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The calcicolous vascular flora of New Zealand

Life forms, taxonomy, biogeography and conservation status

Geoffrey M. Rogers, Shannel P. Courtney and Peter B. Heenan

New Zealand Government

Department of Conservation
Te Papa Atawhai

Cover: A pedestal remnant of Otekaike Limestone at Awahokomo in the Waitaki Valley typifies the plight of many eastern South Island limestone habitats. It is a severely degraded ecosystem, stripped of most of its regolith by wind-ablation and invaded by weeds, particularly the yellow-flowered stone crop (*Sedum acre*) and the blue-flowered viper's bugloss (*Echium vulgare*). Yet, it supports the highest concentration of narrow-range calcicoles in New Zealand, with five Awahokomo endemics and five narrow-range taxa that are shared with other Otekaike Limestone outcrops of the Waitaki Valley (see also Molloy et al. 1999), along with the basicole *Chaerophyllum basicola* (Heenan & Molloy 2006). Weed suppression is undertaken by staff of the Department of Conservation/Te Papa Atawhai and the Queen Elizabeth II National Trust/Nga Kairauhi Papa. Wire exclosures protect palatable calcicoles from rabbits. *Photo: Geoff Rogers*.

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The calcicolous vascular flora of New Zealand

Life forms, taxonomy, biogeography and conservation status

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Abstract

This report describes the life forms, taxonomic status, geological biogeography and conservation status of 152 calcicolous taxa in New Zealand, 91 (60%) of which have been formally named. Of the remaining 61 unnamed taxa, 26 are raised in this study with supporting voucher specimens. This is the first endeavour to describe the calcicolous vascular flora of New Zealand which, at 5.6% of the estimated total New Zealand vascular flora, is substantially greater than previously thought. Most calcicoles (91%) are confined to the South Island, with only 13 taxa occurring in the North Island, and 95% of the calcicoles are endemic to regionally-confined geological units, with a richness bias towards units located in West Nelson, Marlborough and Canterbury. In addition, 73% have total habitat areas of <10 ha, likely as a result of adaptation to persistent, isolated, differentiated terrains that provided non-forest habitat throughout the numerous climatic cycles of the Pleistocene. In total, 71 (47%) of the calcicolous taxa are ranked as Data Deficient or Threatened (cf. 14% of the entire flora), 43 (29%) of which are ranked as Nationally Critical. However, 33 (46%) currently receive no form of conservation management. Together, our measures of taxonomic resolution and extinction risk argue for this being a particularly under recognised and threatened flora and ecosystem.

Keywords: calcareous substrates, calcicoles, calcicolous flora, biogeography, threatened plants, New Zealand

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1. Introduction

Few geological substrates have landform, geochemical and/or floristic characters that lead to their recognition as distinct ecosystem types. New Zealand's outcrops of ultramafic rocks are one example, with their extreme geochemistry, vegetation and suites of local endemics (Druce et al. 1979; Lee et al. 1983; Lee 1992) being sufficient for them to be recognised as a distinct type in ecosystem classifications (e.g. Rogers & Walker 2002; Williams et al. 2007; Singers & Rogers 2014) and as floristically highly distinct globally (Kruckeburg 1992, Stevanović et al. 2003; Heads 2008).

Calcareous landforms of limestone, marble and dolomite are also characterised by peculiar landforms and are globally acclaimed for their floras, which are rich in uncommon and threatened species (Pinto da Silva et al. 1958; Wells 1969; Willis et al. 1996; Tribsch & Schönswetter 2003; Tyler 2003; Wang et al. 2005; Clements et al. 2006; Chung et al. 2014), and consequently also appear as distinct types in ecosystem classifications (Williams et al. 2007; Singers & Rogers 2014). Furthermore, Holdaway et al. (2012) rated three landform expressions of calcareous rocks (screes, boulder fields, and cliffs, scarps and tors) as 'Vulnerable' in their ecosystem threat ranking. Therefore, this study investigated the floristic distinctiveness of New Zealand's calcareous substrates.

1.1 Background to New Zealand's calcicolous flora

1.1.1 Calcareous context

Calcareous substrates occur throughout the two main islands of New Zealand, where they exhibit a wide range of sedimentary ages from the middle Cambrian to the early Quaternary. There are two broad types and ages of calcareous outcrops: Paleozoic marbles and crystalline limestones; and Cenozoic limestones (Williams 1982). The oldest known calcium carbonate ($CaCO_3$)-rich deposit is a trilobite-rich, crystalline limestone of Middle Cambrian age (c. 510 Mya) found in the Cobb Valley, West Nelson (Mortimer & Campbell 2014: 173). There are also substantial marble formations of mainly Ordovician age in West Nelson and Fiordland, while the marble at Marble Bay in Northland and Lee River in East Nelson is Permian in age, that at Kakahu Bush in Mid Canterbury is Carboniferous, and that at Dunback in North Otago is Triassic (Christie et al. 2001). The limestone on the east coast of the North Island is mainly shelly limestone and calcareous sandstone of Pliocene to early Quaternary age. The bulk of the limestone in the South Island is older than that of the North Island, being Eocene to Oligocene in age and, along with the West Waikato limestones, correlates with the major, but probably not total, marine transgression of New Zealand during the Oligocene (Nelson 1978; Cooper 1984; Campbell & Landis 2003; Trewick et al. 2006; also see Volume 57, Issue 2 of the *New Zealand Journal of Geology and Geophysics*). An older South Island limestone is the Late Cretaceous to early Oligocene Amuri Limestone, which occurs as a chalky to flinty substrate in Marlborough and Canterbury. Thus, New Zealand marbles are geologically ancient – mainly Paleozoic – while the limestones are predominantly mid to late Cenozoic in age.

Geological investigations of New Zealand's calcareous landforms have primarily focussed on their lithological character and economic potential as a mining resource (e.g. Park 1905; Marshall 1916; Speight & Wild 1918; Bishop 1967; Warren 1969; Moore 1975; Christie et al. 2001; Hollis et al. 2005). In addition, Cotton (1913) described the geomorphology of the Chalk Range, Clarence Valley, Marlborough, while Williams (1978, 1982) and Kenny & Hayward (2009) provided geomorphological descriptions of New Zealand's main karst regions, showing prominent polygonal drainage networks at Waitomo, Punakaiki and Takaka. Williams (1982) suggested that the main drivers of landform evolution were seasonal rainfall patterns, lithology, soil cover and vegetation, as well as glaciation in the case of high-altitude marble at Mt Arthur.

Limestones and marbles are composed predominantly of biologically-derived $CaCO_3$, but their clastic content – sand, silt and clay – can vary, forming the basis of a purity classification. Mortimer & Strong (2014) showed that most New Zealand limestones are of impure to medium purity, with individual very high purity samples being present in only a few formations and the purest samples (median $CaCO_3$ contents = 93–97 wt%) being found in Cambrian to Cretaceous basement terranes (e.g. marbles of Mt Arthur, West Nelson and West Fiordland), Eocene–Pliocene strata of the Chatham Islands and the Eocene Ototara Limestone of North Otago.

1.1.2 Botanical context

The majority of research on New Zealand's calcicolous flora to date has considered taxonomic revisions of genera with calcareous occurrences or calcicolous subsections of genera, sometimes with supporting accounts of their habitats and biogeography (e.g. Connor et al. 1993; Molloy 1994; Heenan 1996, 2009, 2017; Brownsey & de Lange 1997; Heenan & de Lange 1997, 1998; Ford 1998, 2007; Molloy et al. 1999; Sneddon 1999; Garnock-Jones et al. 2000; Glenny 2004; Heenan & Molloy 2006; Breitwieser et al. 2010, 2015; Smissen & Heenan 2011; Lehnebach 2012; Meudt et al. 2013; Sansom et al. 2013; Perrie & Brownsey 2016; Heenan et al. 2018).

In addition, several studies have described the precarious existences of eastern South Island calcicoles in fragmented lowland habitats (Molloy 1994; Heenan & de Lange 1997; Molloy et al. 1999; Millar & Duncan 2003; Heenan & Molloy 2006; Heenan 2009; Lehnebach 2012), while Williams & Courtney (1998) found that c. 50% of the 80 endemic taxa in West Nelson and North Westland were calcicoles. Burrows (1964) highlighted the narrow ranges of a few calcicoles, and Millar & Duncan (2003) investigated the ecological drivers for the distribution of *Pachycladon* [*Ischnocarpus*] *exile*. Bell (1973a, b), Druce et al. (1987) and Druce & Williams (1989) also studied the floras and communities of the prominent calcareous substrates of parts of Nelson and Marlborough.

Of particular importance among studies that have targeted New Zealand's calcicolous flora are:

- The pioneering work of Druce et al. (1987) highlighting the diverse communities and flora of West Nelson's varied calcareous landforms, and Druce & Williams (1989) emphasising the vegetation and floristic distinctiveness of South Marlborough's Amuri Limestone.
- The autecological narrative of *Australopyrum* by Molloy (1994) and the work of Molloy et al. (1999) highlighting the rich and somewhat novel calcicolous flora of Awahokomo, Waitaki Valley, Otago.

1.1.3 Terminology

Molloy (1994) defined a calcicole as 'a wild plant characteristic of limestone and other base-rich parent materials', allowing the inclusion of plants that are found not only on limestone but also on basic volcanics, schists, calcareous mudstones and allied parent materials. However, Molloy (1994) also suggested that 'Perhaps the term "calcicole" should be abandoned and replaced by another such as "basicole", embracing plants showing a preference for all base-rich materials, not just limestone'. However, Ferreira (1963, 1964) provided evidence for a distinction between calciphilous and basiphilous plants based on their field behaviour and experimental tolerances to soil chemistry.

For the purposes of the present study, we have used a narrower definition of calcicole that includes two distinct subcategories: obligate calcicoles, which occur exclusively on limestone, marble and dolomite (rocks of > 50% $CaCO_3$ and/or calcium magnesium carbonate ($CaMg(CO_3)_2$)) and their rendzinas (a fertile, lime-rich soil with dark humus above a soft or hard calcareous layer); and facultative calcicoles, which occur predominantly on those rocks or their rendzinas. These two categories could be viewed as subsets of the basicolous concept – plants that occur on base-rich substrates such as basalts, schists and calcareous mudstones. The first of these categories is more or less akin to the 'obligate calcicole' category of Burrows (1964), the 'strong calcicole' category of Druce et al. (1987) and Druce & Williams (1989), which was used for plants ‘never found away from areas of calcareous rocks’, and the group of plants recognised by Steele (1955) as ‘growing successfully on neutral soils with high calcium supply and in the field [being] strictly confined to limestone’. Our second category has been less recognised previously but is probably broadly equivalent to the ‘weak calcicole’ category of Druce et al. (1987) and Druce & Williams (1989), which was used for ‘those (plants) in certain circumstances found away from such rocks’. We have excluded from our list those taxa that behave as strong calcicoles in some situations but do not strictly conform to the definition of either category, such as *Parahebe linifolia* and *Anenome tenuicaulis* in West Nelson, and *Raoulia beauverdii* in Marlborough. Also excluded are taxa often labelled basicoles showing a preference for base-rich substrates but not exclusively or predominantly calcareous substrates,

1.2 Objective

Burrows (1964) suggested that ‘only a few species [in New Zealand] are obligate or near-obligate calcicoles’, and this view was shared by Druce et al. (1987: 64). However, Molloy (1994) suggested that the overall importance of the calcicolous component of the New Zealand flora has been underestimated, adding that ‘On a broader scale, a critical survey of the indigenous and naturalised florulas of all limestone and base-rich habitats in New Zealand is required’. Therefore, this study sought to profile New Zealand’s indigenous calcicolous vascular flora at a national scale by examining its life forms, present level of taxonomic resolution, biogeographic patterns in relation to a geological classification of calcareous rocks and national conservation status based on published threat ratings of the individual taxa. By presenting such a national perspective on this flora, this study was aimed specifically at the needs of conservation policy, planning and management, whilst contributing to an emerging suite of studies on azonal ecosystems targeting national patterns of plant composition and ecosystem threat syndromes (e.g. ultramafic landforms (Lee 1992), braided rivers (Williams & Wiser 2004), gravel beaches (Wiser et al. 2010) and coastal turf (Rogers & Wiser 2010; Rogers & Monks 2016)).

2. Methods

2.1 Life forms and taxonomic status

To compile a list of the indigenous calcicolous vascular flora of New Zealand, we initially undertook literature and herbarium searches, and consulted with botanical experts. We recognised three taxonomic categories within the emerging list of putative calcicoles: taxa that had been formally named in the scientific literature with descriptions that indicated biogeographic and/or habitat confinement to calcareous substrates; putatively distinct, unnamed taxa that were supported by a voucher specimen (often with an accompanying tag name) and had been referenced in the literature (namely Druce et al. 1987; de Lange et al. 2004, 2009, 2013; Thorsen et al. 2009; Smissen & Heenan 2011); and putatively distinct, unnamed taxa that had been suggested by taxonomists and/or field botanists and ourselves as calcicoles but had not previously appeared in the literature.

