising alluvial landforms following infrequent mechanical disturbances such as debris avalanching in the absence of grazing, we assume that their currently restricted distribution within intermontane valleys and basins is due to their limited ability to tolerate and recover from anthropogenic fire or grazing. We suggest that prehuman plant communities on permanently moist landforms (i.e. terrace and floodplain backswamps that occupy the extreme right of the hydrology/landform gradient in the present vegetation analysis) probably consisted of waterlogging-tolerant woody species such as *Halocarpus bidwillii* and *Leptospermum scoparium*, together with *Chionochloa rubra*, sedges and rushes.

The vegetation of intermontane valleys and basins underwent substantial changes with the deforestation of eastern South Island catchments by deliberate burning of native vegetation following the arrival of Polynesian people around 750 yr BP (e.g. McGlone & Basher 1995). Initially, woody communities were probably replaced by tall tussock grasslands and successional shrublands. However, with repeated fires and the introduction of mammalian herbivores by European pastoralists around 1850, short tussock grasslands expanded their range to occupy older, more stable surfaces that previously supported taller communities. We suggest that while the initial vegetation composition of intermontane valleys and basins (i.e. successional stage) would have varied according to landform age, disturbance frequency and climate, the overall sequence of anthropogenic changes that has occurred has been similar to those in non-alluvial ecosystems in eastern New Zealand (e.g. Rose 1983; Treskonova 1991). This trend involved the destruction of woody vegetation and spread of

tall tussock grassland, followed by a transition to short tussock grassland and, most recently, the conversion to grasslands dominated by exotic species with a high proportion of *Hieracium* species.

6.3 CURRENT TRENDS IN VEGETATION

Some information on more-recent changes in intermontane valleys and basins may be gained from the interpretation of fenceline contrasts. However, the usefulness of this approach is limited. Our sampling was limited to places where differences in management has led to obvious contrasts: fencelines were not sampled where there was no apparent contrast. Therefore, vegetation changes that have occurred on both sides of fencelines remain undetected. The precise causes of fenceline contrasts (e.g. management regimes) are not known, and modification is inferred indirectly from relative native species biomass and native vegetation successional stage. Moreover, our data were limited to a few fenceline sites representing a small fraction of intermontane valley and basin vegetation types.

Nevertheless, our data suggest that the loss of tussock structural dominance and the replacement of native species by exotic species may be continuing in intermontane valleys and basins. For example, in the Lake Stream, Dobson Valley and Dunstan Creek catchments, fencelines separate tall *Chionochloa rubra* or *C. rigida* on one side, from short-tussock-grassland physiognomy on the other (Fig. 7A-C). In the Waimakariri Valley, a fenceline separates grassland dominated by *F. novae-zelandiae* from a sward dominated by the exotic species *Festuca rubra*, *Agrostis capillaris* and *Anthoxanthum odoratum*, in which native tussocks such as *F. novae-zelandiae* are absent. In grazed vegetation in the Eglinton Valley, where the plant community was already highly modified and contained no native grasses when surveyed in 1974, the dominance of exotic species over native forbs increased in terms of richness and biomass over 26 years between sampling occasions (Walker & Lee 2000).

Other evidence for recent changes in vegetation composition is drawn from the exclosures sampled in this study. In the Caples Valley, the native *Poa colensoi* (blue tussock) was abundant within the stock-and-deer exclosure but was not recorded in the vegetation surrounding the exclosure, while in the Acheron Valley, native tussocks accounted for high proportions of vegetation cover within the Isolated Flat and Acheron 1 exclosures, but were entirely and almost absent, respectively, in grazed vegetation outside the fences. Since it is unlikely that native tussocks invaded these exclosures after the fences were erected, we conclude that native tussock cover has decreased outside the exclosures since the time that they were established (although exact establishment dates are unknown, the exclosures appear to be no older than three or four decades, in keeping with the time-span of most Forest Service exclosures).

