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The pattern of declines and local extinctions of endemic inland *Lepidium* species in the eastern South IslandSusan Walker^{1*} , Michael A.C. Harding² and Graeme Loh³¹Manaaki Whenua – Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand²71 Wairoa Gorge Road, RD1, Brightwater 7091³49 Sutcliffe Street, Dunedin 9012

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Abstract: Small patches of habitat for indigenous species that remain in developed landscapes are predicted to lose species over time as extinction debts are paid off and to become transformed by spillover from intensive land uses. In December 2020 we searched for plants of three inland South Island-endemic species of *Lepidium* (Brassicaceae; *L. kirkii*, *L. sisymbrioides*, and *L. solandri*) at previously known locations in Central Otago, the Waitaki Valley, the Mackenzie Basin, and Kura Tāwhiti (Castle Hill, North Canterbury). We recorded whether *Lepidium* populations remained and identified the vascular plant flora of each location. *Lepidium kirkii* was found at six of 14 locations where formerly known and at one new location, but numbered over 50 individuals at only one of these locations. *Lepidium sisymbrioides* was found at five of six locations visited, but we found fewer than four individuals at three of these locations. *L. solandri* was found at five of 12 formerly known locations in Central Otago (but numbered over 50 individuals at only one), at five of five formerly known locations on public land in the Mackenzie Basin, and at the one known location at Kura Tāwhiti. Exotic vascular plant species outnumbered native species at all but one *Lepidium* location in Central Otago and at Kura Tāwhiti, but not in the Mackenzie Basin, where there had been the least habitat loss and land-use intensification. Our results are consistent with theoretical predictions of more local plant extinctions at *Lepidium* locations, and greater transformation of their habitats, in landscapes dominated by intensive land uses and non-indigenous vegetation. We conclude that intensive *ex situ* and *in situ* management is now needed to avoid global extinctions of *L. kirkii* and *L. sisymbrioides*, and local extinctions of *L. solandri* at remaining Central Otago locations and at Kura Tāwhiti. We do not know whether landscape-scale processes still provide for the persistence of *L. solandri* and other dryland species in the Mackenzie Basin or whether intensive land use has already crossed ecological thresholds.

Keywords: Brassicaceae, dryland ecosystems, fragmentation, local extinction, land-use intensification, off-site effects, saline habitat, threatened species

Introduction

Three diminutive and extraordinarily cryptic plants, *Lepidium kirkii* Petrie (family Brassicaceae), *L. solandri* Kirk, and *L. sisymbrioides* Hook.f. (Table 1) are endemic to a few inland regions of New Zealand's South Island and categorised as Threatened – Nationally Critical (de Lange et al. 2018). These *Lepidium* species are ecologically unusual in the New Zealand flora and are part of a distinctive inland South Island dryland flora that is becoming increasingly rare and threatened by extensive loss and modification of indigenous vegetation and habitats (Rogers et al. 2005; de Lange et al. 2009; de Lange et al. 2018). *Lepidium kirkii* is the only species in New Zealand's saltpan flora that occurs exclusively inland (Table 1). *Lepidium solandri* and *L. sisymbrioides* are the world's only dioecious members of the family Brassicaceae (4636 taxa in 340 genera) (Soza et al. 2014; Francis et al. 2021).

Remaining species' populations living in fragmented

landscapes face multiple interacting threats that are immediate (proximate) causes of decline. Inland *Lepidium* species are threatened by direct clearance, fragmentation, and isolation of their habitats and populations, which potentially lead to genetic impoverishment and drift (Frankham 1996), and failures in ecosystem processes (e.g. through loss of pollinators; Aguilar et al. 2006) and reproductive systems (e.g. insufficient available mates; Scobie & Wilcock 2009). Spillover of materials (Didham et al. 2015) and organisms (Blitzer et al. 2012) from surrounding land uses can cause or exacerbate cross-boundary effects such as competition from weeds, pesticide or herbicide damage, herbivory, and seed predation by mammals or invertebrates (e.g. cabbage white butterfly *Pieris rapae*), and/or infections of pathogens (as detected in coastal *Lepidium*; e.g. Armstrong 2007; van Vianen et al. 2013). Lesions of white blister rust (*Albugo*, Chromista), and associated stunted and distorted growth, have been observed on all three inland *Lepidium* species in parts of their remaining geographical ranges. The

Table 1. Habitats and populations of inland *Lepidium* species.

Name	Descriptions
<i>Lepidium kirkii</i>	The natural habitat of monoecious <i>L. kirkii</i> is saline and alkaline soils, which are defined by Allen and MacIntosh (1995) as sites with saline conductivity > 400 μ S, soil horizons pH > 7.0, or known halophytic flora and/or fauna. These habitats are also referred to as salt pans (Allen et al. 1997), saline substrates (Craw et al. 2022), saline patches (Rogers et al. 2000; Rufaut et al. 2018), or the inland saline ecosystem (Williams et al. 2007). Saline soils formerly covered more than 40 000 ha of semi-arid land in the Maniototo ecological district, mid-Manuherikia Valley, and upper Clutha Valley, but cultivation and irrigation had reduced their area to less than 100 ha by the 1990s. This reduction may be the most dramatic in any New Zealand ecological system (Rogers et al. 2000). Fifteen known locations of <i>L. kirkii</i> in Central Otago were recorded by Allen (2000).
<i>Lepidium solandri</i>	Non-salty topsoils near and around the margins of salt pans, exposed or thinly gravel-mantled Tertiary sediments, gravel veneers over schist, and arid outwash and river gravels were formerly major habitats of dioecious <i>L. solandri</i> in Central Otago (Allen et al. 1997). In the upper Waitaki basin (Mackenzie Basin), formerly extensive outwash and alluvial gravel terraces, plains, and fans supported hundreds of subpopulations (groups of two to 50 individuals) in their very driest microsites. The most northern record of <i>L. solandri</i> is from “limestone soils” in the Upper Waipara Gorge. It has been occasionally collected from “Broken River” in North Canterbury since the 1880s (Allen 2000) and now occurs on unstable limestone debris in the Lance McCaskill Nature Reserve (Kura Tāwhiti), and rarely on private, university, and Crown leasehold land in the vicinity of where habitat clearance is continuing (Grove et al. 2021). Earlier names for <i>L. solandri</i> (Heenan et al. 2007) were <i>Lepidium sisymbrioides</i> Hook.f. subsp. <i>sisymbrioides</i> (e.g. Allen 2000), <i>L. sisymbrioides</i> subsp. <i>solandri</i> (Kirk) Thell., <i>L. sisymbrioides</i> subsp. <i>solandri</i> var. <i>typicum</i> Thell., <i>L. matau</i> Petrie, <i>L. sisymbrioides</i> subsp. <i>matau</i> var. <i>lobulatum</i> Thell., and <i>L. sisymbrioides</i> subsp. <i>matau</i> (Petrie) Thell.
<i>Lepidium sisymbrioides</i>	We have the least historical information and understanding of the past habitats of dioecious <i>L. sisymbrioides</i> , which is now found on dry bedrock outcrops or cliffs of diverse origin and on immediately adjacent gravels. The species remained on schist outcrops in the Kawarau Gorge, greywacke outcrops, and river terraces in the Upper Manuherikia Valley, and limestone and basalt outcrops in the lower Waitaki Valley (Allen 2000; Heenan et al. 2007). Earlier names for <i>L. sisymbrioides</i> (Heenan et al. 2007) were <i>L. sisymbrioides</i> Hook.f. subsp. <i>sisymbrioides</i> , <i>L. kawarau</i> Petrie; <i>L. sisymbrioides</i> subsp. <i>ovatum</i> Thell., <i>L. kawarau</i> var. <i>dubium</i> Kirk.

white blister rust has been identified as *A. lepidii* (Cooper & Park 2020), which may be an endemic or indigenous organism. Its dispersal, infection, and effects on host mortality in natural populations, remain little understood.