To test the integrity or veracity of claims that each formally named taxon exhibited calcicolous behaviour, we conducted field surveys that specifically targeted each taxon’s substrate/regolith distribution and also checked for absences on adjoining non-calcareous substrates. To test the hypotheses that the unnamed taxa in each of the other taxonomic categories were calcicoles, we first checked herbarium records (particularly CHR, OTA and WELT) for their morphological distinctiveness, referring also to voucher annotations, and discussed the taxonomic and habitat claims with knowledgeable taxonomists and field botanists. We then conducted field surveys that targeted each taxon's substrate/regolith distribution and also checked for absences on adjoining non-calcareous substrates. The extinct *Myosotis cinerascens* was the only taxon not encountered in the wild, although its historical distribution in Castle Hill basin was targeted during a field survey. All field surveys were conducted between 2004 and 2017.

Some of the formally named and unnamed taxa that were proposed as being calcicoles based on our definitions were rejected following the appraisal of herbarium and field data (e.g. *Chionochloa flavescens* ssp. *lupeola*; Edgar & Connor 2000: 441), resulting in a final list of 152 taxa that included 90 formally named taxa, 36 unnamed taxa that had previously been cited in the literature and 26 taxa raised in this study with supporting voucher specimens.

The calcicolous taxa were categorised into the following life forms, based on Druce (1993): dicotyledonous tree, shrub, liane, fern, grass, sedge, composite herb and non-composite herb. The proportion of each was then compared with that in the entire New Zealand indigenous vascular flora using an updated version of Druce's (1993) masterlist of New Zealand taxa (Courtney 2011).

To summarise the taxonomic status of calcicoles, we simply determined the number of formally named and unnamed taxa. In addition, since the New Zealand flora has a highly skewed distribution of genus richness (Fenner et al. 1997; Rogers & Walker 2002), with a large proportion of monospecific genera and a small proportion of very rich genera, we also examined the taxon richness of genera that contribute to the calcicolous flora and the proportions of calcicolous taxa in each contributory genus.

2.2 Biogeography

To investigate the distribution of calcicolous taxa in terms of calcareous substrates, we drew upon the seamless 1:250 000-scale, digital QMAP database for New Zealand (www.gns.cri.nz/Home/Our-Science/Earth-Science/Regional-Geology/Geological-Maps/1-250-000-Geological-Map-of-New-Zealand-QMAP), which has previously been used to produce a geological map of New Zealand (see Heron 2014). We first compiled a classification of New Zealand's calcareous substrates by selecting areas of limestone and marble (rocks containing $> 50\%$ $CaCO_3$ – these were rarely intermixed with dolomite) from the database, and mapping those substrates of a broadly similar age and landform appearance as colour-coded polygons on 1:1 000 000-scale maps of the North and South Islands (after Smith Lyttle 2014 – based on Turnbull & Smith Lyttle 1999; Fig. 1A & B).[1] These substrate polygons were then subjectively classified into aggregate regional units using free-drawn boundary lines to depict their broad spatial extent.

Next, we investigated the broad elevational distribution of the calcicolous flora by examining the presence of each taxon in different altitudinal belts. To do this, we rationalised the six altitudinal belts of Wardle (1991: 77) into three: a lowland belt, which is equivalent to Wardle's warm temperate belt; a montane belt, which combines Wardle's cool temperate and subalpine belts; and an alpine belt, which combines Wardle's penalpine, alpine and nival belts. It should be noted that some taxa occur in more than one belt.

We also made a subjective estimate of each taxon's areal extent by using three area of occupancy classes: < 1 ha, 1–10 ha and > 10 ha.

Finally, we used linear mixed effects models to test the following hypotheses:

- There is no significant difference in the mean area of occupancy scores between calcicoles that occur predominantly below (lowland and montane) and above (alpine) the treeline.
- There is no significant difference in the number of geological units occupied and the mean area of occupancy scores between obligate and facultative calcicoles.

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[1] Note that because of the scale of data capture and the need to generalise the rock descriptions, the polygon boundaries shown in Fig. 1A & B have been smoothed. Also, although the mapped outcrops are dominated by calcareous substrates, they may also include lesser amounts of other rocks.

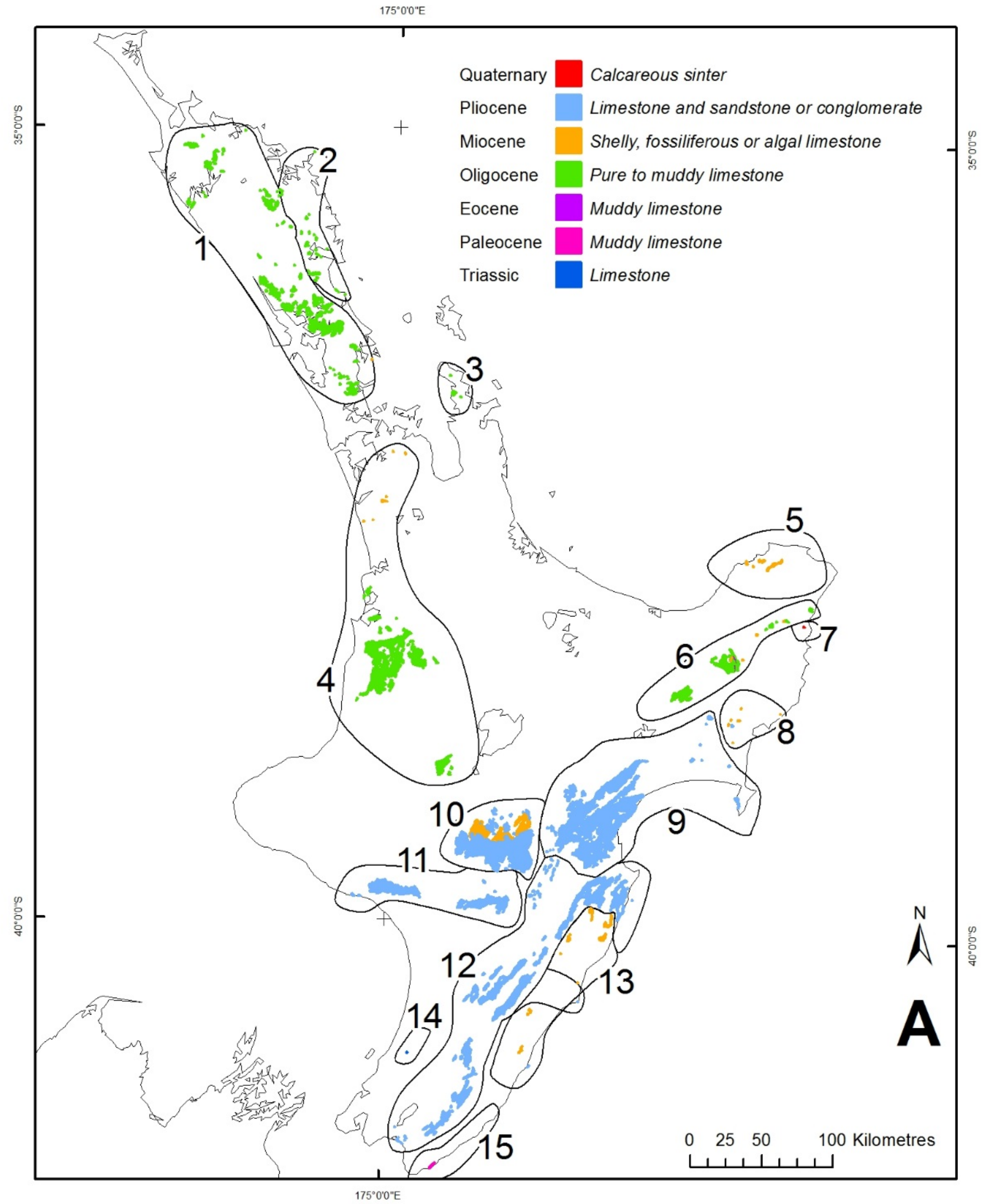

Figure 1. Distributions of the calcareous substrates of New Zealand in A. the North Island and B. the South Island. Maps are drawn at a 1:1 000 000 scale using areas of limestone and marble (rarely intermixed with dolomite) (rocks containing >50% $CaCO_3$) extracted from the 1:250 000-scale, digital QMAP database for New Zealand (Heron 2014; see section 2.2). Calcareous substrates of a similar age and broad landform appearance have been rendered and mapped as colour-coded polygons. Free-drawn polygons were then used to classify these into regional units, the names of which are listed in Table 4.

Our models included random intercepts for the family and genus of each taxon to account for taxonomic relatedness. All other terms were included as fixed effects, with area of occupancy scores being treated as a factor and the number of geological units occupied being included as a continuous variable (in the latter model), and the error terms were assumed to have a binomial distribution. We tested for over-dispersion of the modelled factors (Browne et al. 2005), which was not significant. The estimates represent contrasts calculated directly from the mean parameter estimates. We also estimated 95% highest posterior density (HPD) intervals from the mixed models by simulating the modelled parameter posterior distributions (n = 1000), calculating contrasts for each replicate and using these replicates to estimate the intervals (intervals that do not overlap zero are considered significant). All analyses were carried out in R (R Core Team 2012).

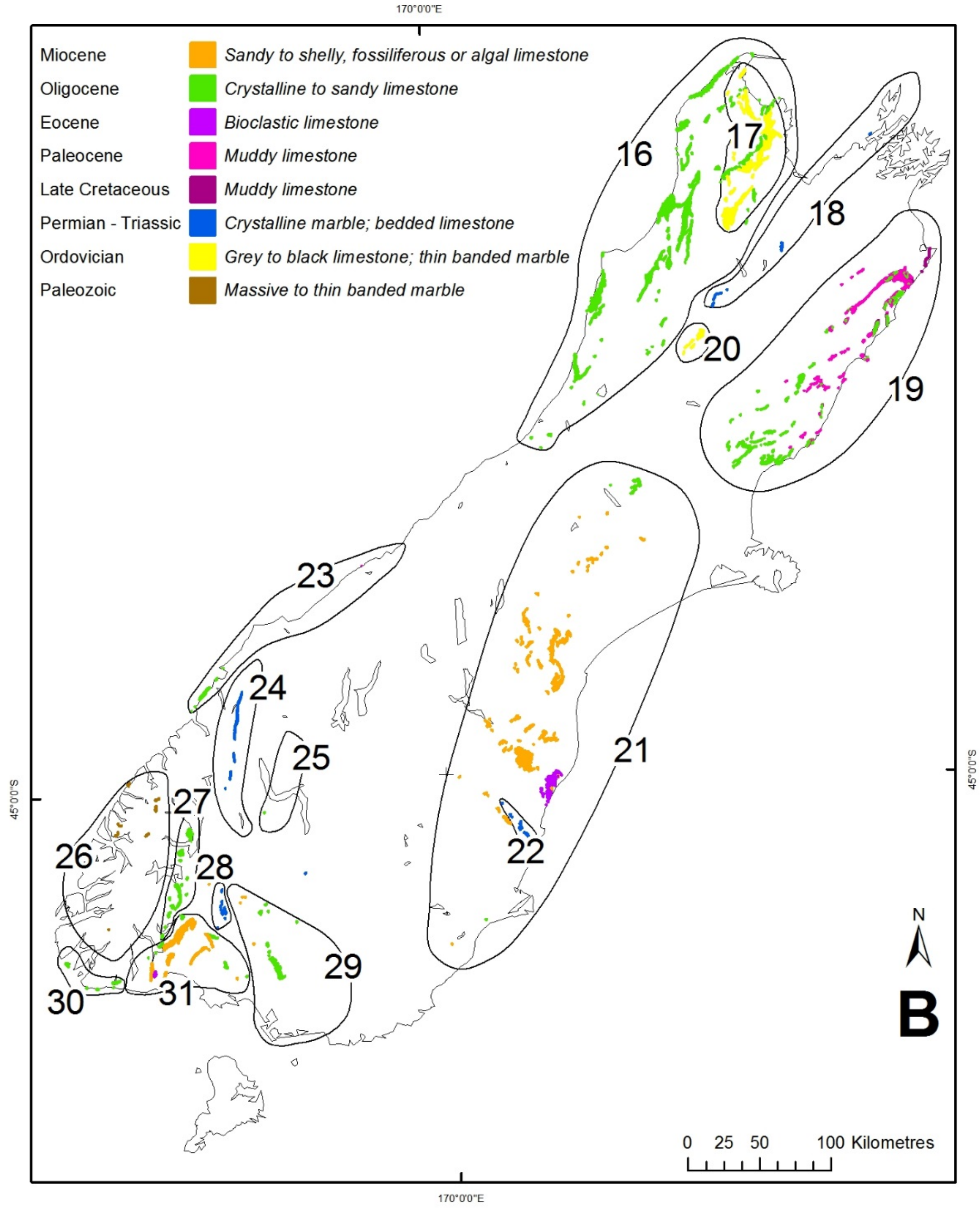

Fig. 1. continued.

