Ecology and conservation status of three "spring annual" herbs in dryland ecosystems of New Zealand

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Abstract The biological and ecological significance of the "spring annual" life-history strategy in the New Zealand flora is examined for *Myosurus minimus* subsp. *novae-zelandiae* (Ranunculaceae), *Ceratocephala pungens* (Ranunculaceae), and *Myosotis pygmaea* var. *minutiflora* (Boraginaceae) in terms of their biogeographies, habitats, population sizes, seed morphologies, plant communities, and relationships with co-occurring exotic taxa. All three have predominantly eastern South Island and lower North Island distributions, two have contracted modern ranges, and all extant populations are centred on Central Otago. The ephemeral wetland habitat of *Myosurus*, the "desert" pavement habitat of *Ceratocephala*, and the turf and gravel habitat surrounding water bodies of *Myosotis* all share a strong summer soil-moisture deficit. These genuine non-forest habitats are compared with farming-induced scabweed or mat vegetation on dry hillslopes as additional facultative habitat for all three taxa. Selection for this growth strategy probably accompanied mountain building in the mid to late Cenozoic with the creation of seasonally dry eastern climates. Small numbers of sites, small population sizes, and habitat vulnerability to weeds and land conversion result in a conservation status of "threatened" for all three taxa. The problem of nesting conservation goals and management strategies for spring annual habitat within the restoration goals for their surrounding, degraded dryland ecosystems is highlighted.

INTRODUCTION

Xeromorphic anatomical features appear in many groups of vascular plants adapted to the seasonally dry environments of eastern New Zealand (e.g., *Carmichaelia**, Wagstaff et al. 1999). However, therophytes (Raunkiaer 1934) or annual species, which complete a life history from seed to seed during a favourable season of the year, are rare in the New Zealand flora (Lloyd 1985; Lee 1995). Within New Zealand's annual plants we categorise just four taxa as "spring annuals" by virtue of possessing an annual life cycle in response to summer soil moisture deficits. *Myosurus minimus* subsp. *novae-zelandiae* (Ranunculaceae) (Garnock-Jones 1986) (hereafter referred to as *Myosurus*), *Ceratocephala pungens* (Ranunculaceae) (Garnock-Jones 1984) (hereafter referred to as *Ceratocephala*), *Myosotis pygmaea* var. *minutiflora* (Boraginaceae),

*Nomenclature of plants follows Allan (1961), Connor & Edgar (1987), Edgar & Connor (2000), and Webb et al. (1988).

and *Crassula tetramera* (Crassulaceae) commence their life cycle by germinating in winter or early spring, flowering and fruiting in spring, and shrivelling and dying in early or mid summer. All four plants are short-statured or prostrate forbs, typically less than 30 mm diam., and of cryptic coloration and texture. Walker (1994) suggested that they occupied local areas of periodically dry saline or shallow soils in Central Otago, which were unable to support taller vegetation. She reported their decline over four years following removal of sheep (*Ovis aries*) and rabbits (*Oryctolagus cuniculus*) from a small number of xeric sites in "induced" habitat that were previously heavily grazed (Walker 2000).

Soil moisture deficits are a predictable seasonal event in eastern South Island's semi-arid environment as well as on many unconsolidated and excessively well-drained soils in slightly more humid districts. There are other strict therophytes in the vascular flora, for instance, *Sebaea ovata*, *Atriplex hollowayi*, and *Euchiton sphaerica*, but they are not classed as spring annuals because their growing season extends from spring to autumn. Others are annuals, but not strictly so, because they may also exist as short-lived perennials, such as *Stellaria decipiens*, *Polygonum salicifolium*, *Drosera pygmaea*, and some of the herbaceous fireweeds (*Senecio* spp.). Numerous other taxa are geophytes or hemicryptophytes, flushing in the warmer seasons of spring to autumn and existing as rhizomes or corms in winter. Some examples are the ferns *Phylloglossum drummondii*, *Hypolepis millefolium*, *Ophioglossum* spp., and *Anogramma leptophylla*, the orchids *Thelymitra* and *Pterostylis* spp., the sedge *Carex coriacea*, the monocotyledonous herbs *Iphigenia novae-zelandiae*, *Hypoxis* cf. *hookeri*, and *Bulbinella* spp., and the dicotyledonous herbs *Drosera auriculata*, *D. binata*, *Gentiana* spp., *Craspedia* spp., *Hypericum* spp., *Gnaphalium luteo-album* var. *compactum*, and *Potentilla anserinoides*. The limited presence of annualism in New Zealand's temperate and semi-arid environments contrasts with its prominence in the floras of arid or desert environments (van Rooyan 1999).

Our study adopted a comparative ecological approach, examining differences in biogeography, habitat, population size, seed biology, community composition, and relationships with co-occurring exotic plants to elucidate the adaptive significance of the spring-annual life strategy in a New Zealand context. From that basis we try to explain each plant's ecosystem and geographic rarity. We restrict our study to *Myosurus*, *Ceratocephala*, and *Myosotis pygmaea* var. *minutiflora*, but exclude *Crassula tetramera* from the group because there is doubt whether it is taxonomically distinct from *C. sieberiana* (C. Ogle pers. comm.) and it is of less conservation concern than the others.

BACKGROUND INFORMATION

Taxonomy and relationships

Myosurus is a cosmopolitan genus, with the New Zealand subspecies distinguished from North American, Australian, and South African *Myosurus minimus* in overall plant size, and features of the scape, receptacle, and achene beak (Garnock-Jones 1986). Garnock-Jones (1986) suggested that *M. patagonicus* of South America is likely to be part of the *M. minimus* complex. Periodically inundated vernal pools are likely to be the habitat for most *Myosurus* taxa (Stone 1959).

Ceratocephala is otherwise a North African and Eurasian genus, with the New Zealand species, *C. pungens*, representing an extremely unusual disjunction from the two widely sympatric Northern Hemisphere species (Garnock-Jones 1984). Although it was previously thought of as naturalised, Garnock-Jones (1984) recognised it as native.

Myosotis is a diverse genus in New Zealand, with 57 taxa recognised by Druce (1993), including 24 which remain undescribed and of uncertain taxonomic status. Allan (1961) listed four varieties within *Myosotis pygmaea* sens. lat. *M. pygmaea* var. *minutiflora* (hereafter referred to as *Myosotis*) is distinguished from the other varieties by minute flowers (0.5–1.0 mm diam.; Simpson & Thomson 1943; Allan 1961), linear oblong and spathulate leaves, and long, shaggy, and spreading hairs. In coastal situations, but less so inland, it has two colour morphs, green and bronze forms, although a green to bronze transition seems to be related to plant maturity. The three other *M. pygmaea* varieties covered by Allan (1961) are *pygmaea*, *glauca*, and *drucei*. A fifth taxon allied to the complex was recognised by Druce (1993), and tag-named *Myosotis* "Volcanic Plateau". It was referred to as *M.* aff. *pygmaea* (CHR 244566) by de Lange et al. (1999). The *Myosotis pygmaea* complex is likely to be the subject of further taxonomic investigation, not least because local races seem to form within

the *M. pygmaea* var. *minutiflora* taxon and *M. pygmaea* var. *drucei* inconsistently has flowers of the distinguishing diameter of *M. pygmaea* var. *minutiflora* (A. Robertson pers. comm.; GMR pers. obs.).

METHODS

Field reconnaissance

We collated herbarium records of spring annuals from WELT, CHR, and OTA and other accounts (e.g., Protected Natural Area Programme reports) as a basis for investigating the present wild status of spring annuals in Southland, Otago, south Canterbury, and throughout the North Island. Where sufficient geographic details were provided, most locations of historical records were visited between 1998 and 2000, and additional surveys were undertaken in likely habitats in the vicinity. Accurate detection was laborious and slow due to the small size, cryptic appearance, and similarities of the study plants with some exotic species common in these habitats: *Myosotis discolor* and *Cerastium fontanum* resemble *Myosotis*, whereas *Aphanes arvense* resembles *Ceratocephala*.

Field sampling

We sampled vegetation within one or more 500 × 500 mm quadrats at sites which were selected on the basis of the presence of one or more of the three spring annual species. Cover of each vascular plant and lichen and cover of litter, soil, and rock was estimated in six cover-classes (1, <1%; 2, 1–5%; 3, 6–10%; 4, 11–25%; 5, 26–50%; 6, >50%). In addition, estimates of combined cover of all vascular plants, and of all non-vascular plants, were made to the nearest 5%. To collect community information at a smaller spatial scale, and to allow preliminary analysis of spatial interactions within the community, we repeated the vegetation sampling procedure within each of 25 subquadrats (100 × 100 mm) within each of the 56 (500 × 500 mm) quadrats. In each subquadrat, the number of *Ceratocephala* and *Myosotis* plants were recorded, but the densely aggregated pattern of *Myosurus* prevented counting them individually.