Some induced tussock grassland communities show a tendency to revert to tall tussock and more woody vegetation where seed sources remain, and given freedom from fire. For example, size and age distributions in populations of *Halocarpus bidwillii* on alluvium in the Mararoa Valley and at Pukaki Downs on outwash plains in the Mackenzie district (S. Walker unpubl. data) suggest that it

is currently reinvading *Chionochloa rubra* grasslands. Tall tussocks of *C. rigida*, and shrubs of *Hebe propinqua*, *H. lycopodioides* and *H. odora* also appear to be spreading in *Festuca novae-zelandiae*—*Poa colensoi* short tussock grasslands in the Mararoa Valley in Southland, while *Ozotamnus leptophyllus*, *Kunzea ericoides* and a range of *Hebe* species appear to be invading *F. matthewsii* short tussock grasslands in the Esk and Nigger catchments in Canterbury. This suggests that there is some potential for the re-establishment of at least unpalatable woody species on alluvial landforms in intermontane valleys and basins, as long as fire is absent.

Taken together, our results suggest that the predominant trend in the vegetation of intermontane valleys and basins is from tall tussock to short tussock grasslands, and from short tussock to exotic-dominated grasslands. Unpalatable native shrub species are increasing in some locations, but this does not appear to be a widespread trend. The vegetation changes in intermontane valleys and basins appear to be recent consequences of mechanical damage to native tussocks and shrubs by grazing, browsing and trampling by feral and domestic herbivores, their replacement by exotic species better adapted to mammalian herbivory, lack of native species recruitment due to seed and seedling predation, competition with exotic species for resources by native propagules, and/or longer-term changes in soil nutrient and organic matter status.

6.4 POST-PASTORAL CHANGES IN VEGETATION

Presently, 28.4% of the surveyed intermontane valleys and basins described in this report lie within public conservation lands. Grazing licences have been terminated and stock have been excluded from some of the surveyed catchments in recent years (e.g. in the Hawdon and Poulter valleys in Canterbury, the Siberia and Dart valleys in Otago, and the Eglinton Valley in Southland). However, many of the remaining intermontane valleys and basins are presently either leased for grazing or lie adjacent to unfenced pastoral lands, so that pastoral use continues in effect.

Some indication of short-term changes that might be expected to follow the removal of grazing can be obtained from a comparison of vegetation samples inside and outside the existing long-term grazing exclosures located within eastern South Island intermontane valleys and basins. However, interpretation of these data is influenced by several considerations.

1. First, the ten exclosures represent a small proportion of the intermontane valleys and basins sampled in the survey. All were positioned in relatively modified vegetation types because the establishment of exclosures has been motivated in the past by a perception of adverse vegetation change. Therefore, results cannot be readily extrapolated to indicate potential consequences of grazing removal in less-modified vegetation types, e.g. more native-species-rich and native-dominated vegetation in intermontane valley heads.
2. Baseline data collected at the time of establishment were not available for most exclosures. Changes in the grazed controls over time mean that the

present species composition of grazed vegetation may not approximate that at the time of exclosure (e.g. Walker & Wilson 2002). Measured differences between ungrazed and grazed vegetation therefore represent results of alternative treatments applied at an undefined starting point, rather than post-pastoral change alone.

3. Dates of exclosure establishment are unknown in many cases, although the maximum age was estimated to be less than four decades. Our data therefore signify only short-term outcomes of grazing removal.
4. None of the exclosure sites presently includes, or is near to, populations of native woody plant species that might indicate potential for their re-establishment.
5. The percentage of native species richness was used as an index of vegetation modification to interpret landscape-scale vegetation gradients (i.e. in the vegetation ordination) where the extremes of intact and highly modified vegetation were represented. However, native species richness and native species richness percentages may actually increase, rather than decrease, with vegetation modification up to a certain point. This is because the abundance of small, shade-intolerant native intertussock species tends to increase following a reduction in the density and stature of taller and larger tussock and shrub species by fire, grazing or other disturbance. Native intertussock species may later be displaced by invading exotic species, so that native richness and native richness percentages decrease again. Native species richness and richness percentage are therefore unreliable and potentially misleading indices of vegetation condition where individual sampling sites at intermediate levels of modification are being compared. For example, in the Dobson, Lake Stream and Dunstan Creek catchments, tall tussock grasslands on one side of fencelines had lower native species richness and native species percentages than adjacent pasture where the tall tussocks had been completely removed. We suggest that native biomass percentage is a more robust index of vegetation modification (albeit more laborious to measure).