2.3 Conservation status

Where available, we obtained the threat ranking of each taxon from de Lange et al. (2013) and used this to compile a conservation status for the calcicolous flora. For those taxa that are not listed in de Lange et al. (2013), we have provided a suggested threat ranking based on the criteria of Townsend et al. (2008) using our personal knowledge, sometimes supplemented with that of botanical experts. We then examined the frequency of taxa ranked as Data Deficient or Threatened by genus in each of the 31 geological units. In addition, we assessed the level of conservation engagement that each Threatened taxon is currently receiving by government environmental agencies by categorising them into three engagement categories:

1. Management to maintain or improve ecological health, which includes protection advocacy
2. Inventory, monitoring and periodic surveillance
3. No taxon-specific management

3. Results

3.1 Life forms and taxonomic status

In our surveys, we recognised 152 calcicoles (Table 1), which represents 5.6% of the 2718 taxa that make up the entire indigenous vascular flora of New Zealand according to Courtney (2011). The dominant life forms in hierarchical order are non-composite herbs, shrubs, composite herbs and grasses, while there are comparatively few sedges, ferns, dicotyledonous trees and lianes (Table 2). There are no gymnosperm or monocot trees or shrubs, rushes, orchids, or monocot herbs (other than grasses and sedges) among the calcicoles.

There are higher percentages of composite herbs, non-composite herbs and grasses in the calcicolous flora than in the entire vascular flora, but lower percentages of ferns and sedges. There are few calcicolous trees, with only the moderately-sized *Hoheria ovata, Pseudopanax macintyrei* and *Sophora longicarinata* being present in the flora, which was perhaps expected since cliffs are a common calcareous habitat and mostly unsuitable for anchoring large trees.

Just 91 (60%) of the 152 calcicolous taxa we recognised have been formally named, which is a much lower proportion than the 83% for the entire flora listed by Courtney (2011) (Table 3 and Fig. 2). Of the 61 unnamed taxa, 35 (23%) have previously been cited in Druce & Williams (1989), Thorsen et al. (2009), de Lange et al. (2004, 2009, 2013) and Smissen & Heenan (2011), while the remaining 26 (17%) are raised in this study as putative taxa with supporting vouchers. There are two or more unnamed calcicoles in each of the following genera: *Craspedia* (15), *Senecio* (6) (Fig. 3), *Carex* (4), *Hebe* (3), *Melicytus* (2), *Brachyscome* (2), *Chaerophyllum* (2), *Coprosma* (2), *Myosotis* (2) and *Ranunculus* (2).

The calcicolous flora includes 57 genera (Table 3), which represents 13% of the 433 genera in the entire flora as listed by Rogers & Walker (2002). Several patterns are evident at the genus level:

- The six genera with the largest numbers of calcicolous taxa are *Craspedia* (15), *Myosotis* (11), *Hebe* (10), *Gentianella* (9), *Carex* (8) and *Senecio* (8).
- Overall, 111 (73%) of the calcicolous taxa belong to 24 genera with high overall richness (>19 taxa in the entire flora): *Asplenium* (3), *Brachyglottis* (2), *Cardamine* (6), *Carex* (8), *Carmichaelia* (2), *Celmisia* (2), *Chionochloa* (2), *Colobanthus* (4), *Coprosma* (2), *Craspedia* (15), *Epilobium* (3), *Gentianella* (9), *Hebe* (10), *Melicytus* (4), *Myosotis* (11), *Parahebe* (2), *Pimelea* (5), *Poa* (4), *Ranunculus* (4) and *Senecio* (8).
- Fifteen genera with moderate to high overall richness (>10 taxa in the entire flora) have 10% or more of that richness represented by calcicoles: *Craspedia* (26%), *Gentianella* (21%), *Brachyscome* (20%), *Chaerophyllum* (20%), *Gingidia* (20%), *Pachycladon* (20%), *Myosotis* (20%), *Senecio* (19%), *Trisetum* (17%), *Cardamine* (15%), *Colobanthus* (14%), *Melicytus* (13%), *Wahlenbergia* (13%), *Pimelea* (10%) and *Montia* (10%).
- Four genera with low overall richness (<4 taxa in the entire flora) have >25% of that richness represented by calcicoles: *Australopyrum* (2 taxa or 100%), *Poranthera* and *Simplicia* (1 taxon each or 50%) and *Botrychium* (1 taxon or 33%).
- Several grass genera with low to moderate overall richness include just one or two calcicoles: *Anthosachne, Australopyrum, Dichelachne, Festuca, Koeleria, Simplicia, Stenostachys* and *Trisetum.*

Table 1. The calcicolous vascular flora of New Zealand. Taxa that have not been formally named but have appeared previously in the literature with a voucher specimen are referenced to a supporting publication. Additional taxa that are unnamed and cited for the first time here are listed according to their probable affinity (e.g. *Celmisia* aff. *gracilenta*) or, where this is unknown or there is a suspected aggregate, names are then listed alphabetically with their affinity noted if known with some confidence (e.g. *Koeleria* cf. *novozelandica* (AK 252546; Awahokomo)). An obligate or facultative rating for each taxon is also shown (for definitions see section 1.1.3).

TAXON	OBLIGATE (o) OR FACULTATIVE (f)
Aciphylla aff. *ferox* (CHR 617083A + CHR 617083C; Mt Cass)[a]	o
Anthosachne sacandros (Connor) Barkworth et S.W.L.Jacobs	o
Asplenium cimmeriorum Brownsey et de Lange	f
Asplenium lepidotum Perrie & Brownsey	f
Asplenium lyalli (Hook.f.) T.Moore	f
Australopyrum calcis subsp. *calcis* Connor et Molloy	o
Australopyrum calcis subsp. *optatum* Connor et Molloy	o
Azorella aff. *haastii* (CHR 212602; Fiordland)[a]	o
Botrychium aff. *lunaria* (CHR 289336; NW Nelson)[b]	o
Brachyglottis compacta (Kirk) B.Nord.	o
Brachyglottis laxifolia (Buchanan) B.Nord.	f
Brachyscome (a) (WELT 10278; Ward)[c]	o
Brachyscome (b) (CHR 518295; Pareora River)[d]	o
Cardamine basicola Heenan	f
Cardamine bisetosa Heenan	o
Cardamine caesiella Heenan	o
Cardamine coronata Heenan	o
Cardamine integra Heenan	o
Cardamine verna Heenan	o
Carex calcis K.A.Ford	o
Carex cremnicola K.A.Ford	o
Carex dolomitica Heenan et de Lange	o
Carex impexa K.A.Ford	o
Carex aff. *testacea* (CHR 510694; Owen)[a]	o
Carex aff. *wakatipu* (a) (CHR 249755; “small, 2-style”)[a]	o
Carex aff. *wakatipu* (b) (CHR 510696; “small, 3-style”)[a] (cited as *Carex* (o) (CHR 249779; aff. *C. wakatipu*; small, 3-style) by Thorsen et al. (2009))	o
Carex aff. *wakatipu* (c) (CHR 275182; Flaxbourne)[a]	o
Carmichaelia astonii G.Simpson	o
Carmichaelia hollowayi G.Simpson	o
Celmisia inaccessa Given	o
Celmisia aff. *gracilenta* (CHR 282958; Te Mata Peak)[c]	o
Chaerophyllum aff. *novae-zelandiae* (a) (CHR 573578; Waitaki)[a]	o
Chaerophyllum aff. *novae-zelandiae* (b) (CHR 580158; Weld)[a]	o
Chionochloa flavicans f. *temata* Connor	o
Chionochloa spiralis Zotov	o
Clematis marmoraria Sneddon	o
Colobanthus squarrosus Cheeseman subsp. *squarrosus*	o
Colobanthus squarrosus subsp. *drucei* Sneddon	o
Colobanthus (f) (CHR 365413; “marble”)[e]	f
Convolvulus aff. *verecundus* (CHR 546302; Awahokomo)[f]	o
Coprosma aff. *cheesemanii* (CHR 469919; “rimicola”)[e]	f
Coprosma aff. *obconica* (CHR 285876; Mount Burnett)[a]	o
Craspedia (a) (CHR 273160; Marfells)[a]	o

Continued on next page

Table 1 continued

TAXON	OBLIGATE (o) OR FACULTATIVE (f)
Craspedia (b) (CHR 277655; marble)[a]	o
Craspedia (c) (CHR 358403; Garibaldi)[a]	o
Craspedia (d) (CHR 489351; Owen)[a]	o
Craspedia (e) (CHR 489432; Mt Cass)[a]	o
Craspedia (f) (CHR 489433; Awahokomo)[a]	o
Craspedia (i) (CHR 395643; Fyfe River)[c]	o
Craspedia (g) (CHR 469764; Pikikirunga)[c]	o
Craspedia (h) (CHR 260312; Gouland Downs)[c]	o
Craspedia (o) (CHR 471883; Loveridge)[c]	o
Craspedia (r) (CHR 313349; Punakaiki)[c]	o
Craspedia (t) (CHR 365392; Chalk)[c]	o
Craspedia (tt) (CHR355129; “calcicole”)[e]	o
Craspedia aff. *uniflora* (c) (CHR 547140B; “Hacket Limestone”)[a]	o
Craspedia aff. *uniflora* (d) (CHR 179342A; “North Canterbury white”)[a]	o
Dichelachne lautumia Edgar et Connor	o
Dracophyllum marmoricola S.Venter	o
Epilobium gracilipes Kirk	f
Epilobium vernicosum Cheeseman	f
Epilobium wilsonii Cheeseman	f
Euphrasia (a) (CHR 471903; “white”)[c]	o
Festuca deflexa Connor	f
Festuca aff. *novae-zelandiae* (AK 252541; Awahokomo)[b]	o
Galium aff. *perpusillum* (CHR 249195; “calcicole”)[e]	f
Gentianella angustifolia Glenny	o
Gentianella astonii subsp. *arduana* Glenny et Molloy	o
Gentianella astonii (Petrie) T.N.Ho et S.W.Liu subsp. *astonii*	o
Gentianella calcis Glenny et Molloy subsp. *calcis*	o
Gentianella calcis subsp. *manahune* Glenny et Molloy	o
Gentianella calcis subsp. *taiko* Glenny et Molloy	o
Gentianella calcis subsp. *waipara* Glenny et Molloy	o
Gentianella filipes (Cheeseman) T.N.Ho et S.W.Liu	o
Gentianella aff. *calcis* subsp. *waipara* (CHR 569771; Earthquakes)[c]	o
Geranium aff. *brevicaule* (CHR 505532; Manahune)[a]	o
Gingidia enysii (Kirk) J.W.Dawson var. *enysii*	o
Gingidia haematitica Heenan	o
Gingidia aff. *haematitica* (CHR 552973; Northwest Nelson)[a] (see Sansom et al. 2013: 2232)	o
Hebe albicans var. (CHR 273484; “glaucophylla NWN erect”)[a]	o
Hebe arganthera Garn.-Jones, Bayley, W.G.Lee et Rance	o
Hebe calcicola Bayly et Garn.-Jones	o
Hebe ochracea Ashwin	o
Hebe recurva Simpson et Thompson	o
Hebe scopulorum Bayley, de Lange et Garn.-Jones	o
Hebe stenophylla var. *hesperia* Bayly et Garn.-Jones	o
Hebe townsonii (Cheeseman) Cockayne et Allan	o
Hebe aff. *albicans* (AK 252966; Mt Burnett)[c]	o
Hebe aff. *treadwellii* (CHR 394533; Bald Knob Ridge)[c]	o
Helichrysum aff. *intermedium* (CHR 274826; Chalk Range)[c]	o
Heliohebe hulkeana subsp. *evestita* Garn.-Jones	o
Heliohebe maccaskillii (Allan) D.A.Norton et Molloy	o
Hoheria ovata Simpson et J.S.Thomson	f

Continued on next page

Table 1 continued

TAXON	OBLIGATE (o) OR FACULTATIVE (f)
Koeleria cf. *novozelandica* (AK 252546; Awahokomo)[c]	o
Leptinella calcarea (D.G.Lloyd) D.G.Lloyd et C.J.Webb	f
Melicytus improcerus Heenan, Courtney, de Lange et Molloy	o
Melicytus obovatus (Kirk) Garn.-Jones	f
Melicytus (a) (CHR 355077; Matiri Range)[c]	o
Melicytus aff. *obovatus* (b) (AK 229988; Mt Burnett)[c]	o
Montia drucei (Heenan) Heenan	o
Myosotis angustata Cheeseman	o
Myosotis arnoldii L.B.Moore	o
Myosotis brockiei L.B.Moore et M.J.A.Simpson	f
Myosotis chaffeyorum C.A.Lehnebach	o
Myosotis cinerascens Petrie	o
Myosotis colensoi (Kirk) J.F.Macbr.	o
Myosotis concinna Cheeseman	o
Myosotis petiolata Hook.f. var. *petiolata*	o
Myosotis saxosa Hook.f.	o
Myosotis aff. *australis* (WELT SP090247, “small white”)[c]	o
Myosotis aff. *brockiei* (CHR 497375; Lake Otuhie)[c]	o
Myrsine argentea Heenan et de Lange	o
Pachycladon exile (Heenan) Heenan et A.D.Mitch	o
Pachycladon fasciarium Heenan	o
Parahebe martinii (Garn.-Jones) Garn.-Jones	f
Parahebe senex Garn.-Jones	o
Pimelea aridula subsp. *oliga* C.J.Burrows	o
Pimelea barbata C.J.Burrows subsp. *barbata*	o
Pimelea declivis C.J.Burrows	f
Pimelea mimosa C.J.Burrows	o
Pimelea traversii subsp. *borea* C.J.Burrows	o
Poa acicularifolia Buchanan subsp. *acicularifolia*	o
Poa spania Edgar et Molloy	o
Poa sudicola Edgar	o
Poa xenica Edgar et Connor	o
Poranthera alpina Cheeseman ex Hook.f	o
Pseudopanax macintyrei (Cheeseman) Wardle	o
Pteris aff. *macilenta* (AK 210045; Punakaiki)[c]	o
Ranunculus mirus Garn.-Jones	f
Ranunculus paucifolius (Kirk)	o
Ranunculus aff. *royi* (CHR 513327; Waihao)[c]	o
Ranunculus aff. *stylosus* (CHR 515131; Manahune)[c]	o
Rubus aff. *schmidelioides* (CHR 325720; “strawberry”)[c]	o
Scandia aff. *rosifolia* (AK 344466; “inland”)[a]	f
Senecio glaucophyllus Cheeseman subsp. *glaucophyllus*	f
Senecio hauwai Sykes	o
Senecio aff. *dunedinensis* (CHR 550250; Leatham)[c]	f
Senecio aff. *glaucophyllus* (a) (CHR 501163; Cape Campbell)[a]	f
Senecio aff. *glaucophyllus* (c) (AK 286230; “South Marlborough Limestone”)[a]	o
Senecio aff. *glaucophyllus* (e) (CHR 437799; Mt Cass)[a]	o
Senecio aff. *glaucophyllus* (g) (CHR 489460 NW Nelson)[c]	f
Senecio aff. *glaucophyllus* (h) CHR 552378; “peneplain”)[a]	o
Simplicia buchananii (Zotov) Zotov	f