To describe and compare the environmental requirements of the three spring annuals, we recorded elevation, slope, aspect, and topographic position at each quadrat. Topographic position was described using the nine-unit land-surface model of Dalrymple et al. (1968). Aspect was converted to degrees north and degrees east, i.e., the "northness" and "eastness" of the aspect. Information on geological parent material and soil class was gathered for each quadrat from the Land Cover Database (Terralink International). In Central Otago, where the ranges and habitats of the three species overlap, we also sampled and analysed soil properties at 21 quadrats in order to better distinguish the habitat preferences of the species. For each soil sample, 10 topsoil cores (25 mm diam., 100 mm deep) were collected randomly over an area of 2 m × 1 m centred on the quadrat. The cores were bulked and chemical analysis of pH, electrical conductivity, cation exchange capacity (CEC), base saturation, Ca, Mg, K, Na, and exchangeable Na percent were undertaken following the methods of Blakemore et al. (1987).

We began fieldwork in spring 1998, and recorded vegetation in 15 quadrats at 10 sites. We surveyed vegetation in 22 quadrats at 13 sites in 1999, and in 54 quadrats at 23 sites in spring 2000 (sites were added as more spring annual locations became known to us). At each known site, sampling was repeated annually in subsequent years at the same position (with the exception of two sites, which were not sampled for logistic reasons in 2000). In total, 56 quadrats were sampled at least once at a total of 23 sites. All data are held in the Landcare Research NIVS database.

Data analysis

Spring annual plant communities

Multivariate analyses were used to examine the occurrence of spring annuals in vegetation types and along environmental gradients within the 56-quadrat dataset. Species composition was averaged over repeated samplings of each of the 56 quadrats. Classification of species composition was carried out by cluster analysis (city-block difference measure, flexible sorting strategy, ß = −0.25; Clifford & Stevenson 1975), which was terminated at the arbitrary eight-group level. We used paired *t*-tests with unequal replication to compare environment and species composition at each of the first seven divisions of the quadrat classification. Detrended correspondence analysis (DCA) ordination (Hill & Gauch 1980) was used to identify the major vegetation gradients in species composition. We then used simple regression to examine the relationships of the first two ordination gradients with environmental factors.

Relationships with environment and other species

The 56 quadrats were sorted according to the presence or absence of each of the three target spring annual species on at least one sampling date. Environmental characteristics of quadrats with and without each spring annual in Central Otago (i.e., where all three species may potentially occupy any site) were compared using *t*-tests with unequal replication. We also calculated average environmental characteristics for quadrats that contained *Myosotis pygmaea* var. *minutiflora* separately for the northern South Island and the North Island populations. Species commonly or seldom associated with each spring annual were identified by repeating the *t*-tests, this time using the cover of each common vascular plant species (average cover > 1%) as the independent variate, and seeking evidence for a significant difference in cover between sites with and without the spring annual. We used the Bonferroni correction for multiple tests.

Small-scale spatial relationships

We tested for spatial clumping in the cover and number of spring annuals at the 100×100 mm scale across the 25 subquadrats within each of the 56 quadrats. Moran's index of spatial autocorrelation ("I"; Cliff & Ord 1981) was computed for each quadrat and tested for significance using the same index calculated for 2000 random distributions of cover and number among the subquadrats. We used spatial regression models (i.e., using a spatial weights matrix to account for spatial autocorrelation) to look for significant relationships between the cover and number of spring annuals and the cover of bare soil, all vascular species, and exotic grasses in the 25 subquadrats of each quadrat. Dependence of spring annuals on the availability of bare ground would be indicated by positive correlation between spring annuals and bare soil. Competition for sites at the 100×100 mm scale would be indicated by a negative correlation between spring annuals and the cover of other plants. Again, *P* values were corrected for multiple tests by the Bonferroni methods.

RESULTS

Distribution of spring annuals

In this section we provide descriptions of historical and modern distribution patterns. A comparison between modern and historical records can be used as a measure of distributional trends only with caution (Fig. 1). The precision of site collection notes on herbarium specimens is uneven and many early collections are too imprecise to map at our scale. Modern records include those verified in the field during the present study, supplemented with vouchered records collected since the arbitrarily selected cut-off year 1985 but not searched for in the present study. Three historical records of *Myosurus* in Marlborough with geographic information on the herbarium labels useful for relocation were not revisited, thus constraining a complete appraisal of present status of all three taxa.

Myosurus

Myosurus extends from the eastern shores of Lake Manapouri through eastern South Island to Cape Palliser in southern North Island (Garnock-Jones 1986). It is concentrated in Otago, with scattered sites in Southland, Canterbury, Marlborough, and Wellington-Wairarapa. William Colenso recorded the taxon from Cape Palliser (Hooker 1852–55) and, likewise, Buchanan (1874) from Ocean Beach, Island Bay, Wellington. Ogle (1985) provided plausible support for a 19th century record by William Colenso from near Cape Kidnappers, Hawke's Bay (WELT 2525). Ogle (1985) and Garnock-Jones (1986) reported few recent vouchers from the larger herbaria.

We located 22 extant populations of *Myosurus* (Fig. 1A), two in the Mackenzie Basin, Canterbury, and the remainder in Otago (Fig. 1B). In eastern Otago, there are five records from Macraes Ecological District (McEwen 1987) (G. Loh pers. comm.) and the remainder are from the Alexandra Basin and lower Manuherikia Valley (5), Flat Top Hill (formerly Bald Hill Flat) (2), the lower slopes of the Old Man Range (2), the Dunstan Mountains (2), Rough Ridge (1), the Maniototo Plain (2), and Arrowtown (1) (Fig. 1B). Historical records with vague locations from Otago include Carrick, Raggedy, Dunstan, and Cairnmuir uplands; Arrowtown; upper Waitaki valley; Ida valley; and Maniototo Plain.

Outside of Otago, there are just two modern records of *Myosurus*, from Maryburn Station in the Mackenzie Basin (CHR 496437; C. D. Meurk pers. comm.). The next most recent record from Canterbury is from 1972 from Killinchy near Lake Ellesmere (not surveyed). Prior to this there are Canterbury records from the 1950s, 1940s, 1920s, and late 19th century, but because of vague location notes none of these was followed up on the ground. Site labels include upper Waitaki Plains, Lake
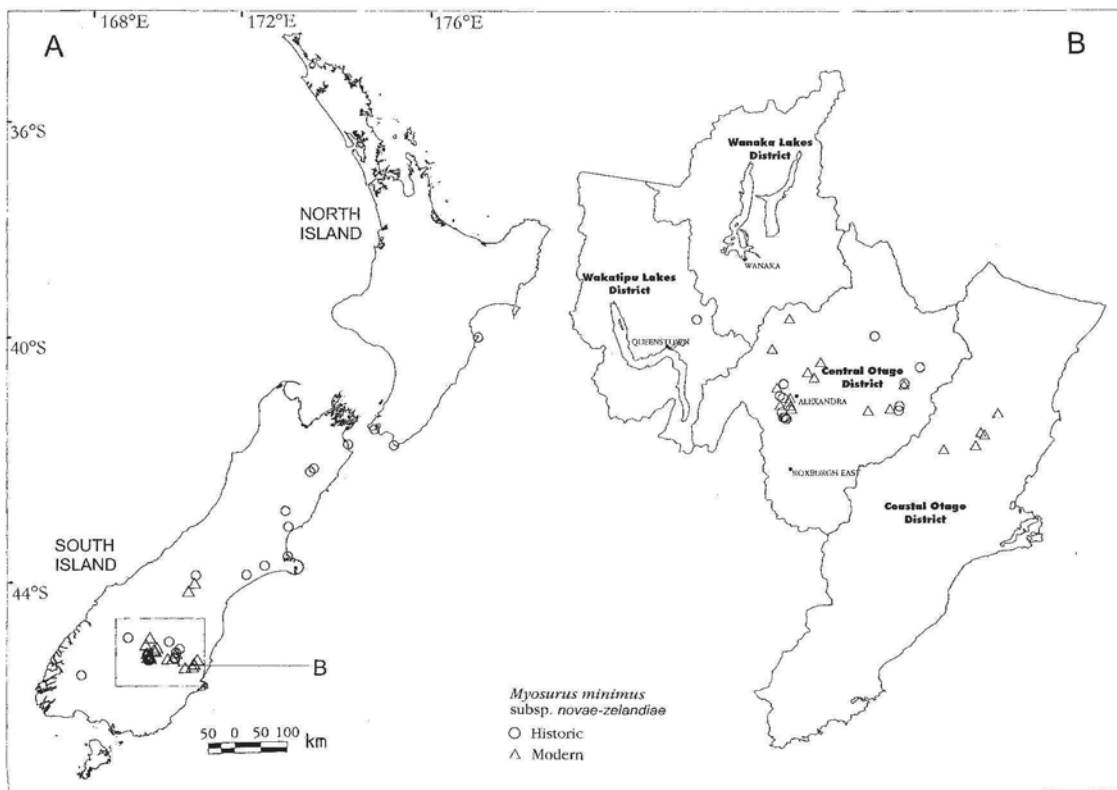
Fig. 1 **A**, Historic and modern distribution of *Myosurus nininus* subsp. *novae-zelandiae* in New Zealand; **B**, Historic and modern distribution in three Otago districts.

Tekapo, Balmoral township and forest, Waipara River near the township, Ashburton River, and Port Hills at Sumner, Banks Peninsula. Three records from the 1940s from Marlborough were also not investigated: two in the upper Awatere valley from Muller and Molesworth Stations and one from the mouth of the Awatere River in the Wither Hills.

