Complementarity of indigenous flora in shrublands and grasslands in a New Zealand dryland landscape

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Abstract: Succession from fire-induced grassland to secondary shrubland vegetation is occurring in parts of deforested dry eastern South Island, New Zealand, but little is known about how the change from herbaceous to woody vegetation alters the indigenous biota. We predicted that development of secondary shrublands would exclude few grassland-specialist plant species and increase indigenous plant 'species occupancy' (the extent to which indigenous species capable of living in dryland landscapes are present) at a landscape scale. We also predicted that taller and denser indigenous plant canopies would facilitate indigenous but not exotic plant species at multiple scales, for example by reducing exotic grass competition or through positive plant–plant interactions. We tested our predictions by sampling vegetation in 100-ha blocks representing a gradient from grassland to mixed 'intermediate' grassland and shrubland to shrubland vegetation at three sites in Central Otago. We found indigenous plant species in shrubland were complementary to those in grassland (additional to the existing set) within and across our study sites, which led to higher indigenous species occupancy in this dryland landscape. Grassland vegetation did not support significant numbers of indigenous plant species complementary to those in shrubland, and we found no evidence that secondary succession displaced indigenous plant species. Shrubland had higher diversity of indigenous plant species than grassland at multiple scales (across sites, within 100-ha blocks and within 144-m^2 plots), and had higher indigenous dominance of composition across sites, but not at smaller (within-block and within-plot) scales. Indigenous dominance of composition within blocks and plots was related to dominance of the physical structure of plant communities by indigenous woody plants or tussock grasses, rather than to development of secondary shrubland alone. Reduced densities of indigenous plant species were related to higher frequencies of exotic grass only where indigenous structural dominance was low, indicating that competitive exclusion of indigenous plants by exotic grasses may depend on degradation of indigenous structural dominance. We conclude that secondary succession from structurally-depleted grassland to mixed indigenous–exotic shrubland is likely to assist the conservation of indigenous plant species in this dryland landscape.

Keywords: biome shift; ecological integrity elements; indigenous dominance; indigenous species occupancy; plant species density; plant species diversity; secondary woody succession

Introduction

Anthropogenic fire-induced grasslands replaced forests and shrublands across much of the drier inland eastern areas of New Zealand's South Island within a few decades of the arrival of humans in the late 13th century (McWethy et al. 2010). The recently-created grasslands are unstable under both pastoral and conservation management, showing changes in species composition and structure over time (e.g. Duncan et al. 1997, 2001; Walker 1997; Meurk et al. 2002; Walker et al. 2003; Rose et al. 2004). In areas that previously supported forest, woodland and shrubland, succession to secondary shrubland vegetation is a relatively common trend (Walker et al. 2009a, b). Mixed indigenous and exotic communities dominated by shrubs and small trees now cover about one-fifth of land not intensively developed within the eastern South Island 'dryland' zone (Walker et al. 2009a). This zone has been defined by Rogers et al. (2005) as LENZ Level IV land environments (Leathwick et al. 2003) with average annual Penman water deficits greater than 270 mm per annum, and covers approximately 39 000 km^2 of the South Island east of the Southern Alps (Walker et al. 2009b).

Here, we ask whether succession to secondary shrubland communities is beneficial for the conservation of the indigenous dryland flora of New Zealand's eastern South Island. Conservation benefit can be considered in different ways, and we use the conservation goal of ecological integrity as defined for New Zealand by Lee et al. (2005, p. 101) as a conceptual framework for our assessment. We consider aspects of two elements of ecological integrity: species occupancy at the landscape scale, and indigenous dominance of plant composition at multiple scales from landscape to plot; we predicted that secondary succession would promote both.

'Species occupancy' as defined by Lee et al. (2005) is the extent to which the diversity of species capable of living at some spatial scale is actually present. Species occupancy measures species numbers relative to a potential reference state of the plants and animals that could potentially occupy an ecosystem, rather than simply numbers of species present. We predicted that developing shrublands in deforested dryland landscapes would offer habitats for plants distinct from those in shorter, non-woody grassland communities, and that these habitats would support indigenous plant species complementary to those in grasslands. Complementarity is 'the gain in biodiversity representation when an area is added to an existing set' (Vane-Wright et al. 1991), and expresses biotic distinctness as a positive biodiversity attribute, capturing 'the sense that complementary faunas or floras form parts of a whole' (Colwell & Coddington 1994). If indigenous shrubland floras are complementary to grassland floras, more of the indigenous plant species capable of living in the landscape will be represented in dryland landscapes that contain shrublands and grasslands than in those with grasslands alone, and species occupancy will therefore be higher. An alternative 'species-displacement' hypothesis, suggested by Rogers et al. (2005), is that the development of secondary woody vegetation in deforested South Island drylands might displace specialist light-demanding indigenous plant species of anthropogenic grassland communities. Displacement of grassland-specialist plants by shrub encroachment has been recorded in anthropogenic landscapes elsewhere, such as in British chalk grasslands (Wells 1969). Landscape-scale species occupancy would be reduced if shrubland development displaced indigenous species without adding complementary species.

'Indigenous dominance' is defined by Lee et al. (2005) as the level of indigenous influence on a community, including its composition, structure and biomass. In secondary successional pathways involving both indigenous and exotic woody species, changes in indigenous dominance of structure or biomass ('indigenous structural dominance') clearly depend on the degree to which indigenous shrubs dominate. Here we focus on the effects of secondary shrubland development on indigenous dominance of vascular plant composition, represented by the percent of plant species present that are indigenous, at different scales. We predicted that effects of secondary woody succession would be asymmetric, fostering higher numbers of indigenous vascular plant species but not of exotic plant species, and thus increasing indigenous compositional dominance.

Our prediction was based on our expectation that the traits of indigenous plant species adapt them better to later-successional vegetation stages, compared with traits of the current resident exotic plant species. Typical traits of late-successional plant species include low fecundity, slow growth, and tolerance of resource-poor conditions (Rees et al. 2001) and are more characteristic of New Zealand's indigenous plant species than of exotic species, which more often have early-successional life-history traits. For example, Craine & Lee (2003) and King & Wilson (2006) showed that introduced grasses and herbs had higher growth rates and lower tolerance of low soil resource availability than indigenous grasses and herbs in the same inland New Zealand South Island environments. Unlike their exotic counterparts, relatively few indigenous grass and herb species of South Island drylands are thought to be obligately early-successional (Rogers et al. 2005), and subfossil investigations suggest a number of indigenous herbaceous species now characteristic of short, open community types grew naturally in understoreys of dry shrublands prior to human settlement (Wood & Walker 2008).