Continued on next page

Table 1 continued

TAXON	OBLIGATE (o) OR FACULTATIVE (f)
Sonchus aff. *novae zelandiae* (CHR 440071; "limestone")[a]	o
Sophora longicarinata G.Simpson et J.S.Thomson	o
Stenostachys deceptorix Connor	f
Trisetum drucei Edgar	f
Trisetum aff. *lepidum* (AK 251835; Awahokomo)[c]	o
Viola aff. *cunninghamii* (CHR 636937; South Marlborough)[a]	o
Vittadinia aff. *australis* (CHR 208561; South Marlborough)[g]	f
Wahlenbergia albomarginata subsp. *flexilis* (Petrie) J.A.Petterson	o
Wahlenbergia matthewsii Cockayne	o

[a] Taxonomic hypothesis created for this study.

[b] Taxonomic reference from de Lange et al. (2009).

[c] Taxonomic reference from de Lange et al. (2013).

[d] Taxonomic reference from de Lange et al. (2004).

[e] Taxonomic reference from Thorsen et al. (2009).

[f] Taxonomic reference from Smissen & Heenan (2011).

[g] Taxonomic reference from Druce & Williams (1989).

Table 2. Frequency of calcicolous taxa by life form. Also shown is the percentage of each life form in the calcicolous vascular flora and the entire New Zealand vascular flora. Note: The percentages of trees and shrubs in the entire flora have been combined.

LIFE FORM	NUMBER OF CALCICOLES	% OF LIFE FORM IN CALCICOLOUS FLORA	% OF LIFE FORM IN ENTIRE FLORA
Dicotyledonous tree	3	2	23
Shrub	30	20	
Liane	2	1	0.0004
Fern	5	3	8
Grass	17	11	8
Sedge	8	5	7
Composite herb	30	20	12
Non-composite herb	57	38	30

Table 3. Frequency (and percentage) of calcicolous taxa per genus arranged in numerically-descending order. Also shown are the number of unnamed calcicoles per genus and the number of unnamed calcicoles that have been ranked as Data Deficient or Threatened by either de Lange et al. (2013) or the present study (see section 2.3).

GENUS	No. TAXA PER GENUS (% OF GENUS)	No. UNNAMED (% OF CALCICOLES UNNAMED)	No. UNNAMED AND DATA DEFICIENT OR THREATENED
Craspedia	15 (26)	15 (100)	8
Myosotis	11 (18)	2 (18)	
Hebe	10 (8)	3 (30)	1
Gentianella	9 (21)	1 (11)	1
Carex	8 (9)	4 (50)	1
Senecio	8 (19)	6 (75)	6
Cardamine	6 (14)		
Pimelea	5 (10)		
Melicytus	4 (13)	2 (50)	2
Poa	4 (7)		

Continued on next page

Table 3 continued

GENUS	No. TAXA PER GENUS (% OF GENUS)	No. UNNAMED (% OF CALCICOLES UNNAMED)	No. UNNAMED AND DATA DEFICIENT OR THREATENED
Ranunculus	4 (7)	2 (50)	2
Asplenium	3 (12)		
Colobanthus	3 (14)	1 (33)	1
Epilobium	3 (6)		
Gingidia	3 (20)	1 (33)	
Australopyrum	2 (100)		
Brachyglottis	2 (6)		
Brachyscome	2 (20)	2 (100)	2
Carmichaelia	2 (6)		
Chaerophyllum	2(20)	2 (100)	2
Celmisia	2 (3)	1 (50)	
Chionochloa	2 (6)		
Coprosma	2 (3)	2 (100)	1
Festuca	2 (18)	1 (50)	1
Heliohebe	2 (25)		
Pachycladon	2 (20)		
Parahebe	2 (9)		
Trisetum	2 (17)	1 (50)	1
Wahlenbergia	2 (13)		
Aciphylla	1 (2)	1 (100)	1
Anthosachne	1 (11)		
Botrychium	1 (33)	1 (100)	1
Clematis	1 (8)		
Convolvulus	1 (25)	1 (100)	1
Dichelachne	1 (20)		
Dracophyllum	1 (3)		
Euphrasia	1 (3)	1 (100)	
Galium	1 (13)	1 (100)	1
Geranium	1 (7)	1 (100)	1
Helichrysum	1 (6)	1 (100)	
Hoheria	1 (13)		
Koeleria	1 (25)	1 (100)	1
Leptinella	1 (3)		
Montia	1 (10)		
Myrsine	1 (8)		
Poranthera	1 (50)		
Pseudopanax	1 (7)		
Pteris	1 (17)	1 (100)	
Rubus	1 (11)	1 (100)	
Scandia	1 (3)	1 (33)	
Schizeilema	1 (7)	1 (100)	1
Simplicia	1 (33)		
Sonchus	1 (25)	1 (100)	1
Sophora	1 (13)		
Stenostachys	1 (25)		
Viola	1 (20)	1 (100)	1
Vittadinia	1 (50)	1 (100)	
Total (% of calcicolous flora)	**152**	**61 (40)**	**38 (25)**

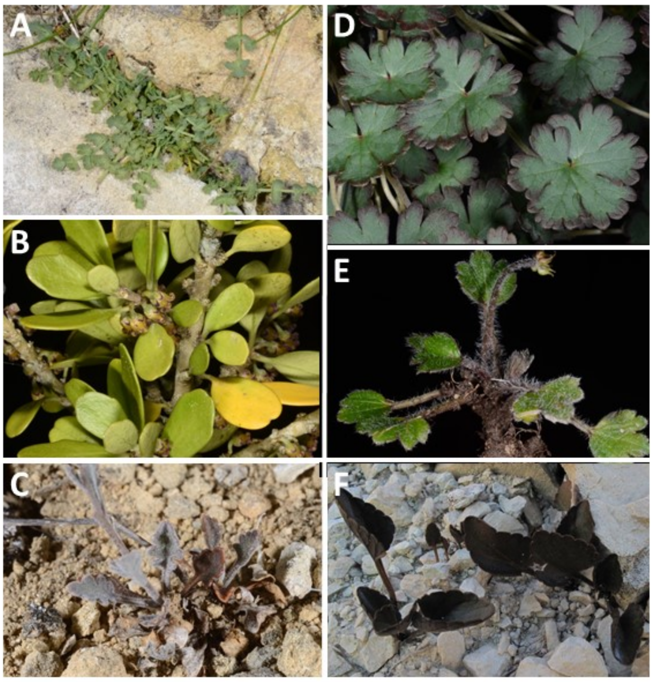

Figure 2. Examples of obligate and facultative named (A–C) and putative unnamed (D–F) calcicolous vascular taxa in New Zealand showing the diverse range of plant morphology in the calcicolous flora. A. *Gingidia enysii* (Kirk) J.W.Dawson var. *enysii* (obligate); B. *Melicytus obovatus* (Kirk) Garn.-Jones (facultative); C. *Pachycladon exile* (Heenan) Heenan et A.D.Mitch (obligate); D. *Geranium* aff. *brevicaule* (CHR 505532; Manahune) (obligate); E. *Ranunculus* aff. *stylosus* (CHR 515131; Manahune) (obligate); *F. Viola* aff. *cunninghamii* (CHR 636937; South Marlborough) (obligate).

3.2 Biogeography

3.2.1 Calcareous biogeography

Among the regions that have been mapped to date, Northland, Waikato, Whanganui, Poverty Bay, Hawke's Bay, Wairarapa, Nelson, North Westland, North and South Canterbury, North Otago, and Southland are prominently calcareous (Fig. 1A & B and Table 4). The most spatially extensive units are the Amuri Limestone unit (Wellman 1959), which stretches across East Marlborough and North Canterbury; an amalgamated complex of South Canterbury–North Otago limestone units, which include more Amuri Limestone; the Tertiary limestones of West Nelson and North Westland; and Te Aute Limestone (Nelson et al. 2003), which effectively ranges from northern Hawke's Bay to southern Wairarapa. Nelson has three distinct units (listed in descending geological age): Ordovician crystalline limestone and marble of the Mt Arthur Group; Permian Wooded Peak Limestone (Waterhouse 1967); and Oligocene limestone, calcareous mudstone and marble of the Tasman Formation. The numerous units in the eastern North Island from East Cape to Cape Palliser are all Tertiary in age, ranging from the Paleocene to the Quaternary.

The frequency of occurrence of calcicolous taxa on each calcareous unit was used to examine taxon-level biogeographic patterns (Table 4). We found that only 13 of the 152 calcicoles occur in the North Island, 9 of which are North Island endemics (3 are restricted to Te Mata Peak, Hawke's Bay; Fig. 4) There is a noteworthy absence of calcicolous taxa on calcareous units north of the Waikato. By contrast, the South Island supports 142 calcicoles, 138 of which are South Island endemics. Four South Island units have relatively high numbers of calcicoles: Mt Arthur Group crystalline limestone and marble (52 taxa); Tasman Formation limestone and marble (43 taxa); South Marlborough–North Canterbury limestone (41 taxa); and Mid–South Canterbury–North Otago limestone (29 taxa). The remaining units have relatively low numbers.

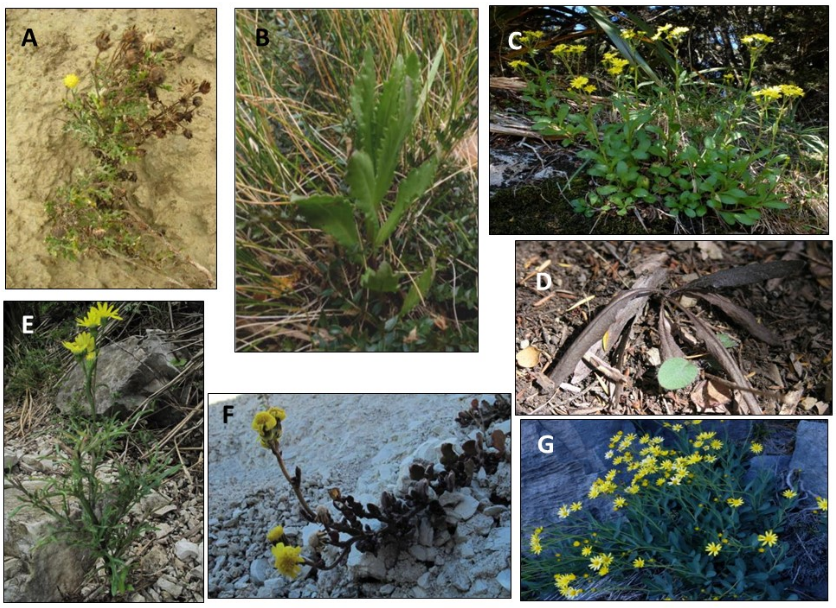

Figure 3. Examples of named and unnamed calcicolous taxa within the genus *Senecio* demonstrating the morphological distinctiveness of unnamed taxa within aggregate groups. A. *Senecio hauwai* Sykes; B. *Senecio* aff. *glaucophyllus* (g) (CHR 489460; NW Nelson); C. *Senecio* aff. *glaucophyllus* (h) (CHR 552378; "peneplain"); D. *Senecio* aff. *dunedinensis* (CHR 550250; Leatham); E. *Senecio* aff. *glaucophyllus* (d) (AK 286230; "South Marlborough Limestone"); F. *Senecio* aff. *glaucophyllus* (b) (CHR 85767; Cape Campbell); G. *Senecio glaucophyllus* Cheeseman subsp. *glaucophyllus*.