Recent detailed searches of the shorelines of Lakes Manapouri and Te Anau failed to rediscover a 1945 record of *Myosurus* from Lake Manapouri (Bennett & Whitehead 1999, 2000). The Island Bay, Cape Palliser, and Cape Kidnapper coasts of the southern and eastern North Island have been thoroughly botanised since the 1950s (A. P. Druce pers. comm.), without success in relocating the Buchanan (1874) or the Colenso 19th century (WELT 22353) records.

Ceratocephala

Garnock-Jones (1984) showed records of *Ceratocephala* at seven sites in Central Otago and the Mackenzie Basin. He noted that there were no vouchered records since 1954, and suggested that this may be because survey of its dry hill-slope habitat in spring is uncommon.

Central Otago holds the six known populations of *Ceratocephala* (Fig. 2), and most have 1–10 individuals. The exception is one Flat Top Hill population comprising 50–70 plants in each of the last two growing seasons. The total population in 2000 was estimated at 83 plants. All populations cover less than 1.0 m^2 in area. The sites are clustered around Alexandra and the Cromwell Gorge of the Clutha River. The extant distribution is similar to the vouchered record (Fig. 2A), except for the three historical collections from the southern Mackenzie Basin (CHR 90270, CHR 48142), which were too imprecise to warrant field investigation.

Myosotis

Allan (1961) recorded *Myosotis* from Wellington's west coast in the North Island and in the South Island at Waimakariri Glacier, Lake Lyndon (Porters Pass), and in Central Otago. Simpson & Thomson (1943)
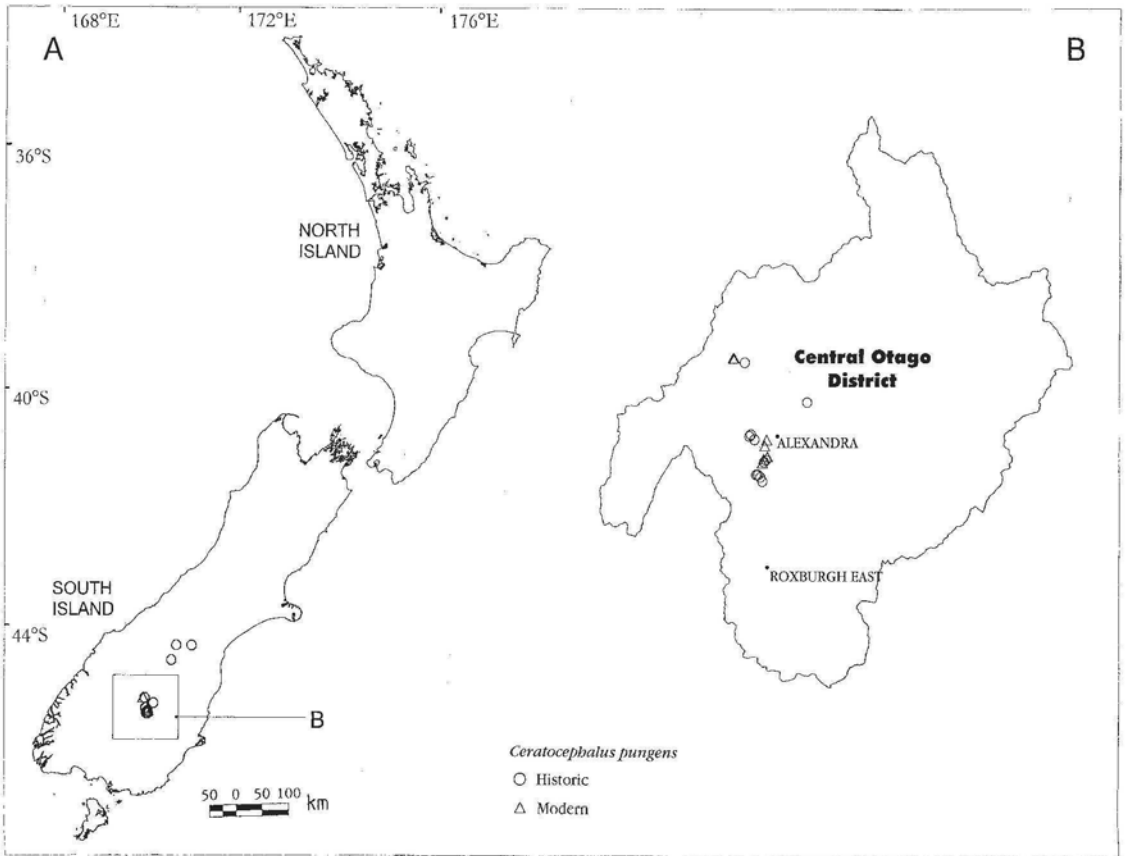
Fig. 2 **A**, Historic and modern distribution of *Ceratocephala pungens* in New Zealand; **B**, Historic and modern distribution in the Central Otago district.

recorded the type specimen (CHR 75725) from "moist gravel at lake shores" of Lake Lyndon, Porters Pass, inland Canterbury.

The present study substantially expands the geographic range and dispersion of *Myosotis* from that of Allan (1961). There are just three modern North Island sites, all coastal: two in Taranaki and one near Cape Palliser (Fig. 3A). There are no modern equivalents of three historic records from the Wellington coast and the northern tip of Kapiti Island. The 16 modern South Island sites are all inland (a 1950 record from the coast at Pahia, Southland, is the only South Island coastal record). The scattered populations in Marlborough and Canterbury are all from the margins of lakes and tarns, including Lake Tennyson, Lake Lyndon, Spider Lakes, an alpine tarn in the Sinclair Range, Rangitata River headwaters, and three from kettle tarns in the Mackenzie Basin. There is no modern record from above Bowenvale, Port Hills, Banks

Peninsula. By comparison, Otago's nine modern populations (Fig. 3B) are mostly on poorly vegetated pavements in degraded mat vegetation, with just one from a turf in a shallow channel on the floor of the Nevis valley. Two populations have recently been lost following proliferation of exotic grasses on recently destocked blocks of depleted dry grassland near Alexandra. Most of the coastal, tarn, and lake margin populations consist of 70 to 300 plants each.

Vegetation patterns and relationships with environment

Eight plant communities containing spring annual plants were derived from cluster analysis (Table 1; Fig. 4A). Five of these (A–E) comprised sites in Central Otago only, and these occupied distinct habitats in terms of measured environmental factors, especially substrate, slope, aspect, and landform (Table 2). The other three communities (F–H)
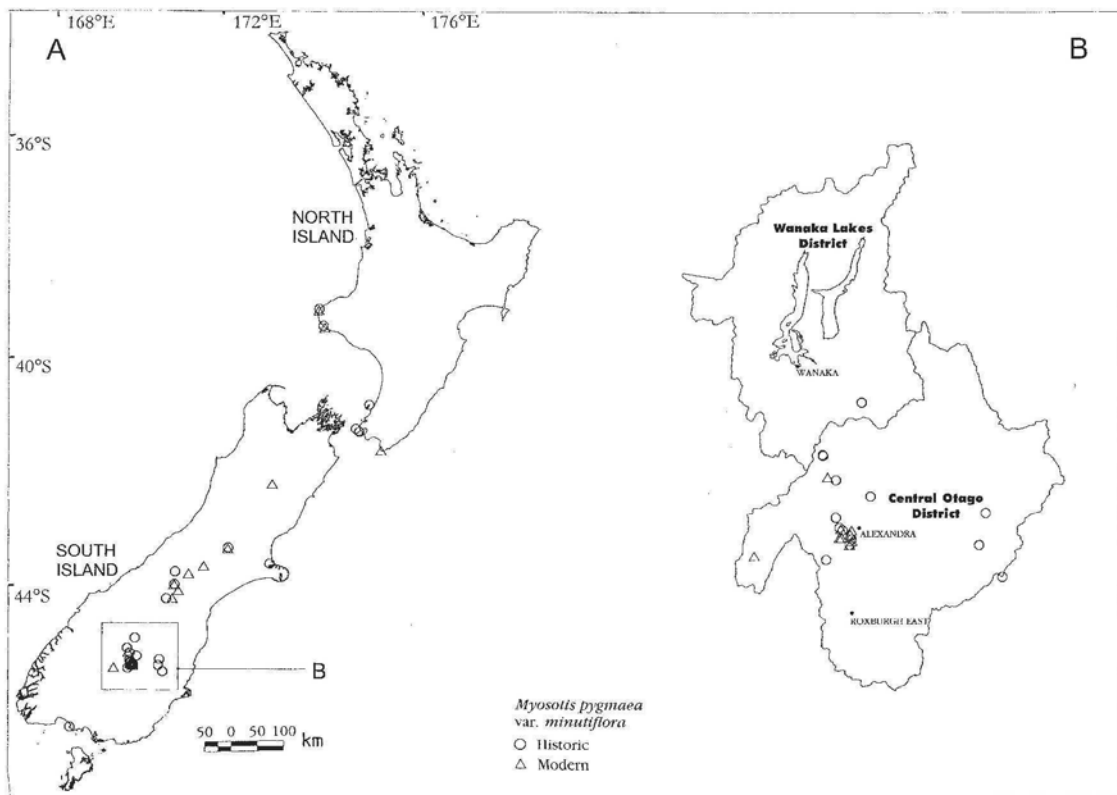
Fig. 3 **A**, Historic and modern distribution of *Myosotis pygmaea* var. *minutiflora* in New Zealand; **B**, Historic and modern distribution in two Otago districts.

comprised coastal and lakeshore turf communities, with quite different plant compositions (Table 1).