A higher-level (ultimate) cause of inland *Lepidium* population declines is likely to be the loss and fragmentation of suitable habitats at the landscape scale. As Hanski (2011) explained, “the ultimate extinction threshold, the one that is treated in metapopulation theory, refers to the point along a gradient of habitat loss and fragmentation where the metapopulation loses viability because colonisations do not suffice to compensate for extinctions.” It is this deficit of colonisations which island biogeography theory (MacArthur & Wilson 1967) applies to predict that small patches of habitat remaining within otherwise developed and converted landscapes will progressively lose species that initially survived. Extinction debt (i.e. the number of inevitable but delayed species extinctions: Tilman et al. 1994) is expected to be greater where habitat loss is more complete, and more rapidly paid by earlier extinctions in smaller and more isolated patches (Diamond 1972).

Landscape-scale habitat loss also leads to deteriorating quality of what habitat remains, because cross-boundary effects increase with decreasing area and increasing habitat fragmentation (Fahrig 2003). Cumulative agricultural intensification has significantly altered surface temperatures, humidity, and evaporative demand at regional scales in semi-arid regions around the world (Nocco et al. 2019 and references therein). Nutrient enrichment from agriculture pervades large areas, including Europe (Stevens et al. 2010),

the USA (Simkin et al 2016), and Australia’s grain production landscapes (Duncan et al. 2008). Nitrogen applied to land in New Zealand increased 629% between 1991 and 2019, and the area of irrigated agricultural land almost doubled between 2002 and 2019, largely in Canterbury, Otago, and Marlborough (Statistics NZ 2021). Habitats occupied by New Zealand’s inland *Lepidium* species are likely to be vulnerable to climatic alteration and spillover of nutrients, other agricultural chemicals, moisture, weeds, and pathogens across their boundaries: vegetation is short-statured and open, there are few topographic barriers to materials travelling on the wind (Walker et al. 2019), and short-statured stress-tolerant dryland species are poorly equipped to compete when stress is ameliorated (e.g. by water or nutrients; Grime 1979). Beyond thresholds of loss and fragmentation in a landscape, positive feedbacks may result in abrupt, landscape-wide loss of specialist taxa, ecological resilience, and management effectiveness (Pardini et al. 2010).

This paper describes remaining inland *Lepidium* populations and their vascular plant communities in the context of the surrounding landscapes and land uses. Our data were collected in the austral summer of 2020/2021, when we surveyed and searched currently known and previously recorded locations and populations of the three species as a first step in a research project to investigate potential proximate causes of decline. Our surveys covered four geographical regions: Central Otago, the Waitaki Valley, the Mackenzie Basin, and Kura Tāwhiti (the Castle Hill basin in the Broken River catchment in North Canterbury) (Fig. 1).

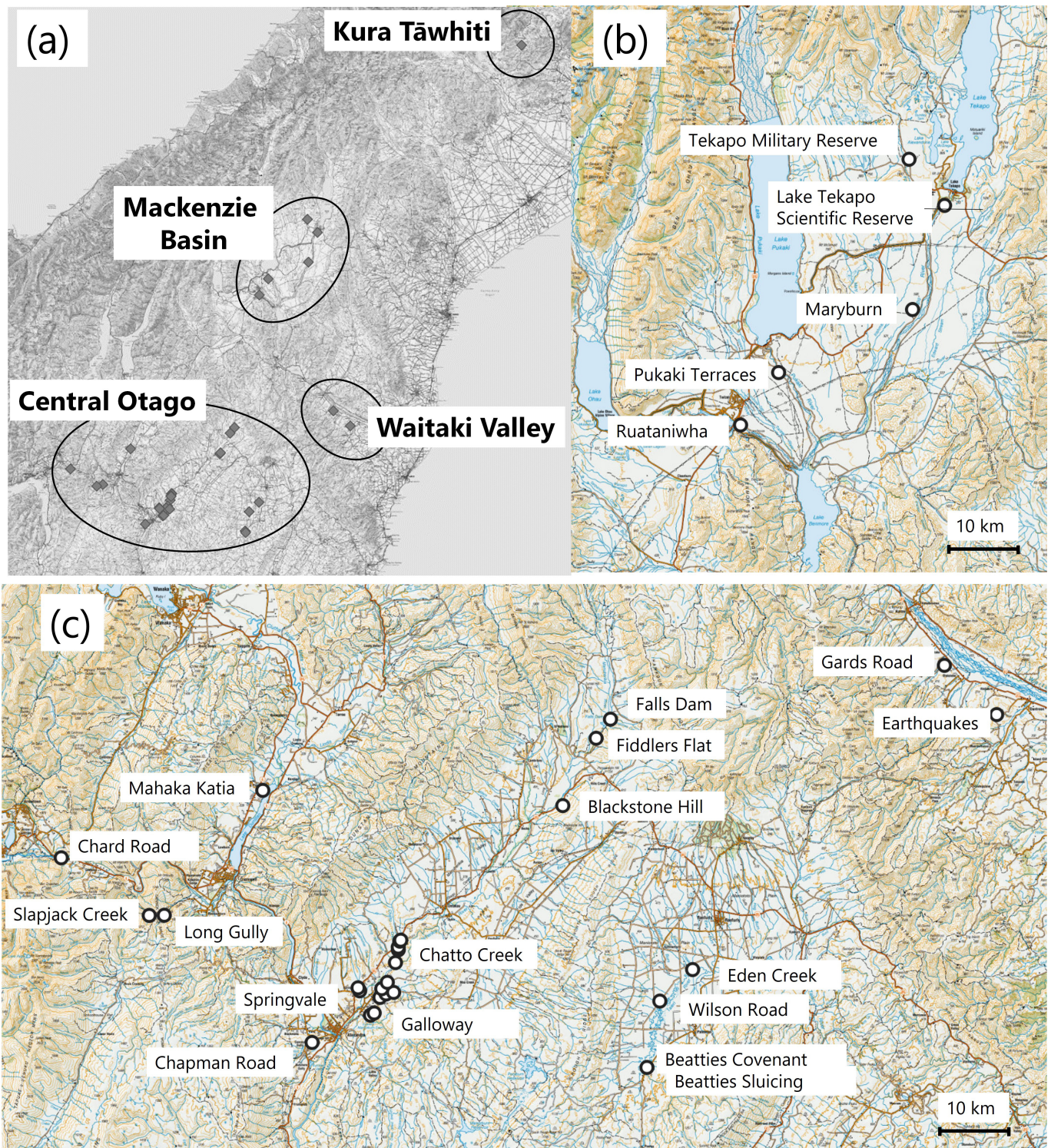


Figure 1. (a) The four geographical regions where inland *Lepidium* species occur (Kura Tāwhiti, the Mackenzie Basin, Waitaki Valley, and Central Otago); (b) locations in the Mackenzie Basin referred to in the text; (c) locations in Central Otago and the Waitaki Valley referred to in the text.