Figure 4. The homoclinal ridge of Te Aute Limestone at Te Mata Peak, Hawke's Bay, which supports three endemic calcicoles. This area is managed as a community park with limited grazing by farm stock, leading to the proliferation of pasture grasses. A. Landscape view of the homoclinal ridge; B. proliferation of pasture grasses; C. *Celmisia* aff. *gracilenta* (CHR 282958; Te Mata Peak); D. *Chionochloa flavicans* f. *temata* Connor; E. *Pimelea mimosa* C.J.Burrows.

Overall, 118 (78%) of the 152 calcicoles are confined to one calcareous unit, indicating a high degree of unit endemism. The frequency of unit endemics shows a similar pattern to total calcicolous richness, with the two Nelson units and the two Marlborough–Canterbury units mentioned above having high numbers of calcicoles and the remaining units having few or no calcicoles. Furthermore, the Marlborough and Canterbury units share the greatest incidence of endemism (78% and 79% of all calcicoles that are present), while the two West Nelson units have somewhat lower levels (56% and 49%).

Table 4. Geological characteristics of 31 calcareous units that support calcicolous taxa in New Zealand (refer to Fig. 1 for unit locations). Also shown are the number of endemic calcicoles and the total number of calcicoles per unit.

UNIT NUMBER	UNIT/FORMATION	REGION	LITHOLOGY	GEOLOGICAL AGE	No. OF CALCICOLES	No. CALCICOLES ENDEMIC TO UNIT (% OF ALL CALCICOLES ON UNIT)	No. CALCICOLES EXTINCT, DATA DEFICIENT OR THREATENED (% OF ALL CALCICOLES ON UNIT)
North Island (see Fig. 1A)							
1	Mahurangi Limestone	Northland	Muddy limestone	Oligocene	–	–	–
2	Whangarei Limestone	Northland	Bioclastic limestone	Oligocene	–	–	–
3	Coromandel Limestone	Coromandel	Flaggy limestone	Oligocene	–	–	–
4	Te Kuiti Group	Waikato	Pebbly, gritty, shelly to sandy limestone	Oligocene to early Miocene	4	1 (25)	–
5	Te Aute Formation	Cape Runaway, Poverty Bay	Limestone, sandstone, mudstone	Miocene	1	–	–
6	Waikohu River Limestone	Poverty Bay	Muddy to bioclastic limestone	Eocene to Miocene	3	–	–
7	Te Puia Springs Sinter	Poverty Bay	Calcareous sinter	Quaternary	–	–	–
8	Patutahi Limestone, Te Aute Formation	Poverty Bay	Shelly limestone	Miocene to Pliocene	1	–	–
9	Te Aute Formation	Northern Hawke's Bay	Bedded, sandy to shelly limestone	Early Pliocene to early Pleistocene	8	3 (38)	3 (38)
10	Unlabelled limestone	Upper Rangitikei River, Waiouru	Alternating limestone, sandstone, mudstone and conglomerate	Miocene to Pliocene	2	–	–
11	Unlabelled limestone	Rangitikei Valley, Whanganui	Shelly limestone	Pliocene	2	–	–
12	Petane Group, Te Aute Formation	Southern Hawke's Bay	Bioclastic limestone	Pliocene	7	3 (43)	2 (29)
13	Whakataki-Castle Point Limestone	Eastern Wairarapa	Sandy to pebbly bioclastic limestone	Miocene	3	1 (33)	–
14	Unlabelled limestone	Otaki River, Horowhenua	Limestone	Triassic	–	–	–
15	Unlabelled limestone	Te Kaukau Point, southern Wairarapa	Well-bedded, muddy limestone	Paleocene	1	–	–

Table 4 continued

UNIT NUMBER	UNIT/FORMATION	REGION	LITHOLOGY	GEOLOGICAL AGE	No. OF CALCICOLES	No. CALCICOLES ENDEMIC TO UNIT (% OF ALL CALCICOLES ON UNIT)	No. CALCICOLES EXTINCT, DATA DEFICIENT OR THREATENED (% OF ALL CALCICOLES ON UNIT)
South Island (see Fig. 1B)							
16	Tasman Formation (plus Nile Group, Takaka Limestone, Matiri Formation)	West Nelson–North Westland	Crystalline to sandy limestone and calcareous mudstone; marble	Oligocene	43	21 (49)	7 (16)
17, 20	Mt Arthur Group	West Nelson	Crystalline limestone and marble	Ordovician	52	29 (56)	11 (21)
18	Wooded Peak Limestone	East Nelson	Hard, bedded marble	Permian	10	3 (30)	3 (30)
19	Amuri Limestone (plus other local units)	South Marlborough–North Canterbury	Shelly, sandy, hard limestone; bedded, hard, fine-grained limestone	Late Cretaceous to Miocene	41	32 (78)	28 (68)
21	Goodwood, Green Valley, Otatara, Otekaike and Amuri Limestones	Mid-South Canterbury–North Otago	Hard/soft, massive to bedded, shelly limestone; sandy limestone and marl	Eocene to Miocene	29	23 (79)	24 (83)
22	Blue Mountain Limestone	Dunback, North Otago	Hard-jointed marble	Permian	–	–	–
23	Jackson Formation, Awarua Limestone	South Westland	Hard bioclastic to micritic limestone	Oligocene	1	–	–
24	Wooded Peak Limestone	Northern Southland, Northwest Otago	Bedded, fine-grained, bioclastic limestone	Permian	1	–	–
25	Bobs Cove Beds	Wakatipu	Bedded, sandy limestone	Oligocene	1	–	–
26	Fiordland Marble	West Fiordland	Marble in schist	Paleozoic	6	2 (33)	2 (33)
27	Tunnel Burn	East Fiordland	Hard, shelly/sandy, bedded limestone	Late Oligocene to Miocene	4	–	1 (25)
28	Glendale Limestone	Productus Creek, western Southland	Limestone, fault zone melange	Permian	1	–	–
29	Forest Hill Formation	Southland plains	Bedded, shelly/sandy, hard limestone	Oligocene	1	–	–
30	Chalky Island Formation	Southwest Fiordland	Bedded, fine-grained limestone or marl	Oligocene	1	–	–
31	McIvor Formation, Clifden Subgroup	Western Southland	Sandy to bioclastic limestone	Eocene to Miocene	1	–	–

A further 27 taxa are effectively regional endemics, being confined to broad regions that contain more than one calcareous unit. Among these, 1 is a Hawke's Bay–Wairarapa endemic (shared on two separate components of Te Aute Limestone), 20 are Nelson endemics, 4 are Marlborough–Canterbury endemics (shared on different components of Amuri Limestone) and 2 are Fiordland endemics (shared on western Fiordland Marble and eastern Tunnel Burn Limestone). Thus, a total of 145 (95%) of New Zealand's calcicoles are regional endemics (118 unit endemics plus 27 broader regional endemics). Overall, Nelson has a large component of that endemism, with 77 calcicoles (or 51% of New Zealand's total) being variously endemic to its three units: 53 are single unit endemics (Table 4), 17 occur on two of the three units (15 of which are shared by the Tasman Formation and the Mt Arthur Group) and just 3 (the trees *Pseudopanax macintyrei* and *Sophora longicarinata*, and the fern *Asplenium lepidotum*) occur on all three units.

At an inter-regional scale, the calcicoles *Myosotis arnoldii* and *Wahlenbergia matthewsii* provide a tenuous biogeographic link between the high endemic centres of Nelson and South Marlborough–North Canterbury. Four taxa span the South Marlborough–North Canterbury and the Mid-South Canterbury–North Otago units: *Australopyrum calcis* ssp. *optatum*; *Galium* aff. *perpusillum* (CHR 249195; "calcicole"); *Myosotis colensoi*; and *Poa acicularifolia* ssp. *acicularifolia*. Two further taxa, *Asplenium cimmeriorum* and *Trisetum drucei* (both of which are facultative), show wide disjunctions between small numbers of North Island and South Island units. Finally, only two taxa, both of which are facultative, are widely distributed: *Asplenium lyallii*, which occurs from the Te Kuiti Group unit southwards to Fiordland and Southland; and *Epilobium gracilipes*, which occurs from the Waihou River unit in Poverty Bay south to Fiordland Marble.

3.2.2 Altitudinal biogeography

The calcicolous flora predominantly occurs below the treeline in lowland and montane belts, with 83 (55%) of the 152 taxa occurring in the lowland belt and 78 (51%) occurring in the montane belt (Table 5). Overall, 113 taxa (74%) occur entirely below the treeline as non-alpine taxa, among which a sizeable group are exclusively lowland (53 taxa or 35%), and 33 taxa (22%) are exclusively montane, with 27 taxa (18%) spanning both belts. By contrast, 39 calcicolous taxa (26%) occur in the alpine belt, 21 (14%) of which are exclusively alpine. Just three taxa span all three altitudinal belts.

Table 5. Frequency (and percentage) of calcicolous taxa in different altitudinal belts (see section 2.2).

LOWLAND		LOWLAND + MONTANE	MONTANE		MONTANE + ALPINE	ALPINE		LOWLAND + MONTANE + ALPINE
Total	Exclusive to belt	Total	Total	Exclusive to belt	Total	Total	Exclusive to belt	Total
83 (55%)	53 (35%)	27 (18%)	78 (51%)	33 (22%)	15 (10%)	39 (26%)	21 (14%)	3 (0.02%)

3.2.3 Area of occupancy

Among the 152 calcicoles, 76 (50%) have an area of occupancy of <1 ha, 33 (22%) occupy 1–10 ha and 42 (28%) occupy >10 ha. Thus, 109 (72%) have an area of occupancy of <10 ha (extinct *Myosotis cinerascens* was not included).

3.2.4 Obligate v. facultative

We categorised 124 (82%) of the calcicolous flora as obligate and 28 (18%) as facultative (Table 1).

3.2.5 Dispersion

We found that taxa that predominantly occur in habitats above the treeline have a significantly greater likelihood of having area of occupancy scores of 2 or 3 than taxa that occur predominantly below the treeline (Table 6). However, there was no significant difference in the number of geological units occupied between the two altitudinal classes of calcicoles. In addition, facultative taxa have a significantly greater likelihood of having area of occupancy scores of 3 (>10 ha) than obligate taxa (Table 7).

Table 6. Parameter estimates and their associated 95% highest posterior density (HPD) intervals for testing the proposition that there is no significant difference in the mean area of occupancy scores between calcicoles that occur predominantly below (lowland and montane) and above (alpine) the treeline. (See section 2.2 for a description of the model parameters.

TERM	MEAN (95% HPD INTERVAL)
Intercept	–2.76 (–3.72 to –1.74)
Factor (area of occupancy 2)	1.24 (–0.1 to 2.58)
Factor (area of occupancy 3)	2.96 (1.79 to 4.19)*

* HPD intervals that do not overlap zero are considered significant.

Table 7. Parameter estimates and their associated 95% highest posterior density (HPD) intervals for testing the proposition that there is no significant difference in the number of geological units occupied and the mean area of occupancy scores between obligate and facultative calcicoles. (See section 2.2 for a description of the model parameters.)

TERM	MEAN (95% HPD INTERVAL)
Intercept	–4.02 (–5.57 to –2.36)
Number of geological units occupied	0.81 (–0.19 to 1.81)
Factor (area of occupancy 2)	1.42 (0.06 to 2.94)*
Factor (area of occupancy 3)	1.91 (0.43 to 3.56)*

* HPD intervals that do not overlap zero are considered significant.

3.3 Conservation status

One of the calcicolous taxa – *Myosotis cinerascens* – has been ranked as Extinct by de Lange et al. (2013), while 73 (48%) have been ranked as Data Deficient or Threatened by de Lange et al. (2013) or ourselves, and 44 (29%) are considered Nationally Critical (Table 8). A further 71 (47%) of the calcicolous taxa have been ranked as At Risk, 67 of which are considered Naturally Uncommon. Thus, 144 (95%) of the calcicolous flora have been ranked as Extinct, Data Deficient, Threatened or At Risk, and only 8 (5%) are considered Not Threatened.

Table 8. Frequency of calcicolous taxa in broad threat categories (bold) and attendant ranks as listed in de Lange et al. (2013) or assessed in the present study (using the criteria of Townsend et al. (2008)). (Note: The Taxonomically Determinate and Taxonomically Indeterminate sections of de Lange et al. (2013) have been combined.)

THREAT CATEGORY (BOLD) AND RANK	NUMBER IN DE LANGE ET AL. (2013)	NUMBER ASSESSED IN PRESENT STUDY	TOTAL
Extinct	1		1
Data Deficient	3	3	6
Threatened	42	25	67
Nationally Critical	31	13	44
Nationally Endangered	7	7	14
Nationally Vulnerable	4	5	9
At Risk	57	14	71
Declining	3	1	4
Naturally Uncommon	54	13	67
Not Threatened	7	1	8
Not previously assessed		43	43

Examination of the frequency of Data Deficient or Threatened taxa on the 31 geological units showed that two out of seven and three out of eight calcicoles in two prominent eastern, lower North Island units are in these categories (Table 4). Furthermore, there are very large numbers and proportions of Data Deficient or Threatened taxa on the two eastern units in the South Island: the South Marlborough–North Canterbury unit (28 of 41 taxa or 68%) and the Mid-South Canterbury–North Otago unit (24 of 29 taxa or 83%), with 18 of the 24 taxa in the latter unit being ranked as Nationally Critical. By contrast, only 7 of 43 (16%) and 11 of 52 (21%) of the large numbers of calcicoles in the two West Nelson units at montane to alpine elevations – Tasman Formation Limestone and Mt Arthur Group Marble – have been ranked as Data Deficient or Threatened.