Community A invariably contained one of the three spring annual species (Table 1), and occurred on north-facing colluvial footslopes with low soil pH and high base saturation, Ca, Na, and exchangeable Na percent (Table 2; Fig. 4A). It was characterised by the presence of the sub-shrub *Thymus vulgaris*, scabweed (*Raoulia australis*), and *Stellaria gracilenta*, together with more common, widespread species such as *Hypochaeris radicata*, *Myosotis discolor*, *Rumex acetosella*, *Sedum acre*, *Taraxacum officinale*, and *Trifolium arvense* (Fig. 4B). Community B, on west-facing sites of recent soils on alluvial toeslopes (Fig. 4A), often contained all three spring annuals, with *Poa lindsayi*, *Crassula tetramera*, and *Aphanes arvensis* (Table 1). *Ceratocephala* was the only spring annual present in the sparse, species-poor Community C, which occurred on west- or north-facing aspects, steep,

rocky, transportational midslopes and interfluves at mid to low altitude in Central Otago (Fig. 4A). The xerophytic native grass *Poa maniototo*, *Rumex acetosella*, and *Erodium cicutarium* were other characteristic species. Most sites with *Myosurus* were classified as Communities D or E (Table 1). Community D occurred at relatively high altitudes in Central Otago, mainly on toeslopes of loess and alluvium with high soil CEC (Fig. 4A). It almost always had *Trifolium repens*, and often *Plantago coronopus* (Fig. 4B). These sites represent the moderate salinity of salt meanders and salt pans but are modified by farming practices and are vulnerable to weeds. Community E occurred at somewhat lower altitudes, on alluvial toeslopes with high soil pH (Fig. 4A) and moderately high exchangeable Na percent and base saturation, the latter pointing to strong salinity. *Puccinellia rariflorens* and *Atriplex buchananii* were common species (Fig. 4B). *Myosotis* was also recorded at a few of these sites.

Table 1 Occurrences of the 81 most common vascular plant taxa in the 8 plant communities of the quadrat classification of spring annuals (values represent proportion of quadrats occupied on a 10-point scale). n, number of quadrats. Plant name abbreviations are used in Fig. 4.

| Species group | Species | Community | | | | | | | |
		A $n = 14$	B $n = 7$	C $n = 3$	D $n = 11$	E $n = 5$	F $n = 3$	G $n = 5$	H $n = 7$
I	*Acaena agnipila**	1	1						
I	*Hypericum perforatum**	1							
I	*Isolepis* sp.	1							
I	*Eleocharis acuta*				1				
I	*Elynus apricus*	1				2			
I	*Oreomyrrhis ramosa*	1							
I	*Cirsium arvense*	2							
I	*Puccinellia stricta*	1			1				
I	*Puccinellia raroflorens* (PUCRAR)	2				6			
I	*Cirsium vulgare**	4	1		1				
I	*Trifolium dubium** (TRIDUB)	4		3	2			4	
I	*Capsella bursa-pastoris** (CAPBUR)				5				
I	*Rumex crispus**				2				
I	*Cerastium fontanum** (CERFON)				5			4	6
I	*Trifolium repens** (TRIREP)				9			4	6
I	*Plantago coronopus** (PLACOR)		1		5		10		9
I	*Myosurus nininus* subsp. *novae-zelandiae* (MYOMIN)	2	6		10	10			
I	*Spergularia rubra** (SPERUB)	1			5	2	7		
I	*Atriplex buchananii* (ATRBUC)	1				8			
I	*Sonchus oleraceum**					6			
I	*Sagina procumbens** (SAGPRO)		1			4			3
I	*Crassula sinclairii* (CRASIN)						7	4	
I	*Medicago lupulina**						7		1
I	*Polycarpon tetraphyllum**						7		
II	*Anagallis arvensis** (ANAARV)	1	6						
II	*Crassula tetramera* (CRATET)	4	9						
II	*Ceratocephala pungens* (CERPUN)	3	7	10					
II	*Crepis capillaris** (CRECAP)	2	6			6			
II	*Myosotis pygmaea* var. *drucei*	2	3						
II	*Poa lindsayi* (POALIN)		3		1			4	
II	*Aphanes arvensis** (APHARV)	6	9		3	2			
II	*Myosotis discolor** (MYODIS)	6	9		2	2			
II	*Erodium cicutarium** (EROCIC)	6	9	3	6				
II	*Poa maniototo* (POAMAN)	6	3	3					
II	*Sedum acre** (SEDACR)	9	4		1	2			
II	*Trifolium arvense**(TRIARV)	9	10		1	2			
II	*Hypochaeris radicata** (HYPRAD)	9		3	4	10	7	2	6
II	*Taraxacum officinale** (TAROFF)	9	3	3	4	6	3	2	
II	*Myosotis pygnaea* var. *ninutiflora* (MYOPYG)	6	10			4	10	10	10
II	*Rumex acetosella** (RUMACE)	7	7	7	4			10	
III	*Bellis perennis**	2							
III	*Echium vulgare**	1							
III	*Erophila verna**	1			1				
III	*Raoulia beauverdii*	1							
III	*Raoulia hookeri* var. *apice-nigra*	1							
IV	*Chondropsis semiviridis* (CHOSEM)	5	1						
IV	*Raoulia australis* (RAOAUS)	4							
IV	*Thynus vulgaris** (THYVUL)	4							
IV	*Poa* sp. (POASP)	7	1			4			
IV	*Stellaria gracilenta*	4							
IV	*Veronica verna**	4		3	1				*(continued)*

Table 1 (*continued*)

Species group	Species	Community A n = 14	B n = 7	C n = 3	D n = 11	E n = 5	F n = 3	G n = 5	H n = 7
IV	*Malva neglecta**	1							
IV	*Poa pratensis*	1							
IV	*Vittadinia australis*	1							
IV	*Vittadinia gracile**	1							
V	*Galium perpusillum*							6	
V	*Muehlenbeckia axillaris* (MUEAXI)							8	
V	*Hieracium pilosella** (HIEPIL)	1						10	
V	*Linum catharticum**							4	
V	*Geranium sessiliflorum* (GERSES)	1						4	
V	*Oreomyrrhis colensoi* var. *delicatula*							4	
V	*Poa cita*	1						4	
VI	*Carex breviculmis* (CARBRE)							6	
VI	*Cardamine debilis*							6	
VI	*Gnaphalium polylepis*	1						6	
VI	*Epilobium angustum* (EPIANG)							6	
VI	*Iphigenia novae-zelandiae*							6	
VI	*Stackhousia ninina*							4	
VI	*Dichondra brevifolia* (DICBRE)							4	
VI	*Ophioglossum coriaceum*							4	
VI	*Oxalis exilis*							4	
VII	*Senecio lautus*								3
VII	*Disphyma australe*								3
VIII	*Agrostis muscosa*								3
VIII	*Arctotheca calendula**								3
VIII	*Oreomyrrhis* sp. (CHR 364086)								1
VIII	*Colobanthus muelleri*								7
VIII	*Crassula manaia* (CRAMAN)								10
VIII	*Lotus suaveolens** (LOTSUA)								9
VIII	*Selliera rotundifolia* (SELROT)								6
VIII	*Zoysia minima* (ZOYMIN)								10

Communities F, G, and H had just one spring annual, *Myosotis* (Table 1; Fig. 4A). Community F (on coastal gravel at Ngawihi near Cape Palliser), has *Plantago coronopus*, *Hypochaeris radicata*, *Medicago lupulina*, and *Crassula sinclairii*, while Community G (turfs bordering Spider Lakes and Lake Tennyson), is distinguished by the presence of *Dichondra brevifolia*, *Epilobium angustum*, *Carex breviculmis*, and *Crassula sinclairii*. Community H comprises coastal turfs in Taranaki with *Zoysia minima*, *Lotus suaveolens*, *Selliera rotundifolia*, *Crassula manaia*, and *Plantago coronopus*.

Eight species groups were derived from cluster analysis (Table 1). Group I species are relatively uncommon, and their occurrence is poorly predicted in terms of associated species. *Myosurus* is a member of this group, although it occurs across four of the community groups. Group II contains more widespread species than Group I, which occur predictably in Communities A & B, although many also occur (albeit less commonly) in other communities, particularly in Central Otago (i.e., Communities C, D, and E). Group II includes *Ceratocephala* and *Myosotis*, the former a component of three community groups, the latter of six community groups. Groups III and IV are species predominantly of Community A and are seldom recorded outside Central Otago. Species of Groups V to VIII have quite restricted community membership and relate principally to the occurrence of *Myosotis* outside Central Otago.