Half of the sampled exclosures contained native biomass percentages higher than in adjacent grazed vegetation. Four (40%) had higher native grass biomass than adjacent grazed vegetation. Environmental factors, and vegetation parameters such as native biomass and native species richness of grazed vegetation, were poor predictors of these vegetation differences between grazed and adjacent ungrazed vegetation. The absence of a consistent relationship is not unexpected, given that baseline data were not available, and that the exclosures represented a small portion of environments and vegetation types. Ecological lag effects, multiple grazers, diverse natural disturbances and unknown management practices have made it notoriously difficult to establish causal links between vegetation change and environment or management in New Zealand tussock grasslands (McKendry & O'Connor 1990). Our results suggest that the relationships between vegetation composition, modification, present herbivory and environment in intermontane valleys and basins are similarly complex to those in other tussock grassland systems. Therefore, even if monitoring data were to be gathered from a larger, more representative range of intermontane valley and basin ecosystems and vegetation types, under different known management regimes, and over periods of several decades, it is

likely that predictions of vegetation changes following the cessation of grazing in intermontane valleys and basins would still involve a high degree of uncertainty.

Intermontane valleys and basins are perceived to be particularly vulnerable to invasion by weeds, and there is concern that native species will be competitively extinguished by a proliferation of exotic species (especially grasses) if grazing animals are removed (Meurk et al. 1989; McKendry & O'Connor 1990; Widyatmoko & Norton 1997). Our study comprises a relatively modified selection of alluvial vegetation types, in which the biomass proportions of native species were low (< 50% in 80% of sampling sites), i.e. those that might be expected to be particularly prone to competitive exclusion of native species following the removal of grazing. However, the competitive exclusion of native species by exotic species was not a universal outcome of the cessation of grazing in these exclosures. Nevertheless, an increase in exotic grasses following the removal of grazing may be a particular threat to the persistence of certain rare shrubs (e.g. *Carmichaelia stevensonii*, *Hebe armstrongii*, *H. cupressioides*, *Helichrysum dimorphum* and *Olearia hectorii*) in eastern South Island intermontane valleys and basins (e.g. Widyatmoko & Norton 1997). However, shrub recruitment is also likely to be compromised by continued grazing if this is used as a tool to control exotic grass abundance. We therefore suggest that both herbivore exclusion and some other method of exotic grass control may be necessary to ensure the persistence of these species in intermontane valleys and basins.

The evidence of post-pastoral vegetation change assembled in this study addresses only short-term changes following the removal of grazing in highly-modified vegetation. Little research has to date been directed towards assessing the potential for long-term post-pastoral reinvasion of native woody plants, and the re-establishment of more natural woody vegetation compositions and ecosystem processes over a representative range of eastern South Island ecosystems. We suggest that such long-term successional trends, which will unfold over time scales from several decades to centuries, will be more relevant than short-term changes to the management of intermontane valleys and basins for biodiversity goals.

Nevertheless, we suggest some general principles that will apply to the short-term recovery of in situ native species.

1. Native species stature and density. For each set of environmental conditions encountered in intermontane valley and basins, and in each vegetation type, there may be a threshold of density and stature above which each particular native species is able to compete with exotic grass swards, and to recover to dominate the community in the years following grazing-exclosure, but below which short-term recovery is unlikely. For example, at Maryburn on the Mackenzie Outwash Plain, where *Festuca novae-zelandiae* and *Discaria toumatou* cover was relatively high at the time of exclosure (c. 12%, Walker & Lee 2000) native biomass increased relative to exotic species over 10 years following exclosure. In two nearby exclosures where native tussock and shrub cover was lower (c. 5% and 3% cover, respectively) native biomass was lower in ungrazed than in adjacent grazed vegetation after the first decade. Evidence from non-alluvial grasslands (e.g. Meurk et al. 2002) suggests that

taller native species (*Chionochloa rigida* and *C. rubra* and various shrub species) may be better equipped than short tussock species to compete successfully with exotic species and to increase where grazing disturbance is removed, although their reinvasion may be slow where they are sparse or have been largely eliminated. For example, in the Eglinton Valley, tussocks of *C. rubra* and *F. novae-zelandiae* were absent at the time of enclosure (1981), and had not invaded ungrazed vegetation after 26 years (Walker & Lee 2000).