Among the 61 unnamed taxa, 43 have been ranked as Data Deficient or Threatened. The following genera include more than one unnamed taxon in this category which should be given priority for taxonomic resolution: *Brachyscome* (2), *Chaerophyllum* (2), *Craspedia* (8), *Melicytus* (2), *Ranunculus* (2) and *Senecio* (6) (Table 3). In addition, the following genera include one unnamed taxon that has been ranked as Data Deficient or Threatened and so represent further priorities for taxonomic resolution due to their limited demography: *Convolvulus* aff. *verecundus* (CHR 546302; Awahokomo) (Smissen & Heenan 2011); *Botrychium* aff. *lunaria* (CHR 289336; NW Nelson); *Galium* aff. *perpusillum*; (CHR 249195; "calcicole"), *Gentianella* aff. *calcis* subsp. *waipara* (CHR 569771; Earthquakes), *Koeleria* cf. *novozelandica* (AK 252546; Awahokomo) *Sonchus* aff. *novae zelandiae* (CHR 440071; "limestone") and *Trisetum* aff. *lepidum* (AK 251835; Awahokomo).

In total, 23 (15%) of the calcicolous taxa are receiving active conservation management that may include protection advocacy to maintain or improve their ecological health, while a further 26 taxa (17%) are being inventoried, monitored or periodically surveyed. However, the remaining 68% are not currently being actively managed, including 35 (48%) of the 73 Data Deficient or Threatened taxa.

4. Discussion

4.1 Life forms and taxonomic status

New Zealand's calcicolous flora comprises a much larger proportion of the entire vascular flora than previously suggested (Burrows 1964; Druce et al. 1987). The 152 recognised taxa consist of four main life forms – shrubs, composite herbs, non-composite herbs and grasses – the last three of which are present at somewhat greater proportions than in the entire flora. By contrast, life forms that are traditionally recognised as being specialists of low-productivity sites, such as sedges, rushes and orchids, are present at much lower proportions or entirely absent. A predominantly shrub, forb and grass calcicolous flora is consistent with the dominant community compositions that were previously documented for non-forest calcareous landforms by Bell (1973a), Druce et al. (1987) and Molloy et al. (1999).

In total, 61 calcicolous taxa (40%) are currently unnamed, which is a much greater proportion than the estimated 17% of unnamed taxa in the entire flora (Courtney 2011). Possible explanations for this disproportionate number of taxonomically neglected entities include:

- Few botanists have acquired the specialist knowledge of this ecosystem's flora that is required to confidently recognise taxonomic curiosities or novelties.
- Most botanists are regional specialists, limiting inter-regional or national perspectives.
- There is a reluctance among botanists to engage with unnamed taxa because investigating and erecting new taxonomic hypotheses requires more effort than working with the more predictable and convenient named taxa.
- There is a tendency for botanical databases to exclude or subordinate unnamed entities to an inferior status, leading to their general obscurity.
- Substantial effort is required to search for typically small populations of indigenous plants within limestone vegetation that is dominated by naturalised species.

Taxonomic uncertainty reduces the likelihood that threatened taxa and their habitats will be prioritised for conservation investment. Fortunately, there has been a trend to taxonomically resolve the status of individual or small groups of putative calcicoles over the last 25 years (see section 1.1.1). However, preliminary morphological or phylogenetic studies have suggested that several genera that are characteristic of basicolous substrates include species aggregates or complexes that contain numerous unresolved calcicoles, such as *Chaerophyllum novae-zelandiae* [*rigidum*] (Heenan & Molloy 2006), *Schizeleima haastii* and *Senecio glaucophyllus* (SPC and PBH, unpubl. data). Thus, 31 of the 57 contributory genera still require taxonomic investigation. Assuming that our putative estimations are correct, the taxonomic resolution of taxa in just 3 of those 57 genera (*Carex* (4 taxa), *Craspedia* (15 taxa) and *Senecio* (6)) would reduce the proportion of unnamed taxa from 61 or 40% of the flora to 37 or 24%.

4.1.1 Taxonomic patterns

We identified several taxonomic patterns within the calcicolous flora:

- A high proportion of the calcicolous flora (73%) belongs to 24 species-rich genera (Table 3) that are recognised as having recently radiated in response to the new habitats provided by the Kaikoura Orogeny (Fenner et al. 1997). Although the remaining 27% belong to much less species-rich genera, only *Australopyrum* is included in the group of monospecific genera, which includes 175 or 40% of the 433 genera in New Zealand (as recognised by Rogers & Walker 2002).
- The 17 calcicolous grasses identified here (cf. eight in Molloy (1994)) belong to ten genera. Eleven of these calcicoles are members of a guild of grass genera with low to moderate species richness that contain just one or two calcicoles each: *Anthosachne, Australopyrum, Dichelachne, Festuca, Koeleria, Simplicia, Stenostachys* and *Trisetum*. These genera belong to a suite of native grasses that have adapted to the novel, high-nutrient, steepland and often rocky niches that were provided by uplift during the Kaikoura Orogeny. The remaining six calcicolous grasses belong to *Chionochloa* and *Poa*, both of which are species-rich genera that have radiated across a wide range of niches, including the widespread, low-nutrient alpine grasslands.
- Five genera have radiated on the calcareous substrates of the northern South Island, with a high proportion of their calcicolous taxa occurring there:
  - *Myosotis* (9 of 11 taxa)
  - *Craspedia* (14 of 15 taxa)
  - *Hebe* (8 of 10 taxa)
  - *Senecio* (7 of 8 taxa)
  - *Carex* (the eight calcicolous carices of West Nelson and South Marlborough are the only calcicolous sedges, five of which are confined to Ordovician marble and dolomite)

The observation of several closely related calcicoles in close proximity to each other also suggests that parapatric evolution (i.e. speciation within groups of sister taxa) has occurred on calcareous substrates:

- *Gentianella astonii* ssp. *astonii* and *G. astonii* ssp. *arduana* occur on separate but adjacent exposures on South Marlborough and North Canterbury Amuri Limestone (Glenny 2004).
- Large-leaved forms of *Gentianella bellidifolia*, which are now recognised as a distinct species (*G. angustifolia*), and *G. filipes*, which speciated from *G. divisa* and *G. corymbifera*, are found on Mt Arthur Group Marble (Glenny 2004).
- *Colobanthus squarrosus* ssp. *drucei* and *C. squarrosus* ssp. *squarrosus* occur on the Tasman Formation Limestone and the Mt Arthur Group Marble in West Nelson, respectively.

It is also likely that *Carex* aff. *wakatipu* (c) (CHR 249755; "small 2-style") and *Carex* aff. *wakatipu* (d) (CHR 510696; "small 3-style") are sister taxa, although both have largely sympatric distributions on Mt Arthur Group Ordovician Marble and indurated limestone of West Nelson.

4.2 Biogeography

4.2.1 Geological age of calcareous landforms

We found a highly variable density but a high fidelity of calcicoles across the 31 geological units, which raises questions about their evolutionary origins. Molloy (1994) commented that ‘it would be useful to know more precisely when the various limestone outcrops were first exposed to weathering and plant colonisation, as much of the speciation recorded so far from limestone must stem from these times’. McGlone (1985) and Lee (1992) suggested that geologically-stable areas in New Zealand have retained a greater proportion of older taxa and, by implication, older endemics, whereas less stable areas have evolutionarily young floras and young endemics. Thus, it follows that more stable regions, such as Northland, West Nelson and Otago, would have more diverse floras retaining older elements than the geologically younger regions of the lower North Island and central South Island. As Molloy (1994) implied, the best way to test this hypothesis may be by examining the geomorphic ages of calcareous landforms – and this pool of 152, mostly unit-endemic taxa is well suited to such a task. Although few studies have deliberately addressed the geomorphic evolution of calcareous landforms, inferences can be made from work targeting the tectonic history of New Zealand, particularly the axial ranges of both main islands (e.g. Adams 1985; Whitehouse 1988; Williams 1991, 2014; Campbell & Johnston 1982; Tippett & Kamp 1995).

The lower North Island is one region where lithological and landform ages have been studied. Eight of the nine endemic North Island calcicoles occur in the footprint of the lower North Island marine transgression of Miocene–Pliocene depositional age (Kamp 1982), and all eight of these calcicoles occupy Te Aute Limestone and associated units of late Miocene–Pliocene age (Beu et al. 1980), which is part of the marine transgression stratigraphy. However, the sedimentary strata’s subsequent exhumation occurred much later, in the mid to late Pleistocene (Ghani 1978; Katz 1979; Pillans et al. 1982; Kamp 1988; Williams 1991), making these eight taxa evolutionarily quite young.

The other North Island endemic, *Hebe scopulorum*, along with the disjunct *Asplenium cimmeriorum*, occupy crystalline limestones of Oligocene depositional age in West Waikato, a region that escaped the lower North Island marine transgression (Stevens 1974; Suggate et al. 1978) but is still of late Cenozoic age (Kear & Schofield 1959). Consequently, these two calcicoles are likely to be somewhat older than the eight taxa that occur immediately to the south.

Northland’s limestone outcrops support no recognised calcicoles despite this being an ostensibly geomorphically-stable region. However, there has only been a substantial amount of emergent land here since the Pliocene (McGlone 1985: fig. 7) and, perhaps more importantly, tall forest fringed and shrouded any limestone outcrops that occurred in this low-relief landscape, reducing the opportunities for adaptation and perpetuation of a non-forest calcicolous flora on well-lit, cliffed outcrops.

In the South Island, the subducted parts of the early to mid Cenozoic peneplain of basement rocks were veneered in 1–2 km of marine sediments at the start of the Kaikoura Orogeny in the late Cenozoic (Williams 2014). All of the eastern South Island calcareous strata and their calcicoles occupy denudation relicts of that sedimentary veneer (for Canterbury, see Browne & Field (1988)). In Marlborough and North Canterbury, calcareous components of the sedimentary overlay are common throughout the lowland eastern or coastal margins, but their presence reduces inland until only isolated relicts remain at montane elevations adjacent to the axial mountains, such as at Castle Hill basin and the Chalk Range. This declining presence inland reflects an inland gradient of increasing uplift, tectonic dislocation, precipitation and thus erosion as a result of the formation of the axial ranges (Tippett & Kamp 1995; Williams 2014: fig. 4.11). Inland strata may also have slightly older emergent ages given the high concentrations of calcicoles on isolated inland outcrops. By contrast, in South Canterbury–North Otago, this inland tectonic and precipitation gradient is less pronounced as uplift rates have been low and uniform across the late Cenozoic sediments that cap the basement Otago peneplain, which remains remarkably intact (Forsyth 2001).

Calcareous landforms in Nelson and North Westland are a combination of early to mid Cenozoic basement peneplain strata and the late Cenozoic sedimentary overlay. Nelson's indurated Wooded Peak Limestone is a subdued lowland part of the early to mid Cenozoic basement peneplain (Waterhouse 1959) and hosts only a modest number of calcicoles. By contrast, the Mt Arthur Group Marble, which stretches from Mt Owen north to the Pikikiruna and Wakamarama Ranges, represents blocks of the early to mid Cenozoic basement peneplain that were uplifted along north-northeast-trending faults (Campbell & Johnston 1982) and supports a rich array of calcicoles. The Tasman Formation limestones of West Nelson–North Westland are parts of the thin veneer of late Cenozoic cover beds that overlay the basement peneplain, which have been preserved as gently to steeply dipping sedimentary sequences in fault-angle depressions, even at montane elevations. Thus, the calcicole-rich Matiri Tops are an uplifted plateau remnant, while the much less calcicole-rich remnants at Westhaven (Whanganui Inlet) in Golden Bay and in North Westland (e.g. Punakaiki) represent lowland blocks that have been heavily dissected by rivers (Campbell & Johnston 1982). Finally, a small remnant of indurated limestone at Parapara Peak in the northern Tasman Mountains is the only remaining vestige of a once extensive Permian sedimentary sequence associated with the basement peneplain as preserved in West Nelson (Cooper 1984: 27).

Uplift of the Fiordland massif commenced in the Oligocene and intensified c. 12 Mya, resulting in estimated total denudation thicknesses of c. 2.5–6 km (House et al. 2002). West Fiordland's marbles are scattered, thin beds inter-fingered with dominant gneiss (Turnbull & Jongens 2010). Fiordland Marble and its few calcicoles only exist at alpine elevations because they are associated with Paleozoic gneissic metasediments and granitic gneisses, which are much more resistant to erosion than the Mesozoic schists, greywackes and argillites of the axial mountains further north (Williams 2014). While the marble's highly crystalline composition would militate against dissolution in this high-rainfall environment, its surface expression will have been spatially dynamic over geological timeframes due to the continuous and substantial denudation and glacial scouring. Finally, a contrast can be drawn between the few Fiordland calcicoles that occur on Ordovician marble separated by 460 km of dextral slip along the Alpine Fault (Wellman 1979; Sutherland & Norris 1995) and the rich calcicolous flora that is associated with West Nelson's Mt Arthur Group Ordovician Marble. We attribute this difference simply to Pleistocene glaciation having a greater effect in Fiordland than in West Nelson's marble ranges.