We also expected that indigenous plant species, being more tolerant of low resource availability, were more likely than exotic plant species to be facilitated by positive plant–plant interactions (Callaway 1995) within shrubland canopies. Facilitation is expected to occur more frequently in more stressful environments (Bertness & Callaway 1994) and plays a greater role in succession in dry biomes than in mesic biomes (e.g. Walker & Chapin 1987). A variety of mechanisms might operate in New Zealand's dryland shrublands. For example, shrubs could provide structural support for lianes and perches for birds dispersing fleshy-fruited seeds, enhance plant establishment and survival through microclimate amelioration, or create physical barriers protecting palatable plants from herbivory. Shrubland canopies could also facilitate indigenous plant species by reducing competition from exotic light-demanding species, especially exotic grasses. A prominent conundrum in the conservation of dryland grassland communities is that exotic grass swards are thought to reduce or exclude indigenous plant species (e.g. Rose 1983; Meurk et al. 1989, 2002; Rogers et al. 2005), but livestock grazing to suppress competition from exotic grasses can also have unwanted collateral effects on indigenous plants (e.g. Treskonova 1991; Walker 1997). Fostering secondary shrubland development potentially offers an alternative to grazing as a plant conservation management approach if, as we predicted, dry shrubland canopies suppress exotic grass competition and increase the diversity of indigenous plant species present.

To test our predictions, we sampled the plant communities of different grassland and secondary shrubland vegetation states in the dryland region of Central Otago in the eastern South Island. We compared 1-km^2 blocks of vegetation of low, intermediate and high woodiness respectively (hereafter grassland, intermediate, or shrubland block-level woodiness) in three different sites. We assumed biotic differences between blocks arose through different management (fire, grazing, pest) histories, and that environmental factors influencing the biota were similar within sites. We did not address causes or timescales of transitions, but simply contrasted the characteristics of alternative states that had developed in similar environments, and assessed their contributions to ecological integrity at different scales. We first investigated the complementarity of the indigenous floras of shrubland and grassland to determine their different contributions to species occupancy at landscape and site scales. We then examined effects of woodiness on numbers of indigenous plant species and indigenous compositional dominance at scales from sites to plots. At small (plot) scales, we also investigated the interacting effects of exotic grasses and indigenous structural dominance on densities of indigenous plant species (numbers of species per unit of area sampled). We apply our results to discuss the implications of successions to secondary shrubland on the conservation of the indigenous dryland flora in this landscape.

Methods

Survey design

Sites

We searched for candidate study sites in Central Otago in which we could identify three blocks of at least 1 km^2 that (1) represented a gradient of vegetation woodiness from grassland with cover dominated by exotic or indigenous grasses and herbs, to an intermediate mosaic or mixture of grassland and shrubland, to shrubland with cover dominated by shrubs and/or trees, and (2) were similar in slope, aspect, and elevation. The few sites meeting these criteria were all situated on faces of the district's north-east to south-west trending mountain ranges within the same group (Type H 'Mackenzie Basin and Central Otago hillslopes') of the eight-group environmental classification of drylands (Rogers et al. 2005). We selected three sites for study (Bendigo, Blackstone Hill and Cambrian; Fig. 1) that represented the greatest variety of environments

Table 1. Location (average latitude and longitude of the three blocks) and sampling dates at the three study sites, and averages (and ranges) of physical characteristics and climate variables at the coordinates of each of the 30 sampled plots. Degrees north and east (where 180° represents both due north and due east) are transformations of corrected compass bearings taken at each site. Slope is derived from a 25-m digital elevation model, and climate variables from interpolated national climate surfaces (Leathwick et al. 2003; Leathwick et al. unpubl. data).

Site	**Bendigo**		**Blackstone Hill**		**Cambrian**	
Latitude, Longitude	169.37E, 44.94S		169.84E, 44.97S		169.72E, 44.89S	
Sampling dates	8–12 March 2007		5–9 December 2007		8–11 February 2008	
	Average	Range	Average	Range	Average	Range
Physical						
Elevation (m)	625	512 to 702	624	460 to 762	736	623 to 868
North aspect (° N)	109	10 to 170	124	0 to 180	85	0 to 180
East aspect (° E)	68	5 to 180	49	5 to 120	110	50 to 164
Slope (°)	13.9	2.6 to 31.3	17.5	8.3 to 25.2	25.3	9.9 to 35.4
Topographic shelter (°)	12	4 to 27	9	5 to 15	14	6 to 26
Rock outcrop area (m^2)	1.8	0 to 14.5	2.3	0 to 23.7	1.3	0 to 19.1
Climate						
December solar radiation (MJ m^{-2} day^{-1})	23	22.99 to 23.08	22.8	22.72 to 22.84	22.8	22.79 to 22.88
Penman water deficit (mm)	531	486 to 617	487	411 to 600	354	280 to 415
Annual extreme minimum temperature (°C)	−9.6	−10.0 to −8.5	−9.7	−10.4 to −8.7	−9.8	−10.7 to −9.3
Days of air frost in July (days)	20.8	19.0 to 21.9	20.7	20.1 to 21.7	19.4	17.8 to 21.0