Myosurus was present in four plant communities, but occurred predominantly in Communities D and E (Table 1). Few other species tended to preferentially co-occur with *Myosurus*. Its characteristic associates were small in number and included lichens (excluding *Chondropsis semiviridis*), *Trifolium repens*, *Cerastium fontanum*, *Spergularia rubra*, and *Capsella bursa-pastoris* (these species were seldom or never recorded with *Myosotis* or

Ceratocephala). Consequently, many species typical of depleted scabweed or mat vegetation were seldom or never recorded with *Myosurus*.

Community C contained *Ceratocephala* exclusively amongst the annuals, although it was also a minor component of Community B. *Ceratocephala* was associated with few species (Table 1). It commonly co-occurred with the lichen *Chondropsis semiviridis* (67% of sites), *Poa maniototo* (50%), and *Crassula tetramera* (50%). It seldom co-occurred with *Myosurus* and was never recorded with *Trifolium repens*, *Spergularia rubra*, *Cirsium vulgare*, *Atriplex buchanani*, *Capsella bursa-pastoris*, or *Puccinellia raroflorens*. In other words, it is not associated with salt-tolerant communities.

Table 2 Geophysical properties of plant communities and quadrats containing spring annual taxa. Derivation of mean north aspect and mean east aspect is described in the Methods. LCDB, Land Cover Database. *n*, number of quadrats.

Property	Community							
	A $n = 14$	B $n = 7$	C $n = 3$	D $n = 11$	E $n = 5$	F $n = 3$	G $n = 5$	H $n = 7$
Spring annual (%)								
Myosurus minimus subsp. *novae-zelandiae*	21	57		100	100			
Ceratocephala pungens	29	71	100					
Myosotis pygmaea var. *minutiflora*	57	100			40	100	100	100
Physical (average)								
Altitude (m a.s.l.)	360	291	340	509	240	20	844	21
North aspect (°)	141	90	107	94	73	83	114	36
East aspect (°)	96	30	43	92	53	83	148	91
Slope (°)	8	9	19	4	5	2	11	2
Physiography (%)								
Interfluve	7	14	33			100	20	
Seepage slope	14	29		9			80	100
Convex creep slope	7			9				
Transportational midslope			67	18				
Colluvial footslope	64							
Alluvial toeslope	7	57		64	100			
Parent material (%: from LCDB)								
Alluvium				36			60	
Greywacke						100		
Lake sediments							40	
Loess				18				
Schist	100	100	100	45	100			
Wind-blown sand								100
Soil type (%: from LCDB using Hewitt 1993)								
Recent	43				100			
Semi-arid	64	57	67	64	100			
Brown						100		
Brown-loamy	29							
Pallic	7			36				
Ultic							100	
Raw		33						
Soil properties	$n = 3$	$n = 5$		$n = 7$	$n = 5$			
pH	8.0	6.1		6.2	7.7			
Electrical conductivity	3.0	0.2		0.3	2.6			
Cation exchange capacity	9.6	9.4		18.4	8.6			
Base saturation	210.7	82.0		76.6	109.4			
Ca	16.2	4.9		7.8	3.9			
Mg	3.7	1.4		3.2	3.5			
K	0.7	0.9		1.4	0.5			
Na	3.6	0.7		1.7	1.4			
Exchangeable sodium percent	31.1	6.3		1.0	14.9			

A

B

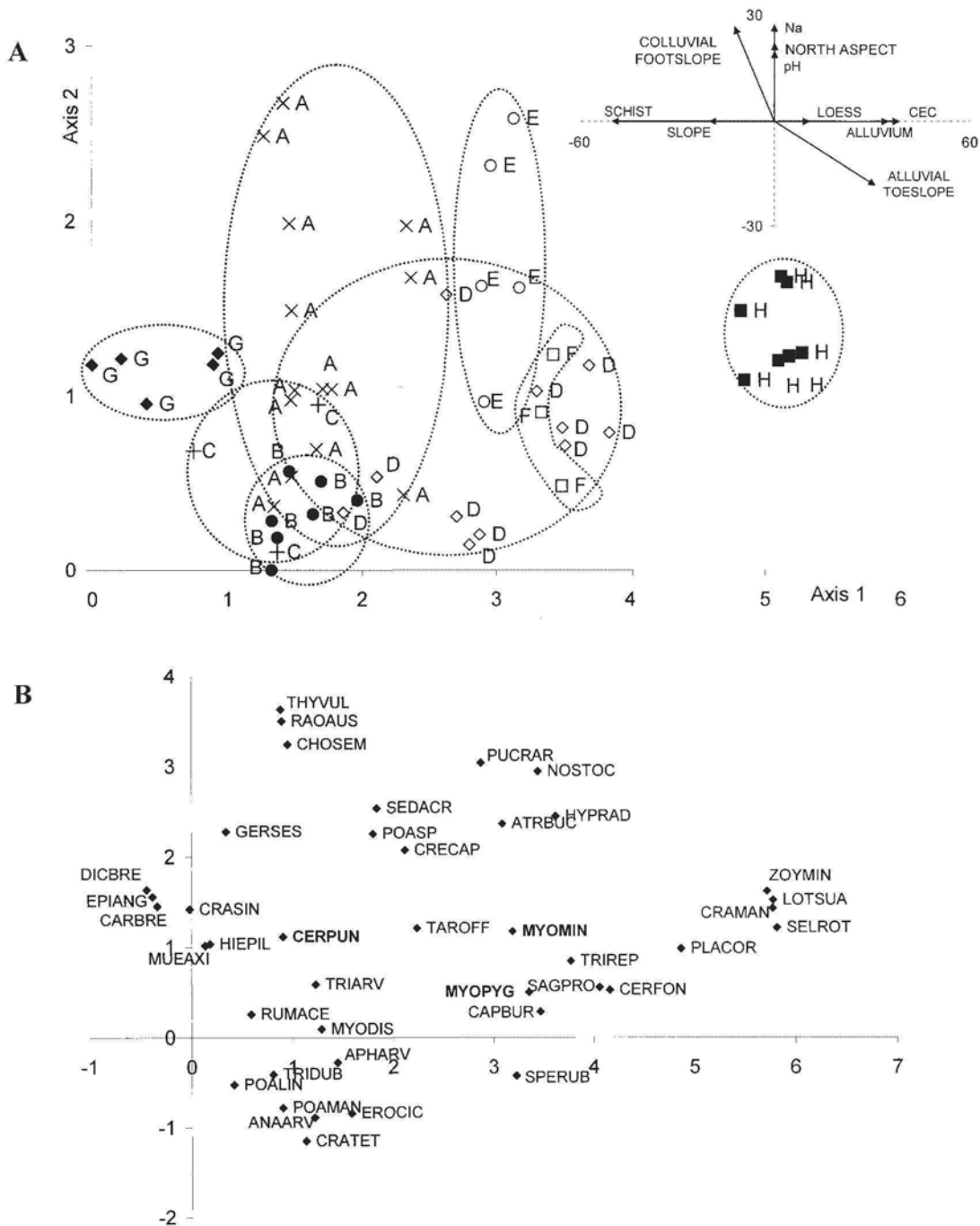**Fig. 4**   **A**, Positions of sites and communities from the cluster analysis classification on a DCA ordination and **B**, positions of species on Axes 1 and 2 of the DCA ordination of species composition (axis units are standard deviations). The inset vector plot shows, for the Central Otago sites only (Communities A to E), the direction, and the percentage of the variation explained by, significant correlations of environmental variates with Axes 1 and 2 (axis units are % variation explained). Plant name abbreviations in B are given in Table 1. NOSTOC = *Nostoc* sp.

Myosotis is a component of six community groups. Given its dual habitat and wide geographic spread, the large number of species it was recorded with is not unexpected (Table 1). Common associates in its Otago sites were *Trifolium arvense* (94%), *Aphanes arvensis* (82%), *Myosotis discolor* (82%), and *Erodium cicutarium* (76%) and, to a lesser extent, *Sedum acre*, *Poa pratensis*, *Poa*

Table 3 Geophysical properties of quadrats containing spring annual taxa. Derivation of mean north aspect and mean east aspect is described in the Methods. LCDB, Land Cover Database. *n*, number of quadrats.

| | *Myosurus mininus* ssp. *novae-zelandiae* | *Ceratocephala pungens* | *Myosotis pygmaea* var. *minutiflora* | | |
	Central Otago *n* = 24	Central Otago *n* = 12	Northern Central Otago *n* = 17	South Island *n* = 5	North Island *n* = 10
Spring annual: % (no.)					
Myosurus mininus subsp. *novae-zelandiae*	100 (24)	33 (4)	35 (6)		
Ceratocephala pungens	25 (6)	100 (12)	35 (6)		
Myosotis pygmaea var. *minutiflora*	25 (6)	50 (6)	100 (17)	100 (5)	100 (10)
Physical (average)					
Altitude (m a.s.l.)	407	321	314	844	21
North aspect (º)	92	116	111	114	50
East aspect (º)	74	65	61	148	89
Slope (º)	4	10	8	11	2
Physiography (%)					
Interfluve		25	12	20	30
Seepage slope	4		24	80	70
Convex creep slope	4	8			
Transportational midslope	8	17			
Colluvial footslope	8	17	29		
Alluvial toeslope	75	33	35		
Parent material (%: from LCDB)					
Alluvium	17			60	
Greywacke					30
Lake sediments				40	
Loess	8				
Schist	75	100	100		
Wind-blown sand				70	
Soil type (%: from LCDB)					
Recent	13	25	18		30
Semi-arid	63	50	71	60	
Brown				60	
Brown-loamy	4	17	6		
Pallic	21		6		
Ultic					70
Raw		8			
Soil properties	*n* = 17	*n* = 6	*n* = 8		
pH	6.8	6.0	6.9		
Electrical conductivity	1.1	0.3	1.8		
Cation exchange capacity	13.1	9.0	9.2		
Base saturation	91.9	79.8	134.8		
Ca	5.9	4.6	9.1		
Mg	3.0	1.4	2.6		
K	1.0	0.8	0.8		
Na	1.5	0.6	1.5		
Exchangeable sodium percent	12.5	4.9	15.1		

maniototo, *Crassula tetramera*, *Crepis capillaris*, *Anagallis arvensis*, *Stellaria gracilenta*, *Myosotis pygmaea* var. *drucei*, *Sagina procumbens*, *Acaena agnipila*, and *Hieracium pilosella*. At its locations outside Otago, it co-occurred with distinctly different assemblages of species (see descriptions of Communities F, G, and H above).