4.2.2 Formation of calcareous landforms

The composition of a calcareous landform reflects:

- Its lithology (characteristics of rock that reflect the depositional environment), stratigraphic position within sedimentary sequences before emergence and degree of induration.
- When surface expression of the sedimentary unit occurred.
- Tectonic dislocation in the form of uplift, folding and faulting.
- The weathering rates of the different facies or lithology.

The interplay between these factors has led to a wide compositional variation in calcareous landforms – massive, bedded and/or jointed, crystalline, shelly, and marl or muddy limestone – which often results in several individually named member units occurring within regional sedimentary sequences (e.g. see Kear & Schofield (1959) for the Oligocene Landon series limestones of West Waikato). In addition, travertine, tufa and sinter (the chemical deposition of limestone from carbonate-rich freshwater) produce their own distinct landforms and micro-reliefs, as seen in the travertine at Miner River, Nelson, which has formed from creeks draining Wooded Peak outcrops. Thus, textural and associated edaphic variations in the rock produce diverse calcareous habitats for plants.

Despite most of New Zealand's late Cenozoic limestones having undergone little metamorphic transformation (Marshall 1916), many act as erosion-resistant caps to plateaux, hogsbacks, homoclinal ridges, cuestas, mesas and buttes in mildly deformed sedimentary strata (Cotton 1942: 89) – the Thousand Acres Plateau and Mt Misery plateau of West Nelson are prominent examples (Heine et al. 1987). As plateaux and homoclinal ridges erode to form relictual cuestas, mesas and buttes, these erosion-resistant limestone caps would provide habitat continuity for calcicole evolution, particularly on scarp and talus exposures. However, in high-rainfall environments, these impervious caps result in poorly-drained soils that have a near-neutral pH at the basal contact with the limestone transitioning to strongly acidic topsoils (Heine et al. 1987). Thus, a resistance to erosion combined with a susceptibility to corrosion leads to the formation of rock pavements with shallow, deeply-weathered soils that possess a strong vertical geochemical gradient. Scarp and talus slopes can be the only edaphic expression of limestone in extensive calcareous plateau topography. Consequently, in a flora of 488 vascular taxa occupying 225 km^2 of Tertiary calcareous landforms of West Nelson, only 11 were classified as strong calcicoles (Druce et al. 1987).

4.2.3 Karst as a calcicole habitat

The fluted surface texture of karst develops in relatively pure and hard carbonate rocks in relatively wet climates (Williams 1978, 1982). In the North Island, karst is prominent on Whangarei Limestone in East Northland, on Te Kuiti Group Limestone of West Waikato and sparsely on Te Aute Limestone from Hawke's Bay to southern Wairarapa. In the South Island, karst is prominent on (after Williams 1978, 1982; Kenny & Hayward 2009):

- Mt Arthur Group Marble and Dolomite of West Nelson at the Burnett Range, Wharepapa / Arthur Range and Mt Owen.
- Tasman Formation Limestone of West Nelson and North Westland at Punakaiki, Paturau and the Mt Arthur Tableland (Heine et al. 1987).
- Sparsely on Amuri Limestone from North to South Canterbury.
- Sparsely on Forest Hill Limestone of Southland.
- Sparsely on the thin beds of marble in West Fiordland.

Solution weathering of carbonate rocks by carbonic acid is greater within soil water that contacts the rocks than in atmospheric rainwater (Williams 1978; Gunn 1981), and is also accelerated by fungi, cyanobacteria and lichens (Danin 1992). Today, much karst has been exposed by the clearance of prehuman forests, with a consequent loss of interstitial soil. A clint and grike relief is typical of the most crystalline substrates, whereas karstic features of softer rock have been labelled as pancake at Punakaiki, pot-holes in North Canterbury Limestone by Zotov (1941), and bedrock, pavement, cups and saucers, scallops, and fissures at Awahokomo by Heenan & Molloy (2006).

Karst relief is prominent on the alpine exposures of marble at Wharepapa / Arthur Range and Mt Owen, West Nelson (Williams 1982). Glacial ice in cirque basins and attendant valleys has subdued or rounded the surface relief compared with the more deeply-dissolved karstic relief that is seen on ice-free topography (see Campbell & Johnston 1982: 290, plate 15.5). Such ice-free sites presumably provided habitat for the large range of alpine calcicoles during the last, and previous, glaciations.

Most calcicoles of karst, and calcareous landforms in general, are chomophytes, i.e. adapted to fissures, crevices and rendzina accumulation zones such as ledges rather than the unbroken faces of massive exposures. Furthermore, where land clearance has greatly increased the potential habitat for non-forest calcicoles, they continue to demonstrate high site fidelity to their original, non-forest exposures rather than expanding their range.

4.2.4 Calcicoles with bimodal substrate distributions

Five of the facultative calcicoles we identified had bimodal substrate distributions, occurring predominantly on calcareous rocks but also on base-rich ultramafic rock. These included *Asplenium cimmeriorum* (Brownsey & de Lange 1997), *Cardamine basicola, Melicytus obovatus, Myosotis brockiei* and *Myosotis chaffeyorum* (Lehnebach 2012). In addition, a sixth facultative calcicole, *Coprosma* aff. *cheesemanii* (CHR 469919; "rimicola"), occurs predominantly on West Nelson Limestone and Marble but is also found on Nelson's ultramafic Mineral Belt and Lockett Conglomerate, a base-rich rock of West Nelson at Ruby and Diamond Lakes (SPC, pers. obs.). *Chaerophyllum basicola* also has a bimodal substrate occurrence on calcareous and ultramafic rocks but has been excluded from our facultative calcicole category because three of its four sites are ultramafic outcrops (Heenan & Molloy 2006). Thus, we recognise seven taxa as being bimodal basicoles, six of which are calcicoles.

4.2.5 Physiography as a driver of calcicole evolution

At a regional scale, climate and landform structures have interacted to strongly influence calcicole biogeography. Calcicoles have only evolved where calcareous landforms create substantial light gaps in the forest – for instance, *Hebe scopulorum* occurs on pedestals of Te Kuiti Group Limestone that emerge above the tall podocarp-broadleaved forest in West Waikato. In regions below the treeline with equivalent calcareous landforms, calcicole richness and endemism are much greater in eastern rain-shadow environments than in equably-wet regions. We attribute this difference to variation in the forest structure and composition, whereby dryland forest with its light canopies and dappled-light understoreys has fostered the growth of herbaceous calcicoles, whereas closed-canopied, equably-wet forest has been inimical to their colonisation. For instance, calcicole richness is much greater in semi-arid lowland South Canterbury–North Otago than in equably-moist lowland Southland. The richness and endemism of calcicoles are also much greater in alpine regions than in equivalent lowland exposures due to reduced community competition from tall, landform-shrouding vegetation. Thus, upland exposures of Tasman Formation Limestone in West Nelson (e.g. Matiri Plateau) host greater numbers of calcicoles than those of the lowland fault-block depressions (e.g. Westhaven (Whanganui Inlet) and Punakaiki) (SPC, unpubl. data).

Locally-distinct climates will also have played a role in calcicole evolution but only from the standpoint of steep or rocky sites having higher levels of insolation and greater variation in seasonal humidity than adjacent areas covered with taller matrix vegetation. Furthermore, the climatic and edaphic insularity of calcareous exposures below the treeline would have applied equally to tall forest during interglacial times and to low forest, scrub and tussockland in glacial climes. The exception to this primarily non-forest calcicolous flora is a small group of calcicoles that are adapted to shaded forest understoreys, which includes three ferns (*Asplenium cimmeriorum, A. lyallii* and *Pteris* aff. *macilenta* (AK 210045; Punakaiki)), two *Myosotis* taxa (*Myosotis brockiei* and *Myosotis chaffeyorum*) and a grass (*Simplicia buchananii*).

Overall, we consider habitat insularity being a function of differentiated landforms, and climatic extremes to have been the primary driver of calcicole evolution and biogeography. Gene exchange opportunities between outcrops would be curtailed for taxa that have adapted to the lithologically-distinct surface textures of calcareous substrates. The resulting adaptive niche shifts (Joly et al. 2013) into open habitats would have occurred irrespective of changes in the matrix vegetation as a result of climate fluctuations during the Pleistocene. Consequently, 72% of calcicoles have areas of occupancy of <10 ha, reflecting tiny areal extents of differentiated habitat within ostensibly wider areas of suitable calcareous terrain. Indeed, as an example, *Montia drucei* was ranked as having an area of occupancy of <1 ha and has a known areal extent of approximately 50 m^2 within an extensive, apparently suitable area of alpine karst at Mt Arthur and The Twins, West Nelson.

Thus, we believe that the patterns of richness and endemism in New Zealand's calcicolous flora strongly reflect the:

- Emergent age of the calcareous strata.
- Rates of denudation from tectonic uplift and deformation.
- Relief height of calcareous outcrops below the treeline.
- Rainfall gradients, which result in closed-canopied forest in the wet west below the treeline shrouding calcareous outcrops and dryland forest in the rain-shadowed, drier east with open canopies permitting higher illumination of understorey calcareous outcrops.
- Differential rates of glacial denudation of the alpine calcareous strata.

Based on this framework, we argue that the North Island's comparatively low total calcicole richness and endemism compared with the South Island can be attributed to the:

- Geologically younger calcareous strata.
- Comparative absence of upland, differentiated terrain and climates to drive calcareous specialisation.
- Generally thin calcareous beds of insufficient height to provide persistent, non-forest habitat among tall fringing forest in the wet west.

Thus, although Northland was previously recognised as preserving an evolutionarily-old floristic element in terms of Pleistocene extinctions (Lee et al. 2001), it is bereft of calcicoles due to equably-wet tall forest shrouding the low-relief outcrops. Alternatively, geomorphically-young regions such as are seen in the lower North Island, support small numbers of calcicoles that are concentrated in eastern districts with prominent exposures of limestone and open-canopied, dryland forest.

In the South Island, rich assemblages of calcicoles are concentrated in:

- The fault-block-delineated mountains of West Nelson that have preserved, uplifted remnants of a diverse range of limestone and marble habitats.
- High-relief, lowland and montane exposures in eastern Marlborough and Canterbury where dryland, open-canopied forest prevails.

Alternatively, few calcicoles occur in wet, lowland districts with low-relief calcareous exposures, such as in Southland and Westland. The differential effect of Pleistocene glaciation is evidenced by the fact that few calcicoles occur on alpine Ordovician marble in Fiordland whereas a rich assemblage is found at equivalent altitudes on Ordovician marble of the Mt Arthur Group in West Nelson. Furthermore, tectonic deformation of the axial ranges in between has accelerated the removal of any calcareous sedimentary strata in that uplift footprint. Finally, precipitation and its influence on the dissolution of limestone may be an additional factor that accelerates denudation rates of calcareous substrates in the wet west and at higher altitudes.

Thus, the combined effects of key evolutionary drivers on only a few geological units, particularly those in the alpine and eastern parts of the South Island, have caused them to become endemic-rich, albeit with constituent taxa that occupy a diverse array of geomorphically-distinct habitats. This explanation for the highly endemic calcicolous flora agrees with McGlone et al. (2001), who concluded that endemic plant centres are associated with differentiated terrain and climates providing isolation, distinctive environments and habitat continuity that are conducive to speciation.

4.3 Conservation status

A comparison of the area of occupancy of calcicoles that occur predominantly above or below the treeline showed that the former are more likely to have larger spatial extent scores. There are two possible explanations for this: the expanse of non-forest alpine habitat is greater above than below the treeline or calcicoles that occur below the treeline have suffered a greater contraction in their habitat as a result of anthropogenic influences. We also found that large numbers and proportions of the calcicoles that are found in the two eastern South Island units that occur entirely below the treeline in agriculturally-modified landscapes are ranked as Data Deficient or Threatened – 68% on the South Marlborough–North Canterbury unit and 83% on the Mid-South

Canterbury–North Otago unit. By contrast, only 16% and 21% of taxa that occur in the two West Nelson units at montane to alpine elevations in comparatively unmodified landscapes are ranked as Data Deficient or Threatened. Thus, it appears that anthropogenic factors may contribute to the smaller area of occupancy scores for calcicoles that occur below the treeline compared with those that occur above.

We found that 35 (48%) of the 73 Data Deficient or Threatened calcicoles currently receive no form of management. There are several possible reasons for this:

- They were taxonomically unrecognised prior to this study.
- An unresolved taxonomy suppresses their conservation profile. Many of these taxa belong to genera that require major taxonomic revision, which will demand considerable and sustained investment, such as *Craspedia, Myosotis* and *Senecio*. Fortunately, however, systematics revisions are currently being undertaken for all three of these genera.
- Management is deemed unnecessary because although the small total population size meets one or other of the maximum population size criteria of the Threatened plant ranks of Townsend et al. (2008), the habitat has few if any threats or modifications.
- There is a lack of knowledge about restoration techniques or the cost-effectiveness of rebuilding their severely degraded habitats.
- There is intense competition for limited conservation budgets.
- Their conservation status is poorly understood due to access prohibitions on private land.