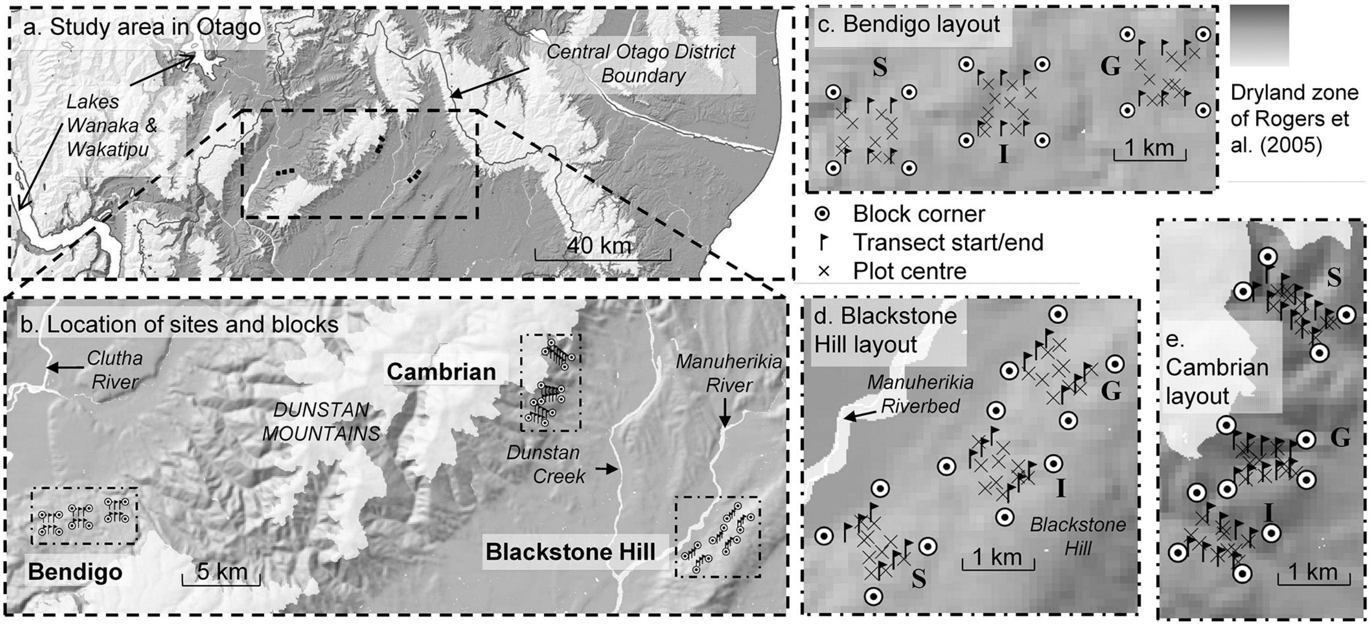

Figure 1. Maps on the left show (a) the study area (dashed outline, with blocks as black rectangles) and (b) the locations of sites (dot-dashed outlines) and blocks (corner symbols) and transect ends (flag symbols). Maps on the right show the layouts of blocks, transects and plots at (c) Bendigo, (d) Blackstone Hill, and (e) Cambrian sites (all with dot-dashed outlines). The grey background is the dryland zone of Rogers et al. (2005), and italics denote key geographic features. S, I and G denote shrubland, intermediate and grassland blocks, respectively.

and vegetation types (Table 1) of those available. All blocks have been under pastoral management and grazed by sheep since the 1850s, with feral lagomorphs and ungulates present in various combinations and levels of abundance. Historical aerial photographs confirmed the shrubland vegetation at our sites was not relictual, but arose through secondary succession over the last 30 to 70 years, through unassisted spread of early-seral woody plants that were left scattered in the landscape under more frequent pastoral fire regimes (Walker et al. 2004).

Blocks (woodiness levels)

We delimited three 1-km^2 blocks at each site, representing grassland, shrubland and an intermediate mixture of grassland and shrubland cover. All blocks at Bendigo and Blackstone Hill were 1-km^2 squares. At Cambrian, where each block spanned a creek, the vegetation pattern constrained us to sample 1-km^2 sub-rectangular polygons (Fig. 1). In locating our blocks, we did not prescribe a percent woody cover for each level, but instead selected the grassiest and woodiest blocks at each site from aerial photography, satellite imagery, and both aerial and ground-based field inspection. The intermediate block was located where overall woody cover was midway between the extremes.

Sampling layout within blocks

We used a dual (plot and transect) sampling layout designed to correlate with animal sampling techniques in a companion study (Walker et al. 2014 this issue; Wilson et al. 2014 this issue). At each site tessellated grid-stratified sampling was used to randomly position 10 widely spaced plots of 12 × 12 m across each block ('woodiness level'). We also established sampling transects totalling 2 km at each site, parallel to the major slope. At the Bendigo and Blackstone Hill sites, three 667-m-long transects were spaced 300 m apart in each block, orientated north to south and north-west to south-east, respectively. At Cambrian we laid out five, four and six parallel transects in the grassland, intermediate and shrubland blocks, respectively; transect lengths varied from 580 to 260 m, and were spaced 200–275 m apart (Fig. 1).

This survey design allowed us to study plant communities at multiple scales: (1) landscape scale, across the three Central Otago study sites, (2) site scale of three 1-km^2 blocks along a gradient of vegetation woodiness, (3) block scale (1 km^2) sampled on the basis of plots and transects within each, (4) transect scale (multiple linear samples across each block), and (5) plot scale (12 × 12 m samples within blocks).

Data collection

Vegetation sampling

Vegetation was sampled at each plot and along each transect using a modified Scott height-frequency method (Scott 1965). We chose the method for its ability to provide a measure of three-dimensional physical structure and plant species composition in grassland and shrubland, and for its suitability for use at relatively large sampling scales such as 100-ha blocks. In plots, sampling points were spaced at 1-m intervals along five parallel 12-m sampling lines, which were spaced 2 m apart (i.e. 13 points per line × 5 lines per plot = 65 points per plot, $n = 650$ points per block). Along transects, points were spaced at 8-m intervals, and 300 vegetation points were sampled in total in each block at each site. At each sampling 'point' we recorded the presence of all vascular plant species in 10 × 10 × 10 cm vertically contiguous cubes to the maximum height of the vegetation. Each plant species was identified to species and as either indigenous or exotic, and assigned to one of seven vascular plant life-form groups: eudicot (hereafter 'dicot') herbs, grasses, non-grass monocotyledonous ('monocot') herbs, trees and/or shrubs, subshrubs, lianes, and ferns and/or psilopsids.

Frequency variables

A measure of relative abundance (i.e. 'frequency') was calculated for each species as the summed presence of each species in each plot or transect, expressed as a percentage of the number of sampled points in order to allow comparison among plots and transects. The frequency of a species exceeds 100% when it is present, on average, in more than one of the vertically contiguous sampling cubes per point (Scott 1965). We summed frequencies across species to calculate frequencies of our different plant groups for each plot and transect. We used the summed frequency of all woody plant species as an index of plot- or transect-level 'woodiness'. The percent of the total summed frequency that was contributed by indigenous plants was used as a measure of 'indigenous structural dominance' (a proxy for the level of influence of indigenous plants on physical structure of the plant community).

Physical environment

At each plot we recorded: (1) aspect, which we transformed to two variables, degrees north and degrees east, each with range 0°–180°; (2) topographic position in three categories: face, gully or ridge; (3) area of exposed large rock outcrops within a 10-m radius of plot centre in each of four cardinal compass sectors; and (4) the horizon angles at eight cardinal compass points. Horizon angles were averaged to provide a topographic shelter index (McNab 1993); high scores indicate greater shelter and low scores greater exposure (our range was 4° to 27° within a theoretical range of −90° to 90°).

At geographic coordinates of plot-centres and sampling points along transects, we extracted slope from a 25-m digital terrain model (DTM) and four climate variables from 25-m interpolated raster climate surfaces, using a GIS. The four independent (Pearson's rank correlation coefficient $r_s < 0.4$) climate variables were annual Penman water deficit, December solar radiation, annual winter extreme minimum temperature, and average number of days of air frost in July, and were selected from a set of 21 candidate variables (4 moisture balance, 3 solar radiation, 6 temperature and 8 frost) available as climate surfaces (Leathwick et al. 2003; Leathwick et al. unpubl.).