Hypotheses

In 2020 most habitats for indigenous species on the valley floors and lower hillslopes of Central Otago and the lower Waitaki Valley had been converted for land uses such as dairying, cattle or deer farming, horticulture, and lifestyle blocks (Fig. 2). In contrast, areas of potential habitat for

Lepidium and other dryland indigenous plants on the basin floors of the Mackenzie Basin were orders of magnitude larger and less isolated, because conversion to intensive use was less complete. Landscape transformation around Kura Tāwhiti was intermediate between Central Otago and the Mackenzie Basin in 2020: habitat for *Lepidium* and other indigenous species

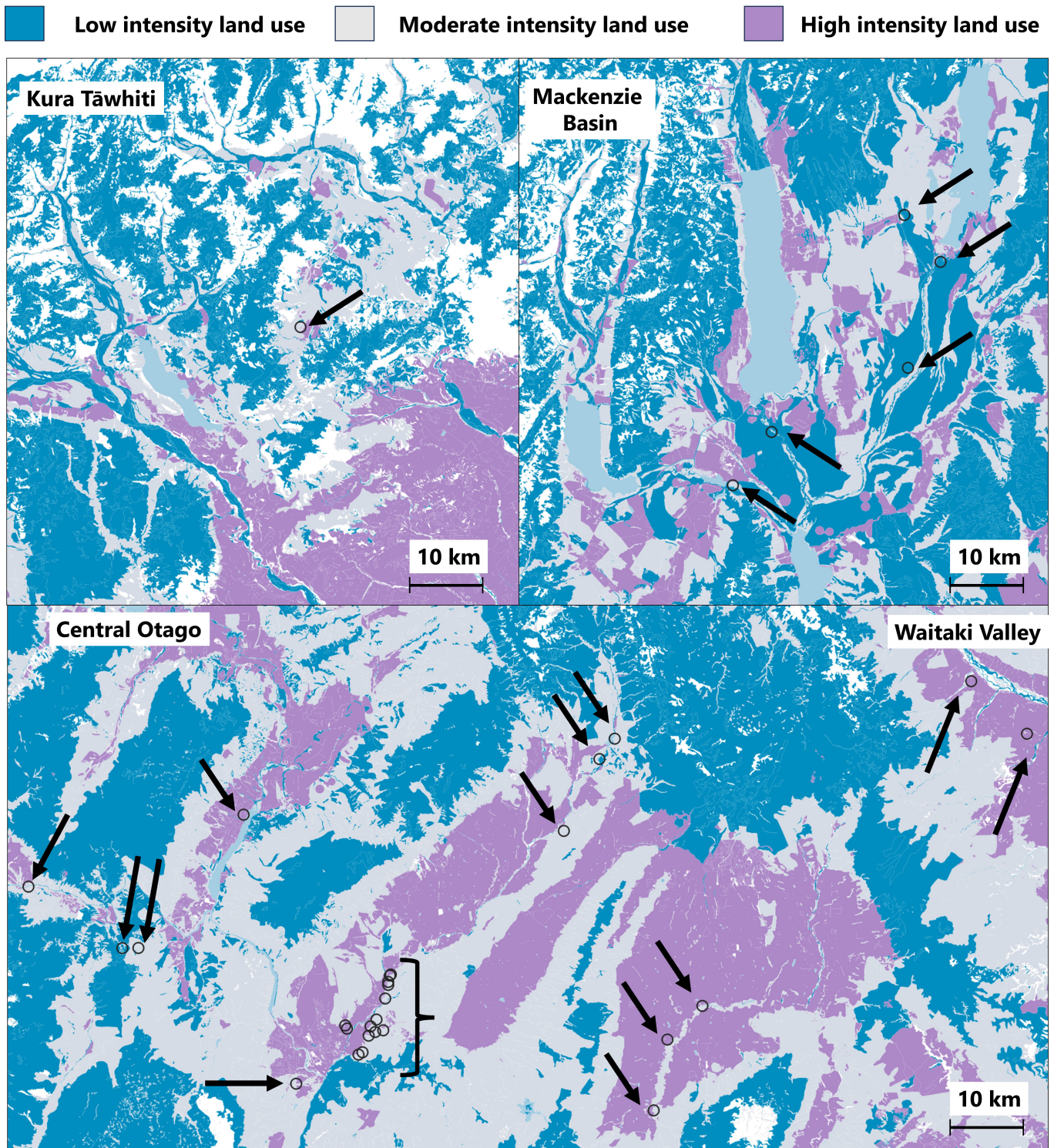


Figure 2. Land use intensity (categorised as low, moderate and high intensity) across the four geographical regions where inland *Lepidium* species occur (Kura Tāwhiti: top left; the Mackenzie Basin: top right; Central Otago: lower left; Waitaki Valley: lower right). Unshaded circles show the 2 km radii around each *Lepidium* location that were used to derive our land use intensity statistics. Black arrows and parentheses are used to emphasise inland *Lepidium* locations.

had become isolated within more-developed land, and the conversion of remaining habitats in the surrounding landscape was ongoing (Grove et al. 2021).

We expected to record fewer indigenous vascular plant species in remaining habitats within more-developed regions, consistent with ecological theory that small patches of

remaining habitat will lose species progressively (MacArthur & Wilson 1967; Diamond 1972; Tilman et al. 1994; Hanski 2011). We also predicted that numbers of indigenous vascular plant species would be lower where local extinctions of *Lepidium* had occurred, consistent with progressive loss of other indigenous species in addition to *Lepidium*.

We expected greater local transformation of habitats within more-developed regions. Specifically, we predicted that vascular plant floras in more developed geographical regions and local landscapes would be more dominated by introduced exotic species and include more exotic ruderal species (*sensu* Grime 1979; i.e. adapted to rapidly acquire soil nutrients from a plentiful pool), reflecting greater alteration of habitats by the surrounding land uses. If local transformation and exotic dominance of habitats contributes to declines and loss of indigenous plant species, we expected that local extinctions of inland *Lepidium* species would have been more frequent at locations with higher proportions of exotic vascular plant species.

Methods

Data

We collated the published and unpublished literature and searched the Allan Herbarium (CHR) for *Lepidium* records, listing previously recorded locations and assembling relevant observer photographs and notes where still available. We then undertook surveys and searches to determine which previously recorded populations remained extant. Fieldwork covered four geographical regions where inland *Lepidium* species are or were known to occur (Figs 1, 2). In Central Otago (but not in other regions) almost all locations of inland *Lepidium* were known in the 1990s and we were able to revisit most of these, and thereby estimate rates of local extinction.

We visited as many locations as we could, mainly between 15 and 24 December 2020 (Appendices S1, S3, S4). At each location, observers searched for *L. kirkii*, *L. solandri*, or *L. sisymbrioides* plants. Where present, individuals were temporarily marked with labelled orange triangles. Full census and gender ratio counts were not attempted because time and (for *L. sisymbrioides*) terrain did not allow exhaustive survey of all locations. However, experienced observers spent enough time at each location to ascertain whether populations remained extant and to record the full vascular flora. We listed each vascular plant species growing within 20 m of observed *Lepidium* plants or their formerly recorded locations. At Kura Tāwhiti we recorded the vascular flora around *Lepidium* plants growing just outside the Lance McCaskill Nature Reserve, not within the recently hand-weeded reserve. We counted numbers of exotic and indigenous vascular plant species at each location from our lists.

We calculated the area of each cover class in the Land Cover Database version 5 (Landcare Research Informatics Team 2019) within radii of 2 km from the centre of each location (Fig. 2). Classes were aggregated into three categories (intensive, intermediate, and low-intensity land use; Fig. 2; Appendices S2, S5), and we calculated the percentage of land within each category within each radius.

Analyses

We used agglomerative clustering function `hclust` from the package `stats` in R (R Core Team 2022) to identify groups of floristically similar locations (classification groups).

Proportions of high- and low-intensity land use within 2 km of locations were compared among geographical regions and classification groups with analysis of variance and Tukey's honest significant difference (HSD) test. Proportions of land use were logit-transformed for these analyses to meet normality

and variance assumptions. To compare numbers of indigenous and exotic species among geographical regions or classification groups we fitted and compared three models with each predictor: (1) a generalised linear model assuming a Poisson distribution, (2) a generalised linear mixed model with an observation-level random effect (OLRE) assuming a Poisson distribution, and (3) a negative binomial model. We selected the best model using Akaike's information criterion corrected for small sample size (AICc; Hurvich & Tsai 1989) and applied Chi-squared or Tukey's HSD tests to assess whether differences between pairwise contrasts were statistically significant. To compare proportions of vascular species that were exotic (representing local exotic dominance of vascular flora) we fitted binomial generalised linear models, in which 'successes' and 'failures' in the dependent variable were numbers of plant species that were exotic and indigenous, respectively, and used chi-squared tests to assess pairwise differences between geographical regions and classification groups. Appendices S7–S11 describe these models and their outputs.