Spring annual habitat characteristics and environmental relationships

We describe the physiographic characteristics of the habitat of each spring annual, based on observation, as well as information on the environmental characteristics of each habitat based on quadrat sampling.

Myosurus

Myosurus is mostly associated with periodically wet depressions and flushes that become parched silty pavements in summer. These winter- and spring-wet depressions and flushes are free of the taller sedges and rushes that dominate many other wetland systems with reliably high water tables. The planar schist landforms of Otago, with their horizontal and massive bedrock overlain by poorly drained, silty soils in a semi-arid climate, promote seasonal pools and flushes. Some of the depressions occupied by *Myosurus* have salty soils (see also Given 1981, p. 97) because surface salts accumulate with the alternate wetting and drying. Just three populations of *Myosurus* remain on the once extensive salt meanders and salt pans on the floors of the Maniototo and Alexandra intermontane basins (Rogers et al. 2000), but the three sites are weed-infested. Each

depression or flush is generally less than 250 m^2 in area, with most populations of *Myosurus* occupying less than 10 m^2 of that. The sites span a range of elevation from the floors of intermontane basins to upper valley slopes near the crests of Otago's block mountains. Consistency in its present habitats (seasonal ponds and flushes and saline patches) suggests that the numerous historical but poorly documented records were from similar seasonally wet/dry depressions, salty or not. A population straddling a rounded spur separating two tributaries of the Manorburn Reservoir on Rough Ridge in Central Otago is a site without a seasonally high water table. Sheep use the area as a nocturnal camp and the mat vegetation is a depleted derivative of the original tall tussock (*Chionochloa rigida*) community. These characteristics point to the site being an opportunistic and atypical extension of habitat.

Myosurus was sampled exclusively on schist substrates in Central Otago (Table 3). It was rarely present with either *Ceratocephala* or *Myosotis* ($P = 0.02$ and $P = 0.08$ by chi-squared tests, respectively). It commonly occurred on gentle slopes (average 4°), more-or-less south-facing aspects, and on schist-derived loess and alluvial soils, mostly on alluvial toeslopes. Soils tended to have lower than average electrical conductivity, base saturation, Ca, Na, and exchangeable Na percent, but higher average cation exchange capacity than sites where it was not recorded.

Thirty-eight percent of the quadrats with *Myosurus* showed that it had a spatially clumped dispersion pattern at the subquadrat scale of 100 ×

Table 4 Number and percentage (in parenthesis) of quadrats with evidence for spatial clumping ($P < 0.05$: autocorrelation) in the cover or number of spring annuals. Also shown are quadrats where the cover and number of spring annuals is significantly correlated with various cover class estimates. +, positive correlation; –, negative correlation.

Taxon	Clumping (autocorrelation)	Cover correlates	Number correlates
Myosurus mininus subsp. *novae-zelandiae*	11 (38%) Cover	2+ (7%) Bare soil 2+ (7%) Total plant cover 1–(3%) Exotic grass cover 1–(3%) Cover *Plantago coronopus*	
Ceratocephala pungens	5 (50%) Cover 1 (10%) Number	3+ (30%) Bare soil	7+ (70%) Bare soil 1+ (10%) Total plant cover
Myosotis pygmaea var. *minutiflora*	4 (16%) Cover 7 (28%) Number	1+, 5– (4%, 20%) Bare soil 1–(4%) Total plant cover 1–(4%) Exotic grass cover	3–(12%) Bare soil 2+, 2–(8%, 8%) Total plant cover 1–(4%) Exotic grass cover

100 mm (Table 4). However, it showed no consistent avoidance or affinity with bare soil or plant taxa (apart from the two other spring annuals).

Ceratocephala

In contrast to the seasonally saturated habitat of *Myosurus*, *Ceratocephala* is specialised to patches of thin, skeletal, summer-dry soils with sparse vegetation cover. A veneer of soil less than 30 mm deep often overlays gently sloping or horizontal platforms of schist bedrock in the foothill tor landscape of Central Otago (McCraw 1965). The unattached lichen, *Chondropsis semiviridis*, is often the most conspicuous plant of the erodible and frost-heave-prone surfaces. *Ceratocephala* completes its life cycle in the short period of intermediate soil moisture between damp and frost-heave-prone winter and the parched extremes of summer. The southern Canterbury records from near Omarama and the Black Forest, Grampian Mountains, indicate that the original range of the species included greywacke pavements, but their equivalence with the veneered soils of the foothills tor landscape of Central Otago is unknown. The site of a recently vouchered record in the upper Clutha valley (CHR 474619) was inundated by the creation of Lake Dunstan in 1994.

Site and soil characteristics for *Ceratocephala* are distinctive. It was sampled exclusively on schist substrates in Central Otago and tended to occur on steeper and more rocky slopes than the average across all spring annual sites (Table 3). It co-occurred with *Myosotis* at half of the recorded sites, although no more frequently than expected at random. Soil pH, electrical conductivity, cation exchange capacity, base saturation, Mg, Na, and exchangeable Na percent were all significantly lower where *C. pungens* was recorded than in those sites where it was not found.

Fifty percent of the quadrats containing *Ceratocephala* showed spatial autocorrelation in its distribution in 100×100 mm subquadrats, i.e., it had a clumped dispersion pattern (Table 4). Furthermore, 30% of the quadrats showed a positive correlation between the cover of *Ceratocephala* and bare soil, and a 70% positive correlation between the number of plants and bare soil.

Myosotis

Myosotis has two habitats. The first is turf communities that border water bodies, including coastal turf on headlands and cliff-tops exposed to salt-laden winds (Rogers 1999) and turfs bordering various ephemeral wetlands, namely kettlehole lakes and tarns, cut-off meander channels of streams, and alpine tarns. In this habitat, *Myosotis* may not behave as a strict spring annual because we recorded it in late June 2001 on its Taranaki coastal turf sites. The second habitat is poorly vegetated and seasonally arid, silty and gravelly pavements bordering beaches, inland lakes, and across the semi-arid intermontane basins of the Mackenzie Basin and Central Otago. In Central Otago, the bare pavement habitat tends to have deeper soils than the bare pavements of *Ceratocephala*, although the two taxa infrequently overlap (Table 3). Bare pavement in driest Central Otago has expanded dramatically from what may have been available in pre-human times. Following the clearance of low forest, scrub, and short tussock (McGlone 2001), pastoral farming has degraded the seral tussockland to mat vegetation of principally *Raoulia* spp. in a mosaic of bare soil. *Myosotis* infrequently co-occurs with *M. pygmaea* var. *drucei* in its dry pavement habitat in Otago (Table 2).

Myosotis was sampled on a variety of substrates, at low elevations in Central Otago and coastal North Island sites, but at > 800 m in Marlborough and Canterbury (Table 3). The eight soil samples from its range in Central Otago, where it was recorded on schist substrates, showed lower than average cation exchange capacity but high base saturation. In Central Otago, it co-occurred with both *Ceratocephala* and with *Myosurus*, although its co-occurrences with *Myosurus* were less frequent than might have been expected at random. In its turf and beach gravel sites in the North Island, Marlborough, and Canterbury, *Myosotis* occurs on moist climate soil types not occupied by other spring annuals (Table 3).

Only a small proportion of quadrats with *Myosotis* showed spatial clumping at the subquadrat scale, although a small proportion of quadrats showed it had some tolerance of other plant cover, including exotic grasses (Table 4).

Seed biology of spring annuals

Achenes of *Myosurus* are boat-shaped, about 1 mm long, with a short subaristate style (or beak) not greater than 0.5 mm long (Webb & Simpson 2001, pl. 115). A tapering, 3–8-mm-long receptacle may contain up to about 80 achenes and is subtended by an elongated scape up to 30 mm long. Achenes of *Ceratocephala* are distinguished by an inflated empty cell on either side of the upper margin, along with a spinous achene beak, which is no longer than the achene and erect or erectopatent (Garnock-Jones

1984; Webb & Simpson 2001, pl. 115). Five to 30 achenes are contained in a glabrous receptacle nestled within the rosette of woolly to hairy, trilobed leaves. Nutlets of *Myosotis* are about 1.2 mm long by 1.0 mm wide, ovate, thickly biconvex, slightly keeled along whole length, and up to five are contained in the cylindrical calyx tube (Webb & Simpson 2001, pl. 45, 47). These dimensions and retention in a tubular calyx seem to make for dispersal by rain splash, surface water, and wind. Observations of recruitment of seedling plants adjacent to mature plants in potted cultivations suggest ready dispersal of seed, probably by wind or rain splash at distances up to 2 m.