Data analyses

Complementarity of shrubland and grassland indigenous floras (landscape and site scales)

Our tests for the complementarity of the indigenous shrubland flora ask 'what is the change in the number of species observed for a given sampling effort if an area contains both grassland and shrubland vegetation, relative to an area containing grassland vegetation alone?'. Conversely, our tests for the complementarity of the grassland flora compared floras in grassland and shrubland to the shrubland flora alone.

We pooled all sampling points from plots and transects in shrubland and grassland respectively. We then drew 1000 random subsets of n points from each habitat, and also undertook 1000 stratified random draws in which half the points were from grassland and half for shrubland ('grassland-plus-shrubland' draws). We counted the number of indigenous plant species observed (S_{obs}) in each draw. We then subtracted the grassland species count from the grassland-plus-shrubland count to determine shrubland complementarity, subtracted the shrubland species count from the grassland-plus-shrubland count to determine grassland complementarity, and calculated the mean differences and 95% confidence intervals over the 1000 draws. We repeated the procedure for each site, for all sites together and for each indigenous plant life-form group. Draws from shrubland and grassland pools were of half the total number of points in each pool ($n = 476$ points for individual-site analyses and $n = 1428$ points for the all-sites analysis). Stratified draws were 238 random points from grassland and 238 from shrubland blocks for individual-site analyses, and 713 points from each level for the all-sites analysis.

Significantly higher S_{obs} in shrubland and grassland together than in grassland alone would indicate the shrubland flora was complementary and increased species occupancy. Alternatively, if shrubland contained only a subset of the flora found in grassland, S_{obs} would be lower in shrubland alone than in the same number of sample points from shrubland and grassland. This result would be consistent with the species-displacement hypothesis and with shrubland development reducing site- or landscape-scale species occupancy. If the grassland flora was complementary to the shrubland flora,

S_{obs} would be higher in samples of points drawn from grasslands and shrubland than from shrubland alone, while a negative difference would indicate that grassland contained only a subset of species found in shrubland.

Effects of woodiness on indigenous dominance of composition (site, block and plot scales)

Our next analyses investigated effects of woodiness on numbers of indigenous plant species and on indigenous dominance of plant species composition at different scales. We follow the terminology of Gotelli & Colwell (2001), using the term 'species density' for numbers of plant species per unit area in small sampling units, and refer to number of species when describing counts of species at larger spatial scales.

For analyses at the scale of sites and blocks, we used a technique similar to our complementarity analyses, in which we pooled sampling points from all plots and transects in each habitat, and compared numbers and indigenous percentages of species in 1000 random subsets of points drawn from shrubland and grassland blocks and levels. Counts of indigenous and exotic plant species (S_{obs}), and indigenous compositional dominance (% species indigenous) in each draw of grassland points were subtracted from those from a draw of shrubland points. We then calculated the mean difference and 95% confidence intervals (based on percentiles) over the 1000 draws. We repeated the method for each site (drawing subsets of $n = 476$ random sampling points from a block) and for the three sites together (drawing subsets of $n = 1428$ points from a level). We also applied the method to determine effects of woodiness level on numbers of species in each indigenous and exotic plant life-form group.

We used generalised mixed models to investigate effects of woodiness at the plot scale. We modelled three plot-level response variables: (*i*) indigenous plant species density (number of indigenous plant species per plot), (*ii*) exotic plant species density (number of exotic plant species per plot), and (*iii*) indigenous compositional dominance (percent of plant species in a plot that were indigenous). Succession increases average plant size, causing numbers of individuals and therefore also numbers of species per unit area to decrease (Gotelli & Colwell 2001). Therefore at small scales, such as our 12 × 12 m plots, later-successional vegetation such as shrubland or forest generally supports lower species densities than early-successional vegetation such as grassland. Higher rather than the expected lower densities of plant species (variables *i* and *ii* above) in woodier vegetation at the plot scale would be consistent with facilitation (positive plant–plant interactions) overriding an expected successional decrease in species density. A change in indigenous compositional dominance (variable *iii*) would be consistent with asymmetric effects of woodiness on densities of indigenous and exotic plant species.

As predictors in these models we used two woodiness variables to represent the extent of secondary succession at different scales. Block-level woodiness predicted effects of context, such as location within a large block of shrubland or grassland; our models contrasted response variables in shrubland and intermediate blocks with those in grassland blocks. Woody-species frequency at the plot level was used to predict the effect of woodiness in the immediate surroundings irrespective of block-level context. This measure was strongly correlated with average and median vegetation height in plots (Pearson's correlation coefficient $r_p = 0.90$). Plot-level and block-level woodiness were not strongly associated ($r_p = 0.45$) because most vegetation was patchy and 12 × 12 m plots can fit within grassy gaps in shrubland and within woody clumps in grassland. As a third predictor, we used indigenous structural dominance (the percent of total summed frequency contributed by indigenous plants) representing the degree to which the vegetation was structurally dominated by canopies of either indigenous tussocks or shrubs.

We fitted a separate model for each predictor. Each model included block nested within site as a random intercept term and plot-level variables east and north aspect, topographic shelter, and rock outcrop area as covariates to account for likely effects of the physical environment. The covariates were selected a priori, retaining the variable with the more likely biological relationship where the Pearson's correlation coefficient between two covariates was ≥0.45 (Appendix 1). All models were fitted using the lmer function in the lme4 package for R version 2.14 (R Development Core Team 2012). Species-density variables were modelled with Poisson error distributions and indigenous dominance with binomial errors (both with log-link functions). We checked graphically for model assumptions, including homoscedacity of residuals, and inspected ratios of residual sums of squares to degrees of freedom to check for overdispersion. We present predictor coefficient means and their 95% highest posterior density intervals (HPDI), which we calculated from 1000 draws from the posterior distribution using the HPDinterval function in the coda package for R.

Effects of woodiness on plant group abundance (transect scale)

We also modelled frequencies of our plant life-form groups in relation to woodiness to investigate facilitation and suppression of different indigenous and exotic plant groups by woody vegetation. Transects traverse multiple vegetation patches within blocks, and provide less patch-specific estimates of plant group frequencies than plots, and were therefore selected as the appropriate sampling unit for the response variable. Woody-species frequency at the transect level was relatively strongly related to block-level woodiness context ($r_p = 0.62$) and we therefore fitted separate models for each woodiness predictor. Frequencies were modelled as Gaussian variables, and each model included block nested within site as a random intercept term and transect averages of our four climate variables as covariates to account for physical environment effects. Models were inspected graphically and coefficient means and HPDIs of predictor effects were reported as for our other generalised mixed models.