2. Presence and vigour of exotic species. The rate of recovery of native tussock species will depend on the resident exotic species and on their competitive abilities, which will be influenced by the environmental characteristics of the site. Mild, high rainfall environments and high-fertility recent alluvial surfaces favour grasses such as *Festuca rubra* (chewings fescue) and *Dactylis glomerata* (cocksfoot), which form dense swards that may competitively exclude native short tussock species if individual tussocks are widely spaced. Summer-dry, cold or infertile environments are less susceptible to invasion by *F. rubra* and *D. glomerata*, but are capable of supporting the grasses *Agrostis capillaris* and *Anthoxanthum odoratum*, and the mat-forming herb *Hieractium pilosella*. The latter species may also slow the re-establishment of native species, especially if they account for high proportions of the cover at the time that grazing is removed.

6.5 MANAGEMENT FOR POST-PASTORAL SUCCESSION

We can predict the prehuman natural vegetation compositions of intermontane valleys and basins in the broadest sense. We suggest that conservation management goals should be similarly broad and non-specific. A primary goal should 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 tussock grassland on more recent landforms. This goal recognises that the trajectories of post-pastoral change that will unfold are uncertain. However, it envisages that an increase in the biomass and dominance of native woody vegetation will provide a more competitive native vegetation physiognomy that is better able to suppress and/or resist invasion by shade-intolerant exotic species. Moreover, a higher proportion of taller, late-successional vegetation will restore some of the former species diversity of intermontane valley and basins, and reinstate more-natural vegetation sequences that link hillside forests with herbaceous communities on the most recent landforms on valley floors. Woody plant communities will have other roles in ecosystem processes, including stabilisation of recent landforms, nitrogen-fixation (e.g. by *Discaria toumatou*), provision of food and habitat for native birds and invertebrate fauna, and shelter and nurse communities for rarer native woody species, e.g. *Carmichaelia kirkii*, *Hebe cupressioides* and *Helicbrysum dimorphum*.

It seems likely that intermontane valley and basin vegetation that is presently dominated by tall native tussock and/or shrub species will retain native dominance following the removal of grazing and the control of feral herbivores. The greatest potential for recovery towards more natural vegetation patterns

incorporating taller, late-successional native woody vegetation exists where woody plant seed sources remain. For example, there is evidence that *Halocarpus bidwillii* (bog pine), *Hebe odora*, and *H. propinqua* may spread from residual populations in some circumstances given freedom from grazing, and *Kunzea ericoides* (kānuka) regeneration is occurring on alluvial terraces in the upper Clutha Valley (S. Walker unpubl. data). Elsewhere, management intervention may be required to reintroduce and re-establish native woody plants where their seed sources have been reduced or removed. Native biodiversity gains are likely to be most difficult to achieve where native biomass is lowest and exotic species are most vigorous. Here, both the continuation of grazing and the removal of grazing may have negative effects on native biodiversity in the short term, and it may be more feasible to encourage long-term succession to native woody vegetation without the community passing through an intervening, successional short- or tall-tussock-grassland stage where tussocks are now sparse or absent. Selective control of woody weeds, e.g. *Rosa rubiginosa* (sweet briar), *Ulex europeaus* (gorse) and *Cytisus scoparius* (broom) may be necessary in some circumstances.