We used generalised linear models to test whether local land use intensity had significant effects on numbers of indigenous species and proportions of species that were exotic across past and present *Lepidium* locations in the four regions. We compared null models (no predictors) of each response variable to models with region, or region and proportion of land under intensive land use, as predictors (Appendices S12–S13). A Poisson error distribution was assumed for the number of indigenous species, and the proportion of exotic species was fitted as a binomial variable with successes and failures being numbers of exotic and indigenous plant species, respectively.

We then asked whether local extinctions of inland *Lepidium* species at Central Otago locations were predicted by the local numbers of indigenous species and proportions of species that were exotic. For these tests we fitted binomial generalised linear models of local extinction, where absence of one of more *Lepidium* species present in the 1990s was coded as one and persistence as zero; null models (no predictors) were compared against models with numbers of indigenous species and proportions of species that were exotic as predictors (Appendices S12–S13).

Residual plots were used to check that all models met the assumptions of linearity and homoscedasticity (i.e. residuals did not show curvature, nor increases or decreases as the predicted values increased).

Results

Survey results

Lepidium kirkii

We found *L. kirkii* at six of fourteen formerly known locations, and at one further location near Chatto Creek (Appendix S3). We found very low numbers of plants (fewer than 20) at all locations, except at Springvale Conservation Area, where more than 50 plants were present. We were able to collect seed at four locations.

Monitoring by the Department of Conservation (DOC) had failed to record *L. kirkii* plants at Upper Galloway or Lower Galloway in recent years (DOC 2017; S. Roselli, DOC, pers. comm.). However, we found a few plants at each location (Appendix S3). Three non-flowering plants were also found at Galloway South 2, which is one of two locations near Lower Manorburn Dam where hundreds of individuals were

present in the 1990s (GL, pers. obs.). We found fewer than 10 individuals (one flowering adult and one group of seedlings on an adjacent private property) at Chapman Road Scientific Reserve, where DOC monitoring had recorded 500 plants in the 2016/2017 summer (DOC 2017). At Chatto Creek, two *L. kirkii* plants on saline soils were found near one historical *L. solandri* record.

We found no *L. kirkii* plants at nine locations where it had previously been recorded (Appendix S3): north of the saltbush plantation at Chatto Creek (CC2); Wilson Road (formerly the largest known population); Beatties Sluicing and Beatties Covenant in the Maniototo; hillslopes below the airstrip near Galloway Station homestead (Galloway Airstrip); Galloway South 1 near Lower Manorburn Dam; two saline sites on Olig Station (Olig 1 and Olig 2); and private property west of the highway at Springvale. Former locations at Rockdale and Dovedale were not visited but appear to have been developed into exotic pasture (Appendix S3).

Lepidium solandri

We found *L. solandri* at 11 locations: five of 11 previously recorded locations in Central Otago, five of five known locations on public land in the Mackenzie Basin, and one location within and around the Lance McCaskill Nature Reserve (Kura Tāwhiti; Appendix S4).

In Central Otago, about 20 individuals remained at Mahaka Katia Scientific Reserve (formerly Pisa Flat, in the Upper Clutha catchment) where hundreds of plants were monitored through the 1990s and early 2000s (Allen 1998; 2000) and as recently as the 2015/2016 summer (DOC 2017) (Appendix S4). The gender ratio was male-biased and the plants were dwarfed and distorted. About 30 plants at Beatties Covenant (a QEII Trust covenant on private land, Maniototo) had a relatively equal gender ratio. Two female plants remained about 1 km to the south at Beatties Sluicing. Three *L. solandri* plants remained on private property near Springvale in the Manuherikia Valley; one was female and bore seed, which germinated. Annual monitoring of this location recorded over 100 plants each year between 2000 and 2008 and then a sharp decline (DOC 2017). We found approximately 50 plants of both genders on a strip of private and public land on Blackstone Hill (treated as two separate locations in our floristic data set). We did not relocate *L. solandri* at any of four previously recorded locations on private land at Chatto Creek in December 2020, but two plants were found at one of these locations in January 2023 (K. Wardle, unpublished data; Appendix S4).

Lepidium solandri had apparently become locally extinct by December 2020 at Eden Creek in the Maniototo, where plants were last recorded in 2016/2017 (DOC 2017); and at Lower Galloway (plants last recorded in 2010/2011), at Wardles, and at three of four former locations at Chatto Creek in the Manuherikia Valley. We were unable to access one further location at Taieri Lake (Maniototo), where the plant had previously been recorded.

Lepidium sisymbrioides

We found plants of *L. sisymbrioides* at five of six formerly known locations searched and were able to collect seed from three of these (Appendix S5).

Three previously tagged plants (one flowering male and two non-flowering plants) were found in Slapjack Creek Conservation Area above the Kawarau Gorge. Here, and at Long Gully (where no plants were found; Appendix S5), the bluff habitat was surrounded by sweet briar (*Rosa rubiginosa*) and

other shrubs, and loose schist slabs made searching hazardous. Two non-flowering plants remained on a road cutting at Chard Road, where Allen (1998) reported collecting seed. Recent searches beside SH6 in the Kawarau Gorge determined that the species no longer occurs at Nevis Bluff (P. Heenan, pers. comm.). We did not access locations documented by Allen (2000) on private land at the Swift Burn nor on the north side of Slapjack Creek (Appendix S5). Most rock crevices that would potentially support *L. sisymbrioides* in the Kawarau Gorge were occupied by culinary thyme (*Thymus vulgaris*) in 2020.

We found about 20 *L. sisymbrioides* plants, with a relatively equal gender ratio, on riparian outcrops and bluffs north of Falls Dam in the upper Manuherikia valley. At Fiddlers Flat we found one previously documented male plant on the terrace surface and another between the terrace and bluffs above the Manuherikia River (we did not search the bluffs).

More than 50 plants remained at Gards Road in the Waitaki Valley, many with obvious *Albugo* symptoms. At Earthquakes there were two known adult female plants and four seedlings. We were unable to inspect a location on private land beside the Hakatamea Highway where an herbarium specimen was collected in 1994 (Appendix S5).

Land use, vegetation characteristics, and *Lepidium* loss

Most of the land use in the 2 km radii surrounding *Lepidium* locations in the Waitaki Valley, Central Otago, and Kura Tāwhiti was of high or moderate intensity (Table 2; Appendices S1 and S2). The Mackenzie Basin was the only region where low-intensity land use surrounded *Lepidium* populations. Plant communities at past and present *Lepidium* locations in Central Otago, the Waitaki Valley, and Kura Tāwhiti supported fewer indigenous vascular plant species, more exotic vascular plant species, and were more dominated by exotic species than those in the Mackenzie Basin (Table 2).

Consistent with our hypotheses, our generalised linear models showed that numbers of indigenous vascular plant species decreased significantly ($P < 0.05$; from 12.2 [95% CI 10.4, 14.4] to 5.9 [4.2, 8.4] species; Fig. 4a), and local exotic dominance of the vascular flora increased significantly ($P < 0.05$; from 55 [50, 60] to 74 [65, 81] percent; Fig. 4b), as the amount of high-intensity land use in the 2 km radii surrounding *Lepidium* locations increased from 0 to 100% (Tables 3 & 4).