Interaction between exotic grasses and indigenous structural dominance (plot scale)

We lastly tested for interacting effects of indigenous structural dominance and exotic grass frequency on densities of indigenous plant species at the plot scale. Structural dominance and exotic grass frequency were not strongly related ($r_p = -0.34$ across plots). We predicted that exotic grasses at constant frequency would reduce numbers of indigenous plant species where indigenous structural dominance was low but not where it was high. We compared four models of indigenous species density at the plot scale, each similar in form to those investigating effects of woodiness on plot-scale variables and assuming a Poisson error distribution. Predictors in our full model (A) were the summed frequency of exotic grasses, indigenous structural dominance, the interaction between these two variables, and the plot physical covariates of aspect, topographic shelter and outcrop area. Models B to

D successively excluded the interaction term, then structural dominance, then summed frequency of exotic grasses. Relative model fits were assessed using Akaike's Information Criterion adjusted for small sample size (AIC$_c$; Akaike 1974; Hurvich & Tsai 1989), which ranks models based on a compromise between model fit and complexity (number of parameters). The best model was indicated by lowest AICc score (Burnham & Anderson 2002).

Results

General vegetation attributes

All blocks supported mixtures of indigenous and exotic plant species. Shrubland was dominated by indigenous *Kunzea ericoides* (kānuka) at Bendigo, exotic *Rosa rubiginosa* (sweet briar) and indigenous *Discaria toumatou* (matagouri) at Blackstone Hill, and by indigenous matagouri, *Coprosma propinqua*, and a variety of lianes at Cambrian (Appendix 2). Three of four tree species recorded – *Griselinia littoralis* (broadleaf), *Melicytus ramiflorus* (māhoe), and *Podocarpus cunninghamii* (Hall's tōtara) – were recorded only at Cambrian, and the fourth (kānuka) only at Bendigo and Cambrian. The most abundant plants in grassland blocks were exotic annual and perennial herbs and grasses at Bendigo, perennial exotic grasses, *Trifolium* spp. and indigenous tussocks of *Festuca novae-zelandiae* (fescue tussock), *Poa cita* (silver tussock) and *P. colensoi* (blue tussock) at Blackstone Hill, and *Chionochloa rigida* (indigenous snow tussock) at Cambrian. Woodiness at plot- and transect-levels (the summed frequency of all woody plant species divided by the number of sampling points) varied from 85% to 177% in grassland blocks, from 155% to 230% in intermediate blocks, and from 222% to 706% in shrubland blocks.

Complementarity of shrubland and grassland indigenous floras

Indigenous plant species in shrubland were complementary to those in grassland: numbers of indigenous species observed (S_{obs}) in random subsets of sampling points from both grassland and shrubland blocks were significantly higher than those observed in random subsets from only grassland blocks at two of our three individual sites (Bendigo and Cambrian) and across all three sites overall (Table 2). Stratified draws of points from grassland and shrubland across our three sites had an average of 21.5 (95% CI 12–30) more species than points from grassland alone.

Some of this observed species complementarity may have derived from inherent spatial turnover between different blocks rather than habitat differences. To provide an indication of background complementarity due to spatial turnover, we reran the analysis comparing the floras of intermediate and grassland blocks. There were 7.2 (95% CI −1 to 16) more species in stratified draws from grassland and intermediate blocks than in draws from grassland blocks alone. This difference represents complementarity from 'background' spatial turnover and development of intermediate shrubland. It seems unlikely, therefore, that spatial turnover alone accounts for the high degree of complementarity of the shrubland flora to the grassland flora that we observed.

Table 2. Complementarity of the indigenous vascular floras in shrubland and grassland (landscape and site scales). The table shows average difference (and 95% confidence intervals) in numbers (S_{obs}) of indigenous plant species in 1000 draws of n random (grassland or shrubland) or stratified-random sampling points (grassland-plus-shrubland). Analyses were performed across all sites ('All sites'; $n = 1428$) and within sites (Bendigo, Blackstone Hill and Cambrian; each $n = 476$). Rows show results for analyses of all vascular species together and individual analyses for each of seven different life-form groups. Confidence intervals not overlapping zero indicate a significant difference at $P < 0.05$. Significant positive differences indicate complementary floras and are in bold.

	Complementarity of the indigenous shrubland flora to the grassland flora (S_{obs} in draws from grassland-plus-shrubland combined minus S_{obs} in draws from grassland only)			
	All sites	Bendigo	Blackstone Hill	Cambrian
All vascular species	**21.5 (12, 30)**	**17.7 (12, 23)**	3.7 (−2, 10)	**11.9 (4, 20)**
Grasses	**5.4 (3, 8)**	**4.7 (3, 7)**	0.8 (0, 2)	0.8 (0, 2)
Dicot herbs	3.9 (−2, 9)	**5.9 (2, 10)**	1 (−2, 4)	0.4 (−5, 5)
Monocot herbs	2.2 (−2, 6)	1.8 (0, 4)	−0.1 (−2, 2)	1.7 (−2, 5)
Trees and shrubs	3.9 (0, 8)	1.9 (0, 4)	0.5 (−2, 3)	4.2 (0, 8)
Lianes	1.2 (−1, 3)	1.1 (0, 2)	0.2 (0, 1)	0.6 (−1, 3)
Subshrubs	1.3 (0, 3)	**1.2 (1, 2)**	0.0 (−1, 2)	1.0 (0, 2)
Ferns and psilopsids	**3.5 (2, 5)**	1.0 (0, 2)	0.2 (−1, 2)	**3.5 (2, 5)**
	(b) Complementarity of the indigenous grassland flora to the shrubland flora (S_{obs} in draws from grassland-plus-shrubland combined minus S_{obs} in draws from shrubland only)			
	All sites	Bendigo	Blackstone Hill	Cambrian
All vascular species	3.3 (−6, 13)	0.3 (−7, 7)	0.6 (−5, 6)	3.9 (−4, 11)
Grasses	−1.5 (−5, 2)	0.1 (−2, 2)	−0.5 (−2, 1)	−0.6 (−2, 1)
Dicot herbs	1.4 (−4, 7)	−0.3 (−5, 4)	0.6 (−3, 4)	2.1 (−2, 6)
Monocot herbs	1.2 (−2, 5)	1.1 (−2, 3)	0.1 (−1, 2)	0.5 (−3, 4)
Trees and shrubs	3.3 (0, 7)	0.8 (−1, 2)	0.2 (−2, 3)	3.0 (−1, 7)
Lianes	−0.7 (−3, 1)	−0.6 (−2, 1)	−0.3 (−1, 1)	0.0 (−2, 2)
Subshrubs	−0.1 (−2, 2)	−0.3 (−1, 1)	0.2 (−1, 2)	0.0 (−1, 1)
Ferns and psilopsids	−0.5 (−2, 0)	−0.5 (−2, 1)	0.0 (−1, 2)	−0.8 (−3, 1)

Across the three sites together, species of fern and/or psilopsid and indigenous grass in shrubland were complementary to those in grassland (Table 2). Species in indigenous grass, dicot herb and subshrub plant life-form groups in shrubland were complementary to those in grassland at Bendigo, while at Cambrian, species of indigenous fern and/or psilopsid in shrubland were complementary to those in grassland. No plant life-form group was less speciose in stratified draws of points from grassland and shrubland than in points from grassland alone.