We know of no evidence to show that the manipulation of domestic stocking rates will achieve sustainable outcomes compatible with suggested conservation goals for intermontane valleys and basins. The idea that there exists some appropriate, low stocking rate that, under particular combinations of environment and vegetation composition, will arrest a further decline in native biodiversity and reduce competition from exotic species (McKendry & O'Connor 1990) is unlikely to be appropriate or practicable for intermontane valleys and basins within public conservation lands. Even if theoretically appropriate grazing intensity thresholds could be defined, vegetation variation from landform to landform within the catchment, natural disturbances, inter-annual variability in climate, the idiosyncratic behaviour of stock, and the presence of fluctuating populations of feral herbivores would ensure that native plant species would be disadvantaged. Moreover, grazing would continue to introduce and transport the propagules of exotic species into and within intermontane valleys and basins, and maintain relatively short, open, disturbed canopies that are more prone to weed invasion (including *Hieracium* species; Rose & Frampton 1999). It will also slow or prevent the recruitment and recovery of taller successional vegetation that might ultimately overtop such exotic species.

6.6 REPRESENTATION IN PUBLIC CONSERVATION LANDS

In many catchments, native forested conservation land borders grazed alluvial valley floors under different tenure (e.g. in the Waterloo, Greenstone, Dart, Hope, Ahuriri, Hopkins, Dobson, Clyde, Lawrence, Hope, Kiwi Stream, Doubtful, Rainbow and Coldwater valleys). This pattern of land tenure reflects the relatively high pastoral value of intermontane valleys and basins, and their allocation to non-conservation land uses. As a result, natural ecosystem linkages and processes across the sequence from hillslope to riverbed have been truncated and modified. The imbalance in the protection of alluvial parts of the

landscape is particularly striking in the Nelson/Marlborough Conservancy, where virtually none of the intermontane valleys and basins that we sampled fall within public conservation lands (Table 3).

The range of environments covered by eastern South Island alluvial systems is only partially represented (Table 4): most intermontane valleys and basins within public conservation lands are close to the Main Divide of the Southern Alps, and experience high rainfall (i.e. environmental types V, VI, VIII). Few of the catchments further east of the Southern Alps, which experience low rainfall (i.e. environmental types I and VI) are included in public conservation lands.

Intermontane valley and basin plant communities and catchment types identified in the present survey are also unequally represented within public conservation lands (Tables 5 and 8 of this report). The most native-dominated plant community identified in this study (native-species-rich *F. novae-zelandiae* grassland; Community A) is the most poorly represented vegetation type; it occurs in both of the environmental types (I and VI) that are most severely underrepresented in public conservation lands. Distinctive catchment groups (E, F, G and H, which comprise five valleys that lie well to the east of the main axial ranges) are also poorly represented.

7. Recommendations

Rather than offering specific mechanisms for management, our recommendations consist of a series of principles that should guide policy formulation.

We recommend that a conservation strategy be developed, specific to intermontane basins and valleys, which aims to protect and manage a full range of environments classified by this study. The areal extent of the protected environment should be increased across all environmental types. However, priority should be given to protecting the more markedly rainshadow environments (environmental types I, VI and IV), which are the least well represented in public conservation lands.

Representation of a greater range of environments, rather than present vegetation types, should be the principal goal of a conservation strategy. Within priority environments, however, catchments with greater potential for the recovery of a variety of native vegetation types should have precedence. Longer catchments tend to contain a wider range of environments and landform types than shorter catchments and hence greater potential for recovery. We have little precise information on resilience; as a general rule, priority should be accorded to the most natural communities.

Whole-catchment ecosystem processes, rather than particular places within a catchment, should be the focus of a conservation strategy. Almost all ecosystem processes of mountain valleys have a downslope component. Consequently, conservation strategies for the valley floors in isolation from catchment slopes will have greater risk of unpredictable outcomes. We recommend that conservation strategies should be formulated for whole catchments, and

especially those highly distinctive catchments in rainshadow environments that are poorly represented in conservation lands (e.g. the Clarence Valley in Marlborough, and the Nevis, Dunstan Creek, and Upper Manuherikia valleys in Otago).

In the absence of a clearer understanding of likely successional trajectories, we can only recommend that goals be set around an increase in native biomass and stature, rather than focusing on the maintenance of the present vegetation states, which are highly modified. Restoration of a greater woody component of the native vegetation should be a priority, as are trends toward recreating the original patterns of the inverted treeline and shrubland communities that were determined by cold-air-inversion, edaphic factors, and flooding disturbance; fire is likely to have been, at most, a very infrequent regulatory factor in prehuman times. Continued pastoral use would, at best, only maintain the present modified vegetation patterns and plant communities, and so is incompatible with these goals.