Also consistent with our hypotheses, two models with similar weight (Table 3) showed that the probability of local extinction of *Lepidium* species in Central Otago decreased significantly ($P < 0.05$) from 0.07 [0.00, 0.57] to 0.74 [0.44, 0.91] as the number of other indigenous vascular plant species at the location increased from 1 to 24 (Figure 4c), and that probability of local extinction increased significantly ($P = 0.05$) from 0.16 [0.03, 0.56] to 0.79 [0.44, 0.95] as local exotic dominance of the flora increased from 40 to 94% (Fig. 4d; Tables 3 & 4).

Classification groups

Agglomerative clustering identified five major groups of locations (A to E) (Fig. 3; Table 2; Appendix S6). Group A was made up of former or current locations of *L. kirkii* and/or *L. solandri* near or on saline soils in Central Otago. Other locations with extant *L. solandri* were split regionally into either Group B (locations in Mackenzie Basin), Group C (low-elevation locations in Central Otago), and Group E (Kura Tāwhiti). Group D comprised habitats of *L. sisymbrioides* in the Waitaki Valley and at lower elevations in Kawarau Gorge.

Table 2. Mean and standard deviations of landscape and vegetation characteristics in the 4 geographical regions and 5 plant community groups identified with agglomerative clustering. The table compares high- and intermediate-intensity land use within 2 km of present or former *Lepidium* populations, and numbers of indigenous and exotic vascular plant species, and the percentage of vascular species exotic in the immediate surroundings within 20 m of the present or former *Lepidium* plants. Superscript letters a to c in common show response variables not significantly different at $P < 0.05$, and Appendices S7–S11 provides details of the analyses used to derive this information.

	High-intensity land use within 2 km (%)	Low-intensity land use within 2 km (%)	No. of indigenous vascular plant species	No. of exotic vascular plant species	Percentage of vascular species exotic (%)
Geographical region					
Central Otago ($n = 26$)	33.0 ± 33.0 ^b	8.5 ± 19.5 ^b	8.5 ± 6.7 ^b	16.4 ± 5.6 ^a	69.3 ± 16.2 ^a
Waitaki Valley ($n = 2$)	100.0 ± 0.0 ^a	0.0 ± 0.0 ^b	9.0 ± 2.8 ^b	18.5 ± 2.1 ^a	67.4 ± 9.5 ^a
Mackenzie Basin ($n = 5$)	0.3 ± 0.6 ^b	79.7 ± 31.5 ^a	21.2 ± 2.7 ^a	11.0 ± 3.7 ^b	33.8 ± 10.1 ^b
Kura Tāwhiti ($n = 1$)	9.2 ^{ab}	0.0 ± 0.0 ^b	13.0 ^b	21.0 ^a	61.8 ^a
Agglomerative clustering group					
A ($n = 15$)	38.4 ± 29.7 ^{ab}	0.2 ± 0.5 ^c	4.6 ± 3.2 ^c	15.1 ± 4.1 ^{ab}	78.1 ± 11.5 ^a
B ($n = 5$)	0.3 ± 0.6 ^c	79.7 ± 31.5 ^a	21.2 ± 2.7 ^a	11.0 ± 3.7 ^b	33.8 ± 10.1 ^d
C ($n = 6$)	46.1 ± 41.0 ^{abc}	0.4 ± 0.7 ^{bc}	12.3 ± 3.3 ^b	21.5 ± 6.9 ^a	62.6 ± 11.6 ^b
D ($n = 4$)	51.5 ± 56.1 ^a	12.6 ± 18.8 ^{bc}	7.8 ± 3.6 ^{bc}	14.3 ± 5.1 ^{ab}	65.2 ± 14.1 ^b
E ($n = 4$)	2.3 ± 4.6 ^{bc}	41.4 ± 30.8 ^{ab}	19.8 ± 5.0 ^a	18.0 ± 4.1 ^{ab}	47.9 ± 9.9 ^c

Table 3. Model comparisons showing Akaike's information criterion corrected for small sample size (AICc); the difference in AICc from the best model (Δ AICc), the cumulative model weight progressing from the best to the worst model (Cum. Wt), and the log-likelihood (LL).

Model and parameters	K	AICc	Δ AICc	AICcWt	Cum.Wt	LL
Response: Number of (all) indigenous plant species						
Region + Proportion of land under a high intensity land use	5	263.17	0	0.98	0.98	-125.51
Region	4	271.24	8.07	0.02	1.00	-130.93
Null model	1	317.12	53.94	0.00	1.00	-157.5
Response: Proportion of vascular plant species exotic						
Region + Proportion of land under a high intensity land use	5	200.63	0	0.97	0.97	-94.24
Region	4	207.32	6.69	0.03	1.00	-98.97
Null model	1	254.11	53.48	0.00	1.00	-125.99
Response: Local extinction of <i>Lepidium</i> species						
Number of other (non-inland- <i>Lepidium</i>) indigenous vascular plant species	2	35.81	0	0.46	0.46	-15.64
Proportion of vascular plant species exotic	2	36.09	0.28	0.40	0.86	-15.78
Null (no predictors)	1	38.21	2.4	0.14	1.00	-18.02

Locations in Group E (Slapjack Creek, Fiddlers Flat, and Falls Dam with *L. sisymbrioides*, and Kura Tawhiti) are all above 500 m elevation.

Lepidium locations in Group B (Mackenzie Basin) and Group E (higher-elevation Central Otago locations and Kura Tāwhiti) supported the largest numbers of indigenous vascular plant species, while locations in Group A had the fewest (Fig. 3; Table 2; Appendix S6). Locations in Groups C and E supported the largest numbers of exotic species, but Group A locations were the most dominated by exotic species (on average 78% of the vascular flora was exotic). Locations in Group B (Mackenzie Basin) were the least dominated by exotic species (average 34% of species), but indigenous species also continued to dominate vascular floras at the three highest-elevation locations of *L. sisymbrioides* in Group E (Slapjack Creek, Falls Dam, and Fiddlers Flat) (Fig. 3).

Halophytic plants in Groups A and C indicate the saline

influence on Central Otago's *L. kirkii* and *L. solandri* habitats. *Atriplex buechananii* (Nationally Vulnerable) was present at most locations, often together with *Puccinellia rariflorens* (Nationally Critical) (Appendix S6). Neither *L. kirkii* nor other halophytes were found at Galloway South 1 (in Group A), where *L. kirkii* had previously been abundant. We also recorded no halophytes near the *L. solandri* locations on Blackstone Hill (in Group C), where specimen CHR 573584 refers to "salt pans" and Nationally Vulnerable *Atriplex buechananii* was recorded by Barkla and Thorsen (2007).

One or more *Lepidium* species had disappeared from two-thirds of the locations in Group A, and few other indigenous plant species were present (Fig. 3; Table 2). Locations in Group C had all retained *L. solandri* but *L. kirkii* was not present on private land at Springvale, Beatties Covenant or Beatties Sluicing, where it was recorded historically along with *L. solandri*. Common weeds at