We found no evidence that grassland floras were complementary to shrubland floras across sites or at any individual site. Numbers of indigenous species observed (S_{obs}) in sampling points drawn from grassland and shrubland blocks together were not significantly greater than in points drawn from shrubland blocks alone, either across the different life-form groups or within any group (Table 2).

Effects of woodiness on indigenous dominance of composition at different scales

Numbers of indigenous plant species varied significantly with woodiness level when calculated across samping units at the large spatial scales of our sampling blocks (Table 3). Significantly-more species of indigenous plant were counted in random points drawn from shrubland than from grassland in all sites combined and in two individual sites (Bendigo and Cambrian). Of the different plant life-form groups, indigenous grasses, dicot herbs and subshrubs were all more speciose in shrubland than in grassland blocks at Bendigo and across all sites, and there were more species of fern and/or psilopsid in shrubland than grassland blocks at Cambrian and across all sites (Table 3). At Cambrian, more species of exotic dicot herb (and therefore also more species of exotic plant in total) were present in shrubland than in the grassland block, while at Blackstone Hill, there were significantly fewer species of exotic grass in the shrubland block than in grassland.

Indigenous dominance of composition (% species indigenous) was significantly higher in shrubland than grassland across all sites, but within only one of our three individual sites (Bendigo) (Table 3). At Cambrian, indigenous compositional dominance was significantly lower in shrubland than grassland. Here, although both exotic and indigenous species were more numerous in points drawn from shrubland than from grassland, the tall-tussock-dominated grassland block had particularly low numbers of exotic plant species (Appendix 3).

At the smaller scales of sampling plots, densities of indigenous plant species (numbers of indigenous plant species per plot) and plot-level indigenous dominance of composition (% species indigenous) were not significantly affected by block-level woodiness (Table 4a). Indigenous plant species density was positively related to woody-species frequency (plot-level woodiness) (Table 4b); on average there was 1.0 [95% HPDI 1.0 – 1.1] more species per plot with every 10 additional woody intercepts per point. Indigenous dominance of composition (% species indigenous) at the plot scale was not significantly affected by either block- or plot-level woodiness, but increased significantly with indigenous structural dominance (the % of total summed frequency indigenous; Table 4c).

No plant group had significantly more species per plot in shrubland or intermediate blocks than in grassland blocks across the three sites (Fig. 2a). Only indigenous trees and shrubs (coefficient mean [95% HPDI]: 0.15 [0.01 – 0.29]), indigenous lianes (0.60 [0.17 – 0.93]), and exotic shrubs (0.36 [0.04 – 0.71]) had significantly more species per plot, in plots where woody-species frequencies were higher (Fig. 2a).

Table 3. Average difference in numbers of indigenous and exotic vascular plant species in shrubland and grassland blocks (landscape and site scales) based on 1000 subsets of *n* sampling points. Parentheses show lower and upper bounds of 95% confidence intervals. Rows show differences in numbers of species in total and within different life-form groups, and differences in the percent of all species indigenous. Confidence limits not overlapping zero indicate a significant difference in numbers of plant species at $P < 0.05$. Significant differences are in bold. The exotic 'Dicot herbs' group included three species of non-grass monocot herbs (i.e. sedges and rushes), which we analysed together with the 57 species of exotic dicot herbs recorded. A similar result was obtained for the analysis using the 57 exotic dicot herbs alone.

	Number of species and indigenous dominance in *n* shrubland points minus number of species or indigenous dominance in *n* grassland points			
	All sites *n* = 1426	Bendigo *n* = 476	Blackstone Hill *n* = 476	Cambrian *n* = 476
Number of indigenous species				
All vascular species	**18.2 (10, 26)**	**17.4 (13, 22)**	3.1 (−2, 8)	**7.9 (1, 15)**
Grasses	**6.9 (4, 9)**	**4.7 (3, 6)**	1.3 (0, 3)	1.4 (0, 3)
Dicot herbs	2.6 (−3, 8)	**6.2 (3, 9)**	0.3 (−3, 4)	−1.7 (−6, 3)
Monocot herbs	1.0 (−2, 4)	0.8 (–1, 2)	−0.3 (−2, 1)	1.2 (−2, 4)
Trees and shrubs	0.6 (−3, 4)	1.1 (0, 3)	0.3 (−2, 2)	1.1 (−2, 4)
Lianes	1.9 (0, 3)	1.6 (0, 2)	0.5 (0, 1)	0.6 (−1, 2)
Subshrubs	1.4 (0, 3)	**1.5 (1, 2)**	−0.2 (−1, 1)	1.0 (0, 2)
Ferns and psilopsids	**4.0 (3, 5)**	1.5 (0, 2)	0.2 (–1, 1)	**4.3 (3, 5)**
Number of exotic species				
All species	2.9 (−2, 8)	−0.4 (−5, 4)	0.7 (−3, 5)	**8.6 (4, 13)**
Grasses	−1.8 (–4, 0)	1.0 (−1, 2)	**−1.9 (−3, −1)**	0.1 (0, 1)
Dicot herbs	4.5 (0, 8)	−1.8 (−6, 2)	2.5 (−1, 6)	**8.4 (4, 13)**
Trees and shrubs	0.4 (–1, 2)			0.1 (−1, 2)
Indigenous dominance of composition				
% species indigenous	**4.0 (1.1, 6.9)**	**15.8 (10.9, 21.5)**	2.6 (−3.5, 8.5)	**−4.6 (−9.5, −0.1)**

Table 4. Coefficients and 95% highest posterior density intervals (HPDI) of effects of woodiness (a, b) and indigenous structural dominance (c) on species densities (number of species per plot) and indigenous dominance of composition (percent of species in a plot that are indigenous) from generalised linear mixed models. Coefficients and HPDI are shown on the scale of the link function (ln). Statistical significance at $P < 0.05$ is indicated by bold text.