To redress our knowledge deficit of the full woody potential of these valleys, we recommend that studies of woody successions be commenced. One starting point would be to examine the demography of shrub species within woody successions that are already underway in relation to landscape patterns. The programme could also investigate techniques to enhance recruitment of native woody species in dense exotic grass swards, and to accelerate native woody successions. Experimental treatments might include species introductions, seed and seedling trials, herbicides, mulch, and/or fertiliser applications. Further knowledge on the successional potential of valleys is likely from the long-term monitoring (c. 10-year intervals) of exclosure plots where full destocking and feral herbivore control is not feasible.

We are still some way from an understanding of the prehuman vegetation of these valleys. We recommend greater attention by landscape historians to these highly distinctive systems to further guide goal setting for conservation.

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9. References

- Allan, H.H. 1961: Flora of New Zealand. Vol. I. Government Printer, Wellington.
- Clifford, H.T.; Stephenson, W. 1975: An introduction to numerical classification. Academic Press, New York.
- Connor, H.E.; Edgar, E. 1987: Name changes in the indigenous New Zealand Flora 1960–1981 and Nomina Nova IV, 1983–1986. *New Zealand Journal of Botany* 25:115–170.
- Dansereau, P. 1964: Six problems in the New Zealand vegetation. *Bulletin of the Torrey Botanical Club* 91: 114–140.
- Dickinson, K.J.M.; Mark, A.F.; Lee, W.G. 1992: Long-term monitoring of non-forest communities for biological conservation. *New Zealand Journal of Botany* 30: 163–179.
- Duncan, R.P.; Webster, R.J.; Jensen, C.A. 2001: Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. *New Zealand Journal of Ecology* 25: 35–47.
- Edgar, E.; Connor, H.E. 2000: Flora of New Zealand. Vol. V. Manaaki Whenua Press, Lincoln.
- Environmental Systems Research Institute 2000. ArcView GIS: The Geographic Information System for everyone. Environmental Systems Research Institute, Redlands, California, United States.
- Goodall, H.G. 1954: Objective methods for the classification of vegetation. III. An essay on the use of factor analysis. *Australian Journal of Botany* 2: 304–324.
- Greig-Smith, P. 1983: Quantitative plant ecology. 3rd Edition. Blackwell Scientific Publications, Oxford.
- Hill, M.O.; Gauch, H.G. 1980: Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Leathwick, J.R.; Stephens, R.T.T. 1998: Climate surfaces for New Zealand. Landcare Research Contract Report LC9798/126 (unpublished). Landcare Research, Lincoln.
- Leathwick, J.R.; Burns, B.R.; Clarkson, B.D. 1998: Environmental correlates of tree alpha-diversity in New Zealand's primary forests. *Ecography* 21: 235–246.
- Lee, W.G. 1981: Botanical report on vegetation exclosures in the Eglinton Valley, Fiordland National Park. Unpublished report, Botany Division, DSIR, Dunedin, held at Landcare Research library, Lincoln.
- Lee, W.G. 1998: The vegetation of New Zealand—functional, spatial and temporal gaps. In: Ecosystems, entomology and plants. *The Royal Society of New Zealand Miscellaneous Series* 48: 91–101.
- McGlone, M.S.; Basher, L.R. 1995: The deforestation of the upper Awatere catchment, Inland Kaikoura Range, Marlborough, South Island, New Zealand. *New Zealand Journal of Ecology* 19: 53–66.
- McGlone, M.S.; Moar, N.T. 1998: Dry Holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. *New Zealand Journal of Botany* 31: 91–111.
- McKendry, P.J.; O'Connor, K.F. 1990: The ecology of tussock grasslands for production and protection. Unpublished report for the Department of Conservation. Centre for Resource Management, Lincoln University, New Zealand.
- Mark, A.F. 1992: Indigenous grasslands of New Zealand. Pp. 361–410 in Coupland, R.T. (Ed.): Ecosystems of the world, 8B. Natural grasslands-Eastern Hemisphere. Elsevier, Amsterdam.
- MathSoft Inc. 1999: S-PLUS. Version 2000. Seattle, Washington, United States.
- Means, J.E.; Harris, R.R.; Sabin, T.E.; McCain, C.N. 1996: Spatial variation in productivity of Douglas-fir stands on a valley floor in the western Cascades Range, Oregon. *Northwest Science* 70: 201–212.

