# Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson

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**Abstract:** The dominant native woody species forming early-successional vegetation on formerly forested sites in lowland New Zealand were kānuka (*Kunzea ericoides*) and mānuka (*Leptospermum scoparium*) (Myrtaceae). These have been replaced extensively by gorse (*Ulex europaeus*, Fabaceae), a naturalised species in New Zealand. Because gorse typically gives way to native broadleaved (angiosperm) forest in about 30 years, it is often considered desirable for facilitating native forest restoration. We tested three hypotheses, derived from the New Zealand literature, on gorse and kānuka: (1) kānuka stands have a different species composition and greater species richness than gorse stands at comparable successional stages; (2) differences between gorse and kānuka stands do not lessen over time; and (3) several native plant taxa are absent from or less common in gorse than in kānuka stands. We sampled 48 scrub or low-forest sites in