	(a) Block-level woodiness		(b) Plot-level woodiness (summed woody-species frequency)	(c) Plot-level indigenous structural dominance (% of total summed frequency indigenous)
	Shrubland vs grassland	Intermediate vs grassland		
Species density (ln number of species per plot)				
Indigenous species density (ln)	0.17 (−0.53, 0.78)	−0.20 (−0.80, 0.54)	**0.02 (0.01, 0.05)**	**1.12 (0.80, 1.51)**
Exotic species density (ln)	0.07 (−0.21, 0.28)	0.21 (−0.04, 0.44)	0.01 (−0.01, 0.03)	−0.29 (−0.57, 0.03)
Indigenous dominance of composition (% of species in a plot that are indigenous)				
Percent species indigenous (%)	0.08 (−0.32, 0.59)	−0.17 (−0.63, 0.24)	0.01 (−0.02, 0.03)	**0.81 (0.27, 1.20)**

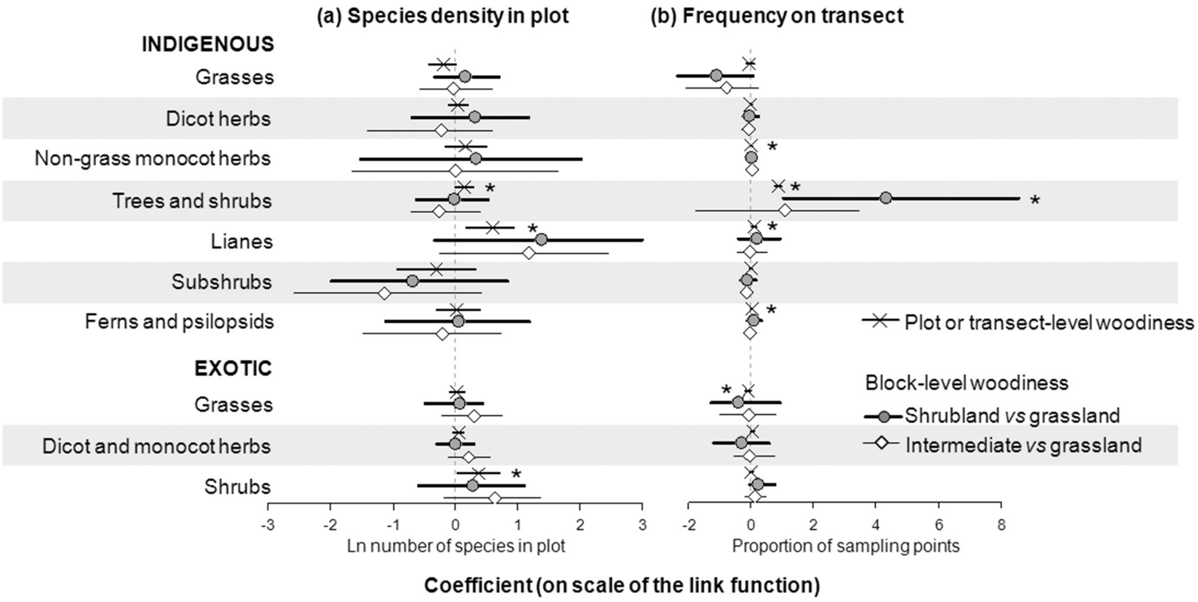

Figure 2. Coefficients and 95% highest posterior density intervals (HPDI) of woodiness effects on indigenous and exotic plant life-form groups. In (a) effects of woodiness on the species density of different plant groups in plots are shown on the scale of the link function (Ln). In (b) effects of woodiness on frequency of different plant groups on transects are shown. Effects of block-level woodiness (shaded circles or clear diamond symbols) and plot or transect-level woodiness (cross symbols) were modelled separately for each plant group. Lower HPDI >0 indicate a significant positive effect; upper HPDI <0 indicate a significant negative effect. Statistical significance at $P < 0.05$ (based on HPDI) is indicated by asterisks *.

Table 5. Candidate models for the plot-scale density of indigenous plant species in 12 × 12 m plots. The best model is indicated by the lowest Akaike's Information Criterion (AICc) score and the highest model weight (equal to proportion of support out of the set of candidate models). ΔAICc = difference in AICc scores between each model and the highest ranking model, *k* = number of parameters. Indigenous structural dominance is % of total summed plant frequency (from height-frequency measurement) indigenous at the plot scale.

Model	Predictors of plot-scale density of indigenous plant species (number of indigenous plant species per plot)	AICc	ΔAICc	Model weight	*k*
A	~Summed frequency of exotic grasses + Indigenous structural dominance + Summed frequency of exotic grasses × Indigenous structural dominance + East aspect + North aspect + Topographic shelter + Outcrop area	115.4	0	0.75	7
B	~ Summed frequency of exotic grasses + Indigenous structural dominance + East aspect + North aspect + Topographic shelter + Outcrop area	117. 6	2.2	0.25	6
D	~ East aspect + North aspect + Topographic shelter + Outcrop area	141.7	26.2	0.00	4
C	~ Summed frequency of exotic grasses + East aspect + North aspect + Topographic shelter + Outcrop area	144.0	28.6	0.00	5

Effects of woodiness on plant abundance

Block-level woodiness affected the frequencies of few plant groups measured along transects. Indigenous trees and shrubs were more frequent on transects in shrubland blocks (median 3.27) than in grassland blocks (median 1.14; coefficient mean [95% HPDI]: 4.33 [1.05 – 8.58]) (Fig. 2b). A greater variety of plant groups was affected by transect-level woodiness (the woody-species frequency on the particular transect; Fig. 2b). Indigenous monocot herbs (coefficient mean [95% HPDI]: 0.01 [0.01 – 0.03]) and indigenous ferns (−0.03 [0.01 – 0.06]) were significantly more frequent on transects with higher woody-species frequencies, in addition to indigenous trees and shrubs (0.86 [0.77 – 0.97]) and indigenous lianes (0.11 [0.17 – 0.05]) (Fig. 2b). Frequencies of exotic grasses were significantly lower on woodier transects (−0.09 [−0.19 – −0.01]).

Exotic grass competition and interaction with indigenous dominance

Our best model of plot-scale densities of indigenous plant species (Model A in Table 5) included an interaction between exotic grass frequency and indigenous structural dominance (% total plant frequency indigenous). The improvement of Model A on Model B (without the interaction term) was relatively modest (ΔAICc = 2.2), however. In Model A the coefficient of the interaction term was positive (coefficient mean [95% HPDI]: 0.29 [0.09 – 0.52]) indicating that exotic grass had a negative effect where indigenous structural dominance was low, and little effect where indigenous structural dominance was greater. Indigenous structural dominance alone had a positive effect on densities of indigenous plant species (0.71 [0.22 – 1.38]), north aspect had a negative effect (−0.10 [−0.17 – −0.02]) but exotic grass frequency alone had no significant effect (−0.08 [−0.26 – 0.06]).