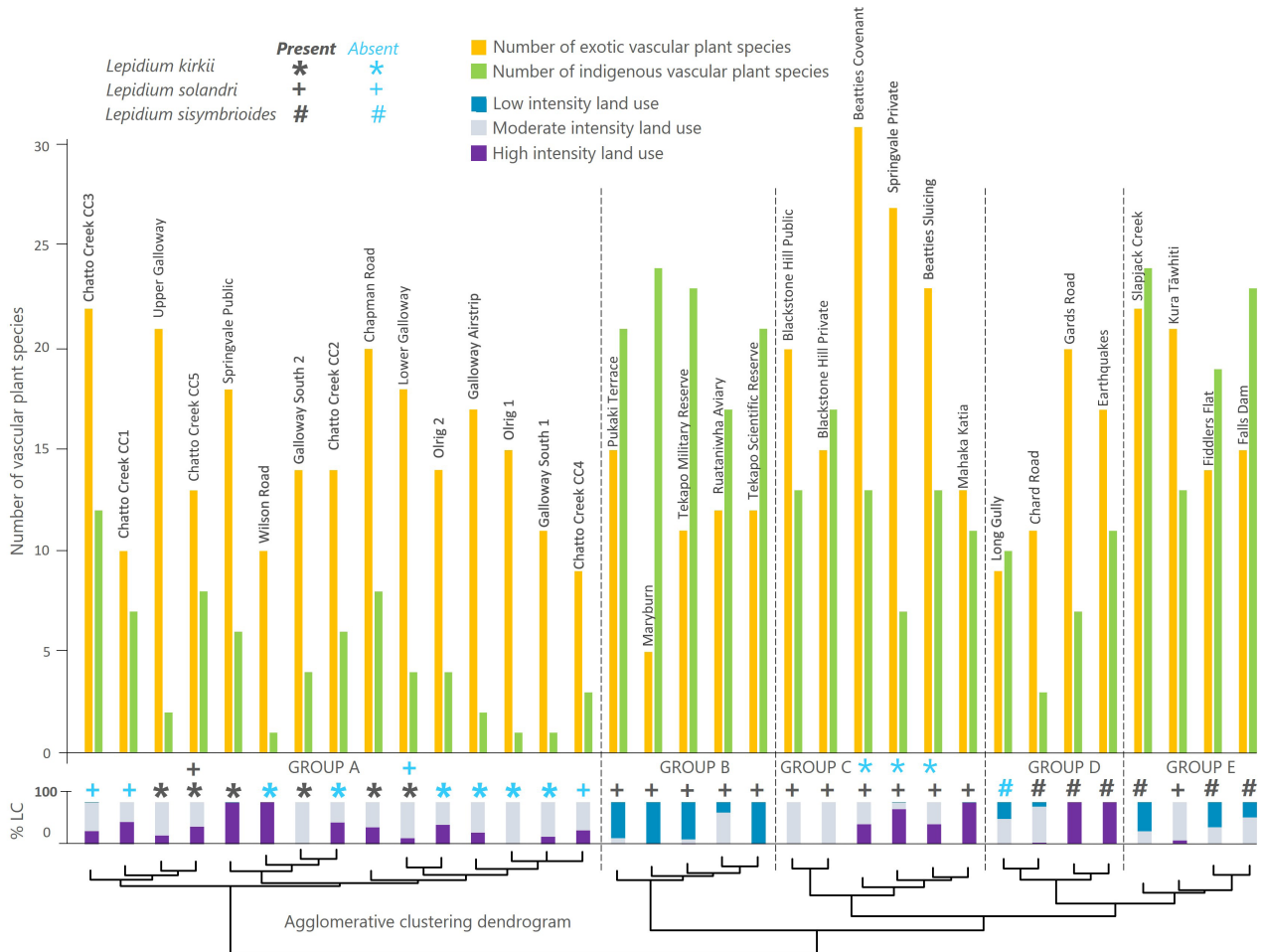


Figure 3. Five groups of former and present-day locations of inland *Lepidium* species we visited, based on agglomerative clustering of the vascular plant composition, with similarity indicated by the dendrogram. The presence or absence of previously recorded inland *Lepidium* species in our surveys is indicated by black and blue symbols, respectively. The lower graph shows the percentage of intensive, intermediate, and low-intensity land use within a 2 km radius of each location. Total numbers of exotic and indigenous vascular plant species identified at each location are indicated in yellow and green bars in the upper graph.

Table 4. Summary of best models, showing the response variables (Response), parameters, parameter estimates (Estimate) and standard errors (Std. Error) and z values and P values (Pr(>|z|)). In all models including the categorical region parameter, the reference region was the Mackenzie Basin.

Model and parameters	Estimate (log scale)	Std. Error	z value	Pr(> z)
Response: Number of (all) indigenous plant species				
Intercept	2.78	0.12	22.38	0.000***
Proportion of land under a high intensity land use	-0.26	0.08	-3.17	0.002**
Central Otago region	-0.70	0.13	-5.27	0.000***
Waitaki Valley region	-0.13	0.34	-0.38	0.707
Kura Tāwhiti region	-0.42	0.29	-1.44	0.150
Response: Proportion of vascular plant species exotic				
Intercept	-0.40	0.19	-2.14	0.033*
Proportion of land under a high intensity land use	0.29	0.10	3.01	0.003**
Central Otago	1.06	0.20	5.28	0.000***
Waitaki Valley	0.55	0.43	1.29	0.198
Kura Tāwhiti	1.06	0.39	2.72	0.007**
Response: Local extinction of <i>Lepidium</i> species				
Intercept	1.21	0.73	1.65	0.099
Number of other (non-inland- <i>Lepidium</i>) indigenous vascular plant species	-0.16	0.08	-1.97	0.048*
Response: Local extinction of <i>Lepidium</i> species (Intercept)				
Intercept	-0.33	0.47	-0.71	0.478
Proportion of vascular plant species exotic	1.110	0.57	1.96	0.050*