DISCUSSION

Habitat relationships

Classification and ordination indicate, firstly, a degree of habitat specialisation and distinctiveness for the three spring annuals, and, secondly, some habitat overlap. We interpret this distinction as indicating, on the one hand, specialisation to genuine non-forest habitats in pre-human landscapes and, on the other, exploitation of sites that are seral and degraded derivatives of the low-forest–scrub–short-tussock communities (McGlone 2001) that occupied the equivalent of forest environments across driest south-eastern South Island in pre-human times. The three genuine non-forest habitats are summarised first. *Myosurus* occupies the floors of ephemerally wet depressions, which include salt aprons, salt meanders, and salt pans of the inland saline ecosystem (Communities D & E). *Ceratocephala* occupies "semi-desert" bare pavement of thin soils that are frost-heaved in winter and arid in summer (Community C). It has no tolerance of salty soils (Rogers et al. 2000). In performing as a spring annual, *Myosotis* is primarily a member of the winter-damp and summer-arid gravel of exposed coasts and lakes (Communities F & H) (Rogers 1999) and the turf marking the water inundation zone at the margin of ephemeral wetlands (Community G). In pre-human times, these four ecosystem types would have been more or less open habitat, with shrubs providing at best sparse cover. Beyond these non-forest ecosystems, all three spring annuals have expanded their habitat range into induced scabweed or mat vegetation in Central Otago that has resulted from degradation of the pre-human low-forest–scrub–short-tussock of dry hillslopes and basin

floors (Communities A & B). Scabweed or mat communities are predominantly patches of *Raoulia* spp. in a matrix of bare soil and rock, the latter comprising skeletal soils, which are stripped of topsoil by wind erosion and frost heave (Hewitt 1996). Grazing by sheep, goats (*Capra hircus*), and rabbits perpetuates scabweed. By virtue of its apparently more readily dispersed seed, *Myosotis* has exploited this habitat to a much greater extent than the more conservatively dispersed *Myosurus* and *Ceratocephala*. Notwithstanding the place of spring annuals in human-induced habitat, in pre-human times, New Zealand's diverse, ground-dwelling avifauna must have maintained a mosaic of bare soil patches within the low-forest–scrub–short-tussock landscapes that prevailed on dry lower hillslopes and basin floors. We conclude that no one non-forest ecosystem or habitat has selected for the spring annual life-history strategy in New Zealand, although all share one common environmental limitation, a seasonal soil moisture deficit.

Spring annual life-history strategy

Why are there so few taxa with this strategy in New Zealand? With three or four taxa, and two of these from monospecific genera, the life strategy constitutes just c. 0.002% of the New Zealand vascular flora. Globally, annual plants are concentrated in deserts (Solbrig 1986; Fox 1990; Polis 1991; Boeken & Shachak 1998). However, the spring annual phenology is extremely rare among annual plants (McKenna & Houle 2000), perhaps because initial low temperatures, followed by rapid onset of resource depletion (drought, canopy closure), select against the strategy of avoiding competition with a short life span. Lytle (2001) suggested that seasonal time constraints and predictable seasonal disturbance regimes select for small size at maturity in annual organisms. The minute size of New Zealand's spring annuals at maturity exemplifies this selection pressure.

Drought-prone environments expose plants to stresses arising from soil moisture deficits, soil salinity, and heat. Plants have evolved a variety of anatomical, morphological, and phenological adaptations to counteract water-deficit stress. They can be divided into mechanisms of drought avoidance (developmental and morphological traits) and drought tolerance (physiological and biochemical adaptations) (Solbrig 1986; Abernethy et al. 1998). The spring annual habit is a drought avoidance mechanism, geared to high productivity and reproductive output. High productivity features

in the drought-escaping ephemerals of deserts are low root-to-shoot ratios, large leaf-surfaces compatible with temperature, and, to avoid mutual shading, widely spaced leaves (Solbrig 1986). Mooney et al. (1976) and Szarek & Woodhouse (1979) found the photosynthetic rates of two desert annuals to be among the highest rates of any known C_3 plant. Among ephemerals, trade-offs take place between drought tolerance and competitive ability (Loria & Noy-Meir 1980). However, investment success in such a balance, selected for in New Zealand's pre-human environments, is now under threat from the competitive pressure of a rich and abundant exotic flora in spring annual communities (Table 3).

Reproductive allocation in desert annuals can be in the order of 50–60% of dry weight of reproductive structures to total dry weight (Loria & Noy-Meir 1980) and is usually higher than in perennials (Cheplick 1998). Reproductive structures, at least by volume, appear to approximate this ratio in *Myosurus* and *Ceratocephala*. The numbers of seed produced in desert ephemerals can also be high (Solbrig 1986). The three spring annuals studied here appear to vary in the numbers of seeds per plant and their dispersal properties. *Myosurus* produces large numbers of seeds that are conservatively dispersed as judged by its population density and dispersion each year across the full breadth of each habitat. *Ceratocephala* invests in small numbers of larger seeds that are also conservatively dispersed. *Myosotis* seeds appear intermediate in number per plant but are widely dispersed. The different strategies will be partly related to the predatory loss of seed, with reported losses in desert annuals from 50% to 95% (Chew & Chew 1970; Soholt 1973; Noy-Meir 1980). As the environment becomes more unpredictable, greater seed carryover from year to year and increased dormancy are expected (van Rooyan 1999). The spinous and beaked achenes in *Ceratocephala* and beaked achenes of *Myosurus* suggest some degree of adaptation to animal dispersal, although barbless spines may provide only temporary attachment to animals (Lee et al. 2001a). Barbless spines may foster entrapment in the ground surface and vegetation, and function as a dispersal-limiting mechanism, where habitats are at small spatial scales. Animal attachment would foster dispersal beyond the confines of microhabitats. In pre-human New Zealand, the feathers of ground-dwelling or ground-feeding birds were the main animal transport mechanism beyond ingestion. The fossil bird fauna of dry north, central, and western

Otago, where the distributions of the three taxa overlap, numbered 62 species (Worthy 1998), including several ground-feeders, such as parakeets (*Cyanoramphus*), flightless goose (*Cnemiornis calcitrans*), takahe (*Porphyrio hochstetteri*), ducks (Anatidae), and wrens (*Xenicus* spp.), as potential seed dispersers. Introduced animals, such as rats (*Rattus* spp.), mice (*Mus musculus*), mustelids, rabbits, hares (*Lepus europaeus occidentalis*), sheep, skylark (*Alauda arvensis*), and several finches (Fringillidae), may have compensated for the curtailed dispersal prospects for *Myosurus* and *Ceratocephala* with extinction of most of the pre-human ground-dwelling avifauna. As a component of winter- and spring-wet depressions, *Myosurus* also has dispersal prospects within mud adhering to the feet of wetland birds. The seed mobility of *Myosotis* from wind and water might have increased with the opening up of dryland vegetation in the last 800 years.

In contrast to drought avoidance by just a few annuals, New Zealand's eastern flora demonstrates a wide range of xeromorphic anatomical features for drought tolerance such as small leaves, leafless stems, waxy cuticles, indumentum, deciduousness, woodiness, deep or tap roots, succulence, and cushion or mat architecture. Some of these features may be secondarily derived from floristic precursors adapted to nutrient-poor and low-productivity habitats in early Cenozoic New Zealand.

Annual plants are not only uncommon in New Zealand, but also elsewhere in the south-west Pacific, namely Australia and New Caledonia (Lee et al. 2001b), despite Australia's extensive deserts. Selection for annualism in New Zealand would have been low on an early Cenozoic archipelago landmass of low relief and predominantly oceanic climate. Lee et al. (2001b) suggested that climate cooling, increasing isolation, and tectonism have each acted to deplete the New Zealand flora, particularly during the mid Cenozoic. Despite late Cenozoic tectonism and the creation of eastern rainshadow environments, limitations imposed by few floristic antecedents, isolation, and absence of true desert conditions seem to have all curtailed the development of an annual plant guild in New Zealand; but, for the few, long-distance dispersal is the likely origin (Lloyd 1985). As mono-specific genera, *Ceratocephala* and *Myosurus* probably arrived in New Zealand with the full expression of the Kaikoura Orogeny in the early Pleistocene (Chamberlain et al. 1999) and, as such, are recent immigrants, in the same period that the flora was loosing cool-intolerant elements (Lee et al.