Discussion

As we predicted, sizeable areas of taller and woodier vegetation increased the variety of indigenous plant species present in the Central Otago dryland landscape. This effect was evident at the landscape scale (across sites) and at two of our three individual sites. We found no evidence to support the alternative hypothesis, that grassland-specialist indigenous plant species are displaced in secondary succession (Rogers et al. 2005), at either landscape or site scales. Plant species complementarity was asymmetric, in that shrubland added significant numbers of plant species to those present in grassland vegetation alone, but grassland vegetation did not add significantly to the species pools recorded in shrubland alone, either across our sites or at any individual site. These results indicate that more of the indigenous plant species capable of living in this dryland landscape are represented when shrubland is present, and hence there is higher indigenous species occupancy (sensu Lee et al. 2005). Our results are also consistent with indigenous plant species of dryland grasslands being relatively well adapted for persistence within or beneath woody canopies and there being few indigenous grassland-specialist plant species (Rogers et al. 2005; Wood & Walker 2008). Successional change in this dryland environment may also be subtle or patchy enough to retain microsites for light-demanding plant species (e.g. Bonet 2004).

Our results were consistent with our prediction that woody vegetation would foster higher numbers of indigenous plant species at a range of scales. Succession to woody vegetation increases average plant size, causing numbers of individuals – and therefore numbers of species – per unit area to decrease at small scales (Gotelli & Colwell 2001). However, our generalised mixed models showed that, in our study area, woodier vegetation had higher densities of indigenous plant species at the scale of our 12 × 12 m plots, contrary to the expected pattern of decreasing densities of plant species in succession. Higher numbers of woody species (trees, shrubs and lianes) per unit area accounted for much of the increase in indigenous species densities in shrubland at plot scales. However, species densities of smaller, lower-growing indigenous plant life-form groups – grasses, dicot and monocot herbs, and subshrubs – were no lower in shrubland than grassland. Indeed, indigenous non-grass monocot herbs (a group including orchids, sedges and rushes) were present at higher frequencies beneath woody canopies than in less woody vegetation. Similarly, at the larger scales represented by our random draws of multiple sampling points within and across blocks, indigenous grasses, herbs and subshrubs were no less speciose in shrubland than grassland, and were significantly more speciose at one site (Bendigo). This pattern of results is contrary to that generally expected in succession internationally, where grasses, herbs and subshrubs typically have allocation strategies that maximise resource capture in conditions of high light and nutrients, and therefore decline through succession (Rees et al. 2001). Together our results are consistent with positive plant–plant interactions (facilitation sensu Callaway 1995) within dryland secondary woody canopies overriding expected successional decreases in the number of species of small herbaceous life-form groups present at both small and large scales.

Some mechanisms of facilitation are suggested by the pattern of plant life-form groups favoured by woody vegetation in our study. For example, provision of more structural support by shrubs and trees might account for higher densities and frequencies of liane species we observed at plot and transect scales. Microclimate amelioration such as buffering from desiccation may explain the higher frequencies of indigenous fern and psilopsid species present. However, those mechanisms cannot explain the facilitation by shrubland of species of indigenous grasses and herbs, which are typically less shade-tolerant and depend on little structural support. For species in these groups, shrubland-to-grassland gradients may represent gradients of human-induced pressures. For example, shrubland habitats may represent or provide refuges from fire, mammalian grazing or other disturbances that lead to rarity or elimination in grassland communities (e.g. Scholes & Archer 1997; Michunas & Noy-Meir 2002).

Fast-growing exotic sward-forming grasses are thought to competitively exclude indigenous plant species in dry grassland habitats, both in New Zealand (e.g. Lord 1990; Walker et al. 2003; Ewans 2004) and elsewhere (e.g. Clarke et al. 2005; Lindsay & Cunningham 2012). We predicted that woody canopies would reduce exotic grasses and their competitive effects on indigenous plant species, and found significantly lower frequencies of exotic grasses with increasing woodiness at local scales. However, densities of indigenous plant species were not generally lower in plots with more exotic grass, but only where exotic grasses dominated plant communities without dense indigenous tussock grass or secondary shrubland canopies. This significant interaction suggests competitive effects of exotic grasses may be countered by positive plant–plant interactions in communities that are structurally dominated by indigenous plant species. It also indicates that the loss of structural dominance, rather than exotic grass invasion, may be the ultimate cause of local loss of indigenous plant species in some dryland environments. Therefore, where the conservation goal for a structurally-depleted dryland plant community is to maintain the diversity of indigenous plant species in the long term, rebuilding indigenous structural dominance may offer an alternative to direct control of exotic grasses through grazing (Meurk et al. 1989) or other disturbance regimes (Meurk & Greenep 2003) that are likely to reinforce low structural dominance.

Our prediction that indigenous dominance of plant species composition (the percent of species that are indigenous) would be higher in secondary woody vegetation was supported at the landscape scale (across our three sites). However, within sites, structural dominance by indigenous plant species appeared to be more important than whether the local plant community was grassland or shrubland. Higher percentages of species were indigenous within plots where the local plant community was structurally dominated by indigenous species, regardless of woodiness. For example, the percent of plant species indigenous in plots was similarly high in the less-woody tall-tussock-dominated grassland block at Cambrian and the nearby tall shrubland block, which both had high levels of indigenous structural dominance (Appendix 3). If structural dominance by indigenous plant species is important for maintaining indigenous plant biodiversity in dryland landscapes, exotic- and indigenous-dominated secondary woody communities may have different effects on indigenous plant biodiversity. We examined only a few of the mixed indigenous–exotic shrublands typical in our study region. Further research would be needed to determine whether the same benefit for indigenous plant species would be realised in secondary succession to more exotic-dominated shrubland types, or in successions through exotic-dominated shrubland to more indigenous woody vegetation states, as described by Sullivan et al. (2007) and Williams (2011) for more mesic environments.

Summary and conclusions

The shrubland states at our sites arose in the presence of pastoral grazing and feral herbivores, and without deliberate intervention. These unassisted transitions to secondary shrubland appear to have positive effects on dryland plant biodiversity. Shrublands supported indigenous species complementary to those in grasslands, and increased the variety of indigenous plant species present within our eastern South Island dryland study area. We found no evidence that indigenous grassland-specialist plant species were displaced or lost in succession. Instead, shrublands supported higher numbers of indigenous plant species than grasslands at a range of scales, and may provide refuges for indigenous plant species that are vulnerable to human-induced disturbances in grasslands. Indigenous vascular plants dominated the suite of species present where the plant community was structurally dominated by indigenous species, whether the dominant life forms were indigenous grasses or shrubs. Reduction of structural dominance by indigenous grasses and shrubs, rather than exotic grass invasion, may be the primary cause of loss of indigenous plant species in dryland plant communities.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Appendix S1. Pearson's correlation coefficients (r) between plot-level predictor variables used in our generalised mixed models.

Appendix S2. Major vascular plant species in sites and blocks.

Appendix S3. Numbers of plant species observed in blocks, and average (± SE) plot-scale species densities observed in grassland, intermediate and shrubland levels across three sites.

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