Within the three broad regions that we recognised as having high levels of calcicolous richness and endemism—West Nelson, South Marlborough–North Canterbury and Mid-South Canterbury–North Otago – there are several isolated outcrops of highly modified habitat that have particularly rich clusters of narrow-range endemics, indicating a significant conservation risk. By unit area, Awahokomo (Fig. 5) in the Waitaki Valley supports the highest concentration of narrow-range calcicoles, with five Awahokomo endemics and five narrow-range taxa that are shared with other Otekaike Limestone outcrops of the Waitaki Valley (see also Molloy et al. 1999), along with the basicole *Chaerophyllum basicola* (Heenan & Molloy 2006). Mt Burnett in West Nelson, the Chalk Range in South Marlborough (Fig. 6), Castle Hill basin in Mid Canterbury, and several exposures in the upper reaches of the Tengawai and Pareora Rivers of South Canterbury (Fig. 7) are additional sites with concentrated, narrow-range endemism that are of considerable conservation concern.

Figure 5. The pedestalled outcrop of Otekaike Limestone (Gage 1957; Forsyth 2001) known as Awahokomo (circled) in the Waitaki Valley, South Canterbury, which supports five endemic calcicoles and five narrow-range calcicoles shared with other areas of Otekaike Limestone in the Waitaki Valley. Also see cover plate.

Figure 6. Chalk Range, South Marlborough. A. Chalk range, which is sandwiched between the Seaward and Inland Kaikoura Ranges, contains numerous calcicoles, many of which are endemic to that Clarence Valley outcrop of Amuri Limestone, which extends south to Limestone and Bluff Hills. B. A steep banded and jointed limestone cliff on the northern Chalk Range, which is the habitat of *Pachycladon fasciarium* (insert), of which less than 30 individuals are known. There is also a historical record of this species from adjacent Ben More. In over a decade of annual monitoring at Chalk Range, only two plants have flowered. The species is characterised by a stout root-stock but is threatened by browsing by goats (*Capra hircus*). Therefore, Department of Conservation staff have erected steel mesh netting (top left and mid and bottom right) to deflect that herbivory.

Figure 7. Goodwood, Green Valley, Otatara, Otekaike and Amuri Limestone outcrops as escarpments, pedestals, pavements and sinkholes (dolines) in Mid-South Canterbury and North Otago. A. Craigmore in the Pareora River catchment has a spectacular array of sinkholes dotting its terraced surface and relictual scrub about its escarpment exposure. B. Manahune in the Tengawai River catchment supports several threatened calcicoles but is devoid of any vestige of its original matrix dryland forest and is grazed by farm stock throughout. C. Taiko in the Pareora River catchment has QEII covenanting offering some protection to its substantial calcicole values. It contains a noteworthy relict, species-diverse dryland forest. D. Waihao Forks, in the Waihao River catchment south of Waimate contains an endemic buttercup calcicole, along with other narrow-range calcicoles; the removal of cattle grazing has fostered a proliferation of rank pasture (the grey-brown coloured matrix vegetation surrounding the limestone blocks and escarpments), which has caused the extinction of the buttercup at one of its two sites.

In this study, we did not investigate the ecological habitats of calcicoles in any detail, particularly in terms of whether they are edaphically constrained and/or competitively confined to the physical character of calcareous landforms. An autecological focus on calcicolous habitats and threats will be necessary for the restoration of species and their guilds. However, wider-scale ecological issues confront ecosystem restoration or revegetation initiatives that involve matrix vegetation and the reconstitution of microclimates. Future studies could also investigate bryophyte and lichen calcicolous floras and their conservation statuses.

5. Conclusions

5.1 Life forms and taxonomy

Our compilation of 152 calcicolous taxa representing 5.6% of the total vascular flora of New Zealand suggests that calcareous landforms have had the greatest substrate influence on vascular plant evolution. Shrubs (20%), angiosperm herbs (58%) and grasses (11%) are the dominant life forms, while there are only three trees, eight sedges, five ferns, two lianes and no rushes or orchids. At the genus level, 57 or 13% of all New Zealand genera contribute to this flora, but only 24 (42%) of these account for 73% of the calcicolous richness. Thus, the calcicolous flora is akin to the entire flora in that a small proportion of genera disproportionately contribute to total taxon richness.

Just 60% of the calcicolous flora has been formally named, compared with 83% for the entire vascular flora. Of the 61 unnamed taxa, 35 have been previously cited in the scientific literature, leaving 26 putative taxa that are cited here for the first time. This level of taxonomic uncertainty is probably unrivalled in other substrate or major ecosystem divisions within the New Zealand flora, with 32 of the 57 contributory genera requiring taxonomic investigation.

5.2 Biogeography

New Zealand's calcareous substrates have two broad lithological origins: crystalline limestone, marble and dolomite of predominantly Paleozoic times (Cambrian, Permian and Ordovician), which are part of the basement rocks that were eroded to form a peneplain in the early to mid Cenozoic; and non-indurated limestones that are part of the 1–2-km-thick sediments that were deposited on the aforementioned marine-transgressed peneplain in the mid to late Cenozoic. Subsequently, the Kaikoura Orogeny has variously uplifted, distorted and denuded that basement peneplain and its marine cover-beds, and so most, if not all, calcareous landforms are of comparatively recent, late Cenozoic geomorphic age.

Although there are good accounts of the geomorphic development of calcareous strata at the regional level, there is a lack of detail around the timeframes of that process. Nevertheless, we classified calcareous substrates into 31 geological units based on their depositional ages and broad landform characteristics. Calcareous substrates are a prominent and widely distributed rock type in New Zealand but are largely absent from the axial ranges of both main islands due to the high denudation rates (e.g. for the central Southern Alps/Kā Tiritiri o te Moana, there is 2–3 km of present relief but there has been 19 km of total erosion since uplift; Williams 2014). We found that these 31 geological units are distributed in near equal numbers between the North and South Islands. However, there is a distributional bias in the calcicolous flora towards the South Island, with 142 calcicoles occurring there compared with only 13 in the North Island.

In addition, we found that 95% of calcicoles are either unit endemics or regional endemics if they span more than one unit, with most South Island calcicoles occurring on:

- Three Nelson–North Westland units, two of which are Paleozoic marble and dolomite, and one of which is late Cenozoic limestone.
- A South Marlborough–North Canterbury limestone unit.
- A Mid-South Canterbury–North Otago limestone unit.

Fiordland also has a small number of endemic calcicoles on both its Ordovician marble and late Cenozoic limestone, while the few North Island calcicoles are clustered on Hawke's Bay and Wairarapa Limestone of late Pliocene–Pleistocene age. There are few, if any, calcicoles on the calcareous units north of the Waikato, in Poverty Bay, in the southwest of the North Island and in Southland.

If there is any bias in the proportions of calcicoles found in the three altitudinal belts compared with the availability of calcareous strata, it is towards the two belts below the treeline (55% lowland and 51% montane cf. 26% alpine). The alpine belt is usually highlighted as hosting many of the novel plant habitats that were created during the Kaikoura Orogeny (Winkworth et al. 2005; Heenan & McGlone 2013). However, the large lowland and montane components of this flora, which principally occupy limestones of the marine cover-beds, indicates that habitat specialisation likely commenced at the earliest emergent ages of these substrates in the late Cenozoic.

A large proportion (72%) of calcicoles have areas of occupancy of <10 ha, despite ostensibly suitable habitats occurring across much greater areas of the geological units they occupy. We argue that the physiography of calcareous landforms can help explain the narrow ranges and apparently high niche specificity of most calcicoles, with habitat insularity as a function of differentiated landforms and the climatic extremes that occur in their open habitats being the primary driver of calcicole evolution and biogeography. Furthermore, this explanation also accounts for the high unit fidelity and the low incidence of vicariant and disjunct distributional patterns within the calcicolous flora.

Only West Nelson and Fiordland host the 26% of calcicoles that have alpine occurrences, despite calcareous substrates being widespread in the South Island. Furthermore, by far the majority of these taxa are West Nelson endemics, which are particularly found on the alpine exposures of Mt Arthur Group Marble. Thus, it seems likely that Pleistocene glaciation had a greater impact in Fiordland, constraining the number of alpine calcicoles that occur on the sparse but widespread alpine exposures of Fiordland Marble – although we also note that botanical exploration and taxonomic studies of the Fiordland flora are not as advanced/well-developed as for Nelson.

In general, we suggest that the following set of physiographic factors best explains the geographically-biased pattern of calcicole richness and endemism:

- The emergent age of calcareous strata.
- The rates of denudation from tectonic uplift and deformation.
- The relief height of calcareous outcrops below the treeline.
- Rainfall gradients that at their wettest inhibit survival of forest understorey grasses and forbs beneath closed canopies and at their driest foster open canopies that are conducive to grass and forb survival.
- Differential rates of glacial denudation of alpine calcareous strata.

5.3 Conservation status

We found that large numbers and proportions of the calcicolous flora are currently ranked as Data Deficient or Threatened (73 taxa or 48% (cf. 14% for the entire vascular flora (de Lange et al. 2013); and of these, 44 taxa or 29% are ranked as Nationally Critical. Although a few of these calcicoles occur on predominantly high-altitude geological units, such as the limestones and marbles of West Nelson, by far the greatest proportion (48) are found on the two eastern South Island units at lowland to lower montane elevations. This is likely due to anthropogenic degradation of habitats below the treeline, such as the loss of matrix forest, which would moderate seasonal extremes in atmospheric and edaphic humidity, combined with weed invasion. In addition, small calcareous sites within these two units can support large concentrations of Data Deficient or Threatened taxa – for instance, at Awahokomo in the Waitaki Valley, all ten of the narrow-range endemics have this conservation status, with nine of these being ranked as Nationally Critical.

5.4 Policy implications

Our measures of taxonomic resolution, conservation status and management engagement all indicate that this is a flora and ecosystem requiring greater conservation attention – indeed, the calcareous ecosystem is likely unrivalled among vascular plants in its level of taxonomic uncertainty and the proportion of its distinct flora that is ranked as Data Deficient or Threatened. Uncertain taxonomies compromise scientific profiles and therefore conservation investment. However, the calcareous ecosystem presents logistical challenges to research and management due to not only its taxonomically-demanding flora, but also the field conditions in which it occurs, including the steep relief, susceptibility to herbaceous weeds and loss of matrix vegetation. In addition, several putative taxa have precarious existences, often having less than 25 individuals, fluctuating population sizes and site occupancies of only a few square metres, which, combined with their specialised niches, renders them highly vulnerable to extinction (Davies et al. 2004). In summary, our floristic critique highlights that the eastern South Island calcareous ecosystem is of preeminent conservation concern.

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Appendix 1

Glossary of scientific terms

Azonal The vegetation of azonal ecosystems is primarily the product of edaphic (of the soil) extremes, such as extreme rock and soil chemistry, extreme heat, and frequent disturbance by water, gravity and wind, which override the otherwise dominant influence of macroclimate. Azonal ecosystems often occur at a small scale and can appear anomalous within the context of the national and regional patterns of vegetation (after Singers & Rogers 2014).

Basicole A plant showing a preference for base-rich rocks and soils. Base-rich rocks have high concentrations of the basal elements in soil chemistry – calcium, potassium, sodium and magnesium.

Bioclastic limestone Bioclasts are skeletal fossil fragments of once living marine or land organisms that are found in sedimentary rocks laid down in a marine environment – especially limestone.

Calcareous rocks and landforms Rocks of >50% $CaCO_3$ and/or calcium magnesium dicarbonate ($CaMg(CO_3)_2$) (the latter in the case of dolomite).

Chomophyte Any plant that grows on rocky ledges or in fissures and crevices.

Clastic content of rock A clast is a fragment of geological detritus – chunks and smaller grains of rock broken off other rocks by physical weathering. Geologists use the term clastic with reference to sedimentary rocks and, in regard to limestone, to particles of sedimentary mud, silt and sand amongst the free calcium carbonate.

Facultative calcicole A plant occurring predominantly on limestone, marble and dolomite (rocks of >50% $CaCO_3$ and/or calcium magnesium dicarbonate ($CaMg(CO_3)_2$)) and their rendzinas.

Gneiss A commonly distributed rock formed by intense metamorphic processes from pre-existing formations that were originally either igneous or sedimentary rocks. It is often foliated (composed of layers of sheet-like planar structures), typically coarse-grained and consisting mainly of feldspar, quartz, and mica.

Lithology Characteristics of rock that reflect the depositional environment, especially its stratigraphic position within sedimentary sequences before emergence and degree of induration.

Marl Lime-rich mud or mudstone.

Melange A mappable-sized breccia containing varied rocks jumbled together with little continuity of contacts.

Obligate calcicole A plant occurring exclusively on limestone, marble and dolomite (rocks of >50% $CaCO_3$ and/or calcium magnesium dicarbonate ($CaMg(CO_3)_2$)) and their rendzinas.

Regolith A layer of loose, weathered deposits, often soil, covering solid rock or bedrock.

Rendzina A fertile, lime-rich soil with dark humus atop calcareous bedrock.