- Meurk, C.D.; Norton, D.A.; Lord, J.M. 1989: The effects of grazing and its removal from grassland reserves in Canterbury. Pp. 72–75 in Norton, D.A. (Ed.): Management of New Zealand's natural estate. New Zealand Ecological Society Occasional Publication No. 1. New Zealand Ecological Society, Christchurch.
- Meurk, C.D.; Walker, S.; Gibson R.S.; Espie P.R. 2002: Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990–2000. *New Zealand Journal of Ecology* 26: 95–103.
- Moore, L.B.; Edgar, E. 1970: Flora of New Zealand. Vol. II. Government Printer, Wellington.
- O'Connor, K.F. 1982: The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology* 5: 97–107.
- Peres, C.A. 1997: Primate community structure at twenty Western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 13: 381–405.
- Planty-Tabbacchi, A.; Tabbacchi, E.; Naiman, R.J.; Defarri, C.; Decamps, H. 1996: Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10: 598–607.
- Rejmánek, M. 1999: Invasive plant species and invulnerable ecosystems. Pp. 79–102 in Sandlund, O.T.; Schei, P.J.; Viken A. (Eds): Invasive species and biodiversity management. Kluwer Academic Publishers, The Netherlands.
- Rose, A.B. 1983: Succession in fescue tussock (*Festuca novae-zelandiae*) grasslands of the Harper-Avoa catchment, Canterbury, New Zealand. *Forestry Research Institute Bulletin* 16.
- Rose, A.B.; Frampton, C.M. 1999: Effects of microsite characteristics on *Hieracium* seedling establishment in tall- and short-tussock grasslands, Marlborough, New Zealand. *New Zealand Journal of Botany* 37: 107–118.
- Rose, A.B.; Platt, K.H.; Frampton, C.M. 1995: Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* 19: 163–174.
- Scott, D. 1965: A height-frequency method for sampling tussock and shrub vegetation. *New Zealand Journal of Botany* 3: 253–260.
- Snedecor, G.W.; Cochran, W.G. 1980: Statistical methods. 7th Edition. Iowa University Press, Ames, Iowa, United States.
- Stace, C.A. 1991: New flora of the British Isles. Cambridge University Press, Cambridge, United Kingdom.
- Treskonova, M. 1991: Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie country, New Zealand. *New Zealand Journal of Ecology* 15: 65–78.
- Walker, S.; Lee, W.G. 2000: Alluvial grasslands in south-eastern New Zealand: vegetation patterns, long-term and post-pastoral change. *Journal of the Royal Society of New Zealand* 30: 69–103.
- Walker, S.; Lee, W.G. 2002: Alluvial grasslands of Canterbury and Marlborough, eastern South Island, New Zealand: vegetation patterns and long-term change. *Journal of the Royal Society of New Zealand* 32: 113–147.
- Walker, S.; Wilson, J.B. 2002: Tests for nonequilibrium, instability, and stabilizing processes in semiarid plant communities. *Ecology* 83: 809–822.
- Wardle, P. 1985: Environmental influences on the vegetation of New Zealand. *New Zealand Journal of Botany* 23: 773–788.
- Wardle, P. 1991: The vegetation of New Zealand. Cambridge University Press, Cambridge, United Kingdom.
- Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988: Flora of New Zealand. Volume IV. Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand.
- Widyatmoko, D.; Norton, D.A. 1997: Conservation of the threatened shrub *Hebe cupressoides* (Scrophulariaceae), eastern South Island, New Zealand. *Biological Conservation* 82: 193–201.
- Wilson, J.B. 1975: Teddybear—a statistical system. *New Zealand Statistician* 10: 36–42.