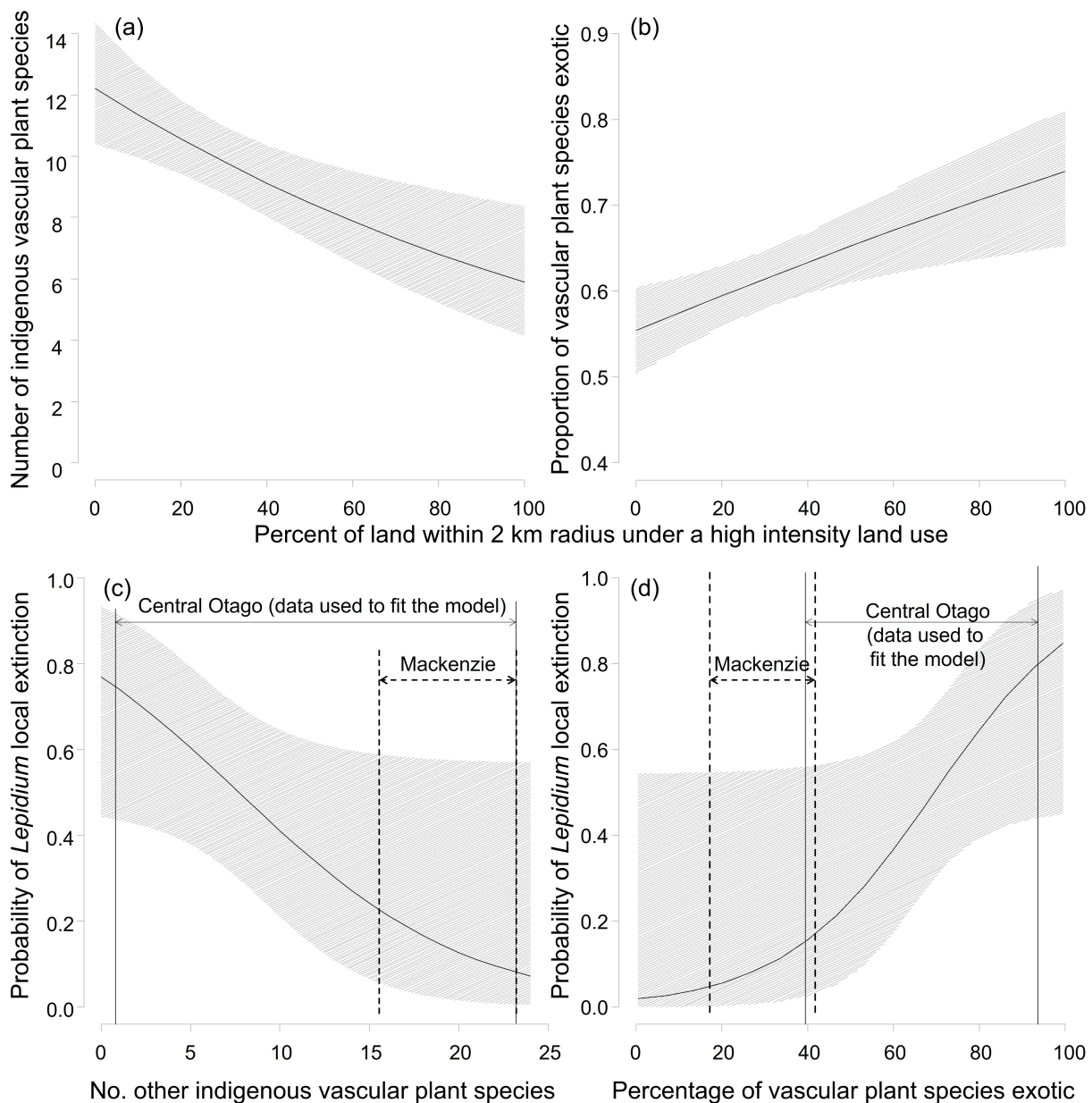


Figure 4. Fitted effects of (a, b) the proportion of land within a 2-km radius under a high intensity land use on the number of indigenous vascular plant species and proportion of vascular plant species that are exotic, respectively, in the full dataset; and (c, d) the number (No.) of other (i.e non-*Lepidium*) indigenous vascular plant species and proportion of vascular plant species that are exotic on the local extinction of one or more inland *Lepidium* species from locations in Central Otago since the 1990s. In (d), we show the range of values recorded in the Mackenzie region and fitted effects for this range for reference, and caution that these values are outside the range of the data from Central Otago which were used to fit the model.

locations in both Groups A and C were *Cirsium arvense*, *C. vulgare*, *Leontodon taraxacoides*, *Lolium perenne*, *Spergularia rubra*, and *Vulpia bromoides*. Group A plant communities often also included exotic *Plantago coronopus*, a distinctive non-native *Puccinellia* species, *Hordeum marinum* subsp. *marinum*, and occasionally *Lepidium africanum* (at Orlig and Galloway airstrip). The invasive grass *Austrostipa nodosa* was present in many locations in Group A, but had so far remained absent from those in Group C.

Blackstone Hill, with the least intensive development nearby of any Group C location, retained indigenous species such as *Coprosma propinqua*, *Discaria toumatou*, *Festuca novae-zelandiae*, *Melicytus alpinus*, *Poa colensoi*, *Raoulia*

beauverdii (Declining), *Stellaria gracilentia*, and *Wahlenbergia albomarginata* (Appendix S6). Mahaka Katia Scientific Reserve supported Nationally Vulnerable *Convolvulus verecundus* and *Muehlenbeckia ephedroides*. At Risk–Declining *Colobanthus brevisepalus*, and *Muehlenbeckia axillaris*, *Poa maniototo*, and *Rytidosperma pumilum*.

Indigenous plant associates of *L. solandri* in the Mackenzie Basin (Group B) included Nationally Vulnerable species *Carmichaelia nana*, *Convolvulus verecundus*, *Muehlenbeckia ephedroides*, *Pimelea sericeovillosa* subsp. *pulvinaris*, and *Raoulia monroi* (Appendix S6), along with *Colobanthus brevisepalus* (At Risk–Declining), *Carex resectans*, *Geranium brevicaulis*, *Luzula rufa* var. *albicomans*, *Muehlenbeckia*

axillaris, and *Scleranthus uniflorus*. The exotic vascular flora included *Pilosella officinarum* and *Rumex acetosella*, but few other exotic species that were common in Central Otago locations were present.

Plant communities at locations with *L. sisymbrioides* (Groups D and E) varied with ecological context and base rock types. Group E clustered communities of densely thyme-invaded schist outcrops at Slapjack Creek with greywacke outcrops at Falls Dam and river gravels at Fiddlers Flat. These locations shared the indigenous shrubs *Coprosma propinqua* and *Discaria toumatou*, grasses *Poa colensoi* and *Anthosachne solandri*, the herb *Wahlenbergia albomarginata*, and the exotic *Hieracium lepidulum*, which were not recorded in the lower-elevation, thyme-invaded Long Gully and Chard Road locations in the Kawarau Gorge, nor on limestone outcrops in the lower Waitaki (Gards Road and Earthquakes) in Group D (Appendix S6). The exotic grass *Austrostipa nodosa* had invaded Gard's Road, Earthquakes, and Long Gully (in Group D) by 2020/2021. Relictual indigenous woody species *Griselinia littoralis*, *Veronica salicifolia*, *Muehlenbeckia australis*, the Nationally Endangered herb *Gingidia enysii*, and the woody weeds *Cotoneaster simonsii* and *Ribes uva-crispa* were recorded only at Earthquakes, and boxthorn (*Lycium ferocissimum*) only at Earthquakes and Gard's Road.

We recorded the indigenous herbs *Anisotome aromatica*, *Celmisia gracilentia*, and *Plantago triandra*, and the exotic *Leucanthemum vulgare* and *Origanum vulgare* only on and around the limestone debris habitat of *L. solandri* at Kura Tāwhiti (in Group E) (Appendix S6). Kura Tāwhiti also shared exotic species such as *Dactylis glomerata*, *Festuca rubra*, *Taraxacum officinale*, and *Trifolium dubium* with limestone habitats of *L. sisymbrioides* in the lower Waitaki Valley; and *Arenaria serpyllifolia* and indigenous *Brachyglottis lagopus* with *L. sisymbrioides* habitats at Falls Dam in the Upper Manuherikia valley. Indigenous silver tussock (*Poa cita*) also occurred at Slapjack Creek and at *L. solandri* locations on Blackstone Hill.

Discussion

Regional patterns

Our data indicate that there have been many population declines and local extinctions in inland *Lepidium* species across their range in the last 30 years. As we expected, across the four regions there were lower numbers of remaining indigenous vascular plant species and greater exotic dominance of local vascular plant associations where land-use intensification and habitat loss had been greater. Local extinctions of inland *Lepidium* in Central Otago had occurred where there were fewer indigenous vascular plant species and a higher degree of exotic dominance in the local vascular plant community.

In 2020, sizeable areas of habitat still existed for *Lepidium* only in the Mackenzie Basin, where only *L. solandri* is present: habitats on public land had not yet been reduced to isolated patches within matrices of intensively developed agricultural land; populations of *L. solandri* remained; floras were dominated by a suite of stress-tolerant indigenous species; and ruderal exotic plant species were all but absent. This was no longer the case in Central Otago, in the Waitaki Valley, and at Kura Tāwhiti, where many or most past habitats of *Lepidium* species across the landscape had been removed and replaced with high- or moderate-intensity land uses.

In Central Otago, populations of *L. kirkii* or *L. solandri* had disappeared from 13 of the 22 patches of former habitat that we visited or surveyed, and cultivation and irrigation had probably extirpated *L. kirkii* at a further two locations. Numbers of other indigenous vascular plants were low in all Central Otago locations at lower elevations, and especially low in those where *Lepidium* species had disappeared completely. A suite of indigenous vascular plant species that co-occurred with *L. solandri* in the Mackenzie Basin and were once more common in undeveloped dryland vegetation across Central Otago (e.g. Ward et al. 1987; Grove 1994) were either absent or very rare across Central Otago *Lepidium* locations in 2020. Although we do not have species lists for locations from earlier years, it seems likely that indigenous plant species other than *Lepidium* have also disappeared from remaining habitat fragments in Central Otago in recent decades, as predicted by theory. There have been similar outcomes in isolated small reserves on the Canterbury Plains: Bowie et al. (2016) reported only “a third of the native vascular plants and 20% of the moss and lichen species recorded [in 1970]”, and Ecroyd and Brockerhoff (2005) reported disappearance of “16 [indigenous] dicotyledonous herbs, two grasses, three orchids, one sedge, one fern, and five shrubs” between 1972 and 2003.