2001b). The failure of *Myosurus* and *Ceratocephala* to radiate here is part of a global pattern of phylogenetic constraint (Garnock-Jones 1984, 1986). Their arrival was probably secured by the provision of erosion-prone pavements and vernal pools in eastern rainshadow regions with the onset of seasonally variable climates. However, the spring annual *M. pygmaea* var. *minutiflora* is the product of divergent evolution of *Myosotis pygmaea* sens. lat. specifically, and the *Myosotis* genus in general, across a range of extreme wet or dry non-forest, and mainly montane to alpine, habitats in the mid-to late Cenozoic. *Myosotis pygmaea* sens. lat., with up to five variants, shows recent radiation across a wide range of non-forest ecosystems from coastal *M. pygmaea* var. *pygmaea* to montane-alpine *M. pygmaea* var. *drucei*. Similarly, the genus *Crassula* has speciated across several non-forest ecosystems, with *C. tetramera* adapted to summer arid habitats. By comparison with the New Zealand flora, the annual habit is prominent among the suite of ruderal and weedy herbaceous species that have successfully invaded disturbed and dry eastern environments. Selection for the annual habit in the continental Northern Hemisphere, from whence much of this flora is derived, was probably spurred by deserts on the one hand and recurrent sheet glaciation and frequent geomorphic disturbance on the other. Both these selection pressures were absent in archipelago New Zealand. Of New Zealand's spring annuals, only *Myosurus* has salt tolerance and is part of a depauperate flora adapted to inland salty soils (Allen & McIntosh 1997; Rogers et al. 2000).

Population variability and habitat viability

In the 3 years of observation, we noted a 4-month difference in the first seasonal appearance of all three plants, from early June to early September. Germination was not synchronous where the plants overlap in Central Otago. *Myosotis* was usually the first to appear, as early as late May or June in turf-stabilised soils buffered against winter frost-heave. *Myosurus* can suffer inundation for several days by spring rains flooding its depression habitat. *Ceratocephala* was consistently the last to germinate, normally appearing in late August to mid September. Germination for all three is likely to be triggered by complex interactions in photoperiod, temperature, and soil moisture. The best germination strategy to adopt in an unpredictable environment is to possess innate seed dormancy, with only a fraction of the population breaking dormancy each year (Cohen 1966; MacArthur 1972). Desert ephemerals

do show dormancy (Solbrig 1986) and only a fraction of the seed is in a condition to germinate every year (Beatley 1967). Delayed germination is a common trait in desert plants in their characteristically stochastic environments (Gutterman 1993).

Our results show differing individual responses by spring annuals to competition from exotic plants across their range of habitats. The clumped arrangement of *Ceratocephala* and its positive correlation with patches of bare soil in most sites suggests that it has little tolerance of other vegetation. It appears to be rapidly outcompeted by exotic species in the absence of grazing. For example, its habitat cover at one site near Alexandra estimated as covering 1000 m^2 in October 1992 (CHR 480322) is now reduced to approximately 0.25 m^2 (G. Rogers unpubl. data), principally due to a proliferation of *Lolium perenne*, *Rumex acetosella*, and *Trifolium arvense* following a reduction in rabbit numbers after the release of RHD (rabbit haemorrhagic disease) in 1997. Our results point to a greater tolerance of exotic plants by *Myosurus* than *Ceratocephala*. Where exotic grasses and forbs are sparsely present, the short life span of *Myosurus* is an effective competition-avoidance mechanism. Its limited occurrences in scabweed or degraded pasture are dependent on continued grazing disturbance and open, abraded, short-statured communities. The joint environmental stresses of a long and uninterrupted period of water inundation in winter followed by prolonged summer soil aridity may be critical to buffer the habitat of *Myosurus* and the turfs of ephemeral wetlands as habitat for *Myosotis* against invasion of exotic grasses and forbs. Salt-tolerant *Plantago coronopus* is an aggressive competitor for *Myosurus* on seasonally damp salty soils in one Central Otago site. Although *Myosotis* is tolerant of the closed, short-statured mostly native vegetation of turfs, it has decreased on Flat Top Hill (Walker 2000), apparently outcompeted by taller swards of exotic grasses (Walker 2000) that colonise its scabweed habitat once this is freed of grazing by sheep and rabbits. In summary, the ephemeral wetland habitat of *Myosurus*, the "desert" pavement habitat of *Ceratocephala*, and the *Myosotis* habitat of turf and gravel surrounding water bodies all appear to have greater resistance to weeds than their shared habitat in scabweed or mat vegetation.

High inter-annual variability in population size is a feature of many annual herbaceous and short-lived perennial plants. *Sebaea ovata* (C. Ogle pers. comm.) and *Myosotis oreophila* (Stanley et al. 1998) are New

Zealand examples. Such variability is problematic in terms of deriving demographic trends and determining a species' conservation status. Patchiness in spring annuals results from dispersing seed, delayed germination of seed banks, and habitat loss. Our monitoring has shown that patchiness is difficult to capture at a quadrat scale of 500 × 500 mm. Evaluation of demographic and habitat trends may require a larger sampling space of several metres, with quadrat placement following a gridded network.

Walker et al. (1999) showed that seasonal changes are small compared with year-to-year changes in vegetation in semi-arid Central Otago. They found that spring vegetation tends to be more variable and less well structured than autumn vegetation, and that spring vegetation contains annual exotic and native taxa not present at other times of the year. This is likely to be partly driven by large within- and between-season variations in temperature and rainfall in Central Otago (Garnier 1951). It may take several decades for vegetation trends to become apparent in semi-arid vegetation (Wiegand & Milton 1996). Wilson (1989) found that the exotic guild of plants tends to determine the structure of communities ahead of the native guild in the upper Clutha catchment of semi-arid Central Otago. He judged that the exotic guild is still increasing and yet to reach equilibrium. Against this background, the early stages of vegetation change in semi-arid, predominantly exotic, grassland at Flat Top Hill, Alexandra, following the removal of sheep and rabbits has shown dramatic compositional shifts, generally increasing biomass, and, specifically, loss of spring-annual habitat (Walker 2000). However, spring annuals on some genuine non-forest habitat beyond the monitored transects are showing stable community composition and the maintenance of bare ground. Nevertheless, increasing biomass in the matrix landscape will mean altered microclimates for the nested spring-annual habitat and, moreover, changed functional relationships.

Protection priorities can be derived for spring annuals using criteria related to degree of threat and representativeness. However, setting conservation goals for spring annuals will need to be site-specific and nested within the higher-level conservation goals for the wider site. For most of dryland New Zealand, ecosystem *restoration* rather than *maintenance* goals will apply and major compositional and structural shifts in vegetation would occur in their implementation. Questions remain over the long-term viability of their genuine non-forest habitats in conservationally managed dryland landscapes. A mix of intensive spring annual and extensive ecosystem-restoration management may therefore prevail for these programmes.

CONSERVATION STATUS

The conservation status of the three plants studied here can be cautiously gauged from a comparison of the range and frequency of historical versus modern records and from population trends from the first period of monitoring in Central Otago. There are fewer modern than historical records for *Myosurus*, with a substantial range contraction outside Otago. Some sites in Otago farmland have disappeared through dewatering, soil cultivation, and weed encroachment (B. Patrick pers. comm.). Prudence suggests that it is premature to claim that *Myosurus* is extinct in Marlborough and northern Canterbury, although the evidence is for at best a critically endangered status there. The species is probably extinct in the North Island because its previous localities have been thoroughly searched without success (Ogle 1985). It is probably extinct in the lakes district of western Southland, perhaps having been adversely affected by water level adjustment from hydro-electric development of Lake Manapouri. There is evidence at several monitoring sites for ongoing weed invasion of its ephemeral wetland and salt pan and salt plain habitat. On its few salt apron sites on conservation land, its habitat is more secure. Based on evidence of habitat destruction and present population depletion by weeds, we support the conservation rank of Threatened-Declining of de Lange et al. (1999).

The evidence from the five known populations and approximately 50–70 plants of *Ceratocephala* between 1998 and 2000 is for a precarious existence. No great change in its geographic status in Otago is evident when comparing historical with modern records; it has always been a very rare species and/ or seldom collected, the latter perhaps partly due to its inconspicuousness. Its south Canterbury status is unknown, following the three mid-20th century collections. At two of its Otago sites near Alexandra, populations have declined due to a proliferation of weeds following removal of grazing herbivores. Another threat is conversion of Central Otago's alluvial terraces and lower colluvial slopes from degraded mat or scabweed to orchards, vineyards, and "lifestyle" blocks. In summary, we are in agreement with the rank of Threatened-Endangered

for *Ceratocephala* (de Lange et al. 1999), reflecting its few populations and evidence for intolerance of an expanding guild of exotics in semi-arid Central Otago.

Historical and modern records suggest little change in the broad geographical pattern of *Myosotis*, although two populations in coastal Taranaki have disappeared. However, preliminary trends from annual monitoring of its two remaining Taranaki populations in coastal turf suggest some losses from expansion of exotic plants. Its continuing presence in Central Otago's scabweed or depleted pasture habitat is probably dependent upon continuing disturbance by sheep and rabbits. Its most secure or stable habitat is seasonally moist gravels bordering lake and sea-coast (e.g., Ngawihi, Cape Palliser, and Lake Lyndon, Porters Pass), where summer drought appears to buffer the habitat against weeds. *Myosotis* was not assessed by de Lange et al. (1999), although it is clearly a deserving candidate for the next review of threatened plants. In view of the evidence for current loss of habitat, we recommend a rank of Taxonomically indeterminate-Declining.

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