Habitats of inland *Lepidium* species are among New Zealand's most edaphically stressful, yet outside the Mackenzie Basin in 2020, exotic plant species dominated floras and most locations supported ruderal species (e.g. *Cirsium arvense*, *Dactylis glomerata*, *Leontodon taraxacoides*, *Lolium perenne*, *Hypochaeris radicata*, *Taraxacum officinale*, *Trifolium dubium*), which are usually absent from high-stress habitats. Dense, exotic grass swards dominated limestone habitats in the Waitaki Valley and intensive hand weeding had recently been undertaken to strip invaded limestone scree in Lance McCaskill Nature Reserve (Kura Tāwhiti). The overall pattern of invasions was consistent with climate amelioration, and/or nutrient and weed enrichment, of formerly high-stress habitats of long-lived, stress-tolerant indigenous plants within landscapes that have been largely converted for intensive land uses, as has been seen overseas (Nocco et al. 2019).

Local-scale threats and intensive management

Actions that address small population sizes, competition from weeds, and changes in substrate characteristics will be needed to maintain species at remaining locations outside the Mackenzie Basin. Establishment of new insurance populations would also be sensible, if possible.

Bolstering the very small population sizes in the wild is prudent for all three species. All germinate readily from collected seed, so *ex situ* propagation and reintroductions are feasible, provided the potential for disease transfer is addressed. In *L. solandri* and *L. sisymbrioides*, dioecy halves the effective population size and confers additional handicaps, which may exacerbate declines when numbers are low. Dioecious plants can suffer pollination limitation, both because they cannot self-pollinate and because only male-to-female pollinator movement directions contribute to seed production (Vamosi et al. 2006). Lack of available mates and pollen can therefore become acute when population sizes are small or skewed. The ability to colonise uninhabited sites is also constrained in dioecious plants because only 50% of the individuals in a population contribute to seed production (the “seed-shadow handicap”; Heilbut et al. 2001; Vamosi et al. 2007).

Weed invasion into Central Otago's saline habitats was occurring with and without the removal of stock. *Plantago*

coronopus was common on saline soils and introduced *Lepidium africanum*—with microhabitat and growth habit similar to endemic *Lepidium*—was growing on saline soils on Olig and Galloway airstrip. Saline soil margins were dominated by *Austrostipa nodosa* or other exotic grasses, often in dense swards, which is consistent with widespread marginal encroachment, as documented by Rufaut (2022). Dense swards of chewing fescue (*Festuca rubra*) dominated *L. sisymbrioides* habitats at Gards Road and Earthquakes; culinary thyme (*Thymus vulgaris*) occupied former rock ledge niches of *L. sisymbrioides* in the Kawarau Gorge; and *A. nodosa* dominated former *L. solandri* habitat at Lower Galloway. Intensive hand weeding has been required to maintain bare surfaces on the limestone debris at Kura Tāwhiti, where other threatened plant species co-occur with *L. solandri* (D. Wotton, unpubl. data) and is likely to be needed elsewhere.

Mechanical exposure of bare surfaces and the addition of carbon to soil surfaces may also be useful to maintain *Lepidium* populations at local scales. Rufaut et al. (2018) noted that salt concentrations that are inimical to many potential competitors of *L. kirkii* (and other halophytes) reduce if saline surfaces are not periodically rejuvenated. They suggested that saline habitats could be restored using an adaptive management approach that mechanically exposes new underlying surfaces of mudstone and clay-altered schist to provide fresh areas of habitat with high salt concentrations. A similar approach has been trialled on limestone substrates in the lower Waitaki Valley which were stripped of deep grass turves before nursery-grown and aggressively hardened plants of *L. sisymbrioides* were planted to bolster local populations (C. Lagrue, DOC, pers. comm.).

Carbon additions to soils have not been trialled and could potentially slow habitat transformation by nutrient spillover and moisture and favour indigenous dryland plant species over the ruderal species that are now invading. Sugar and sawdust additions can increase nitrogen immobilisation by heterotrophic soil microbes and therefore decrease nitrogen availability for early successional plant species (Kulmatiski 2011). Results from Europe and North America show the technique has potential to alter plant community composition and may be a useful tool for restoring some native species at local scales (Eschen et al. 2007; Burke et al. 2013).

Regional- and landscape-scale conversion of indigenous vegetation for intensive land use is likely to be the ultimate cause of observed declines in New Zealand's three endemic inland *Lepidium* species. These changes are probably irreversible in Central Otago, in the Waitaki Valley, and at Kura Tāwhiti. In these regions, it is likely that metapopulation and environmental thresholds have been crossed that remove all possibilities of natural immigration, and that ecological resilience and management effectiveness at remaining *Lepidium* locations will continue to reduce in future (Pardini et al. 2010; Hanski 2011). It is predictable that *Lepidium* and other indigenous dryland-specialist species will continue to be lost from remaining habitat fragments as metapopulation processes unfold and that the ecological character of fragments will continue to change as cross-boundary effects from surrounding land uses develop further. More intense and frequent heat waves, fire, floods, and droughts, and reduced soil moisture brought by climate change (Reisinger et al. 2014), are likely to accelerate species losses and habitat changes.

If, as we conclude, the landscape-scale ecological conditions and processes that once sustained indigenous plant species and communities in Central Otago, in the Waitaki Valley, and at Kura Tāwhiti have gone, there is no

option but to undertake intensive management if *L. kirkii* and *L. sisymbrioides* are to persist at all, and if *L. solandri* is to persist outside the Mackenzie Basin. We do not know yet whether similar thresholds for metapopulations and cross-boundary effects have already been crossed in the Mackenzie Basin so that a similar outcome for all remaining *L. solandri* populations is also inevitable.

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Additional information and declarations

Author contributions: All authors undertook fieldwork. SW was responsible for conceptualisation, writing the original draft manuscript, data analysis, review and editing. MH and GL assisted with writing, review, and editing.

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Data and code availability: Data and code are held in the permanent data storage repository of Manaaki Whenua - Landcare Research (<https://datastore.landcareresearch.co.nz/>) and may be accessed on request to the corresponding author.

Ethics: Sampling protocols were developed with the Department of Conservation and sanctioned by iwi and Tekapo Military Reserve. Permission from the relevant agencies and all private landowners was sought and granted prior to access.

Conflicts of interests: The authors confirm that the research was undertaken in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Land-use intensity levels ascribed to LCDB v5.0 (Landcare Research Informatics Team 2019) land-cover classes within 2 km radii of our *Lepidium* locations.

Appendix S2. Land use intensity (coded as low, moderate or high) across the four geographical areas where inland *Lepidium* species occur.

Appendix S3. *Lepidium kirkii* locations visited or investigated and material collected in Central Otago.

Appendix S4. *L. solandri* locations visited in Central Otago and the Waitaki Valley.

Appendix S5. *Lepidium sisymbrioides* locations visited or investigated in Central Otago and the Waitaki Valley.

Appendix S6. Vascular plant species recorded at locations surveyed for inland *Lepidium* species between December 2020 and February 2021.

Appendix S7. Pairs plot showing the correlations and correlation coefficients between variables used in our analysis across our four geographical regions.

Appendix S8. Pairs plot showing the correlations and correlation coefficients between variables used in our analysis within our Central Otago region.

Appendix S9. Comparisons of attributes between geographic regions and classification groups: Statistical tests and software.

Appendix S10. Comparison of attributes between regions.

Appendix S11. Comparison of attributes between classification groups identified by agglomerative clustering.

Appendix S12. Correlations among landscape and vegetation attributes.

Appendix S13. Generalised linear models: Statistical tests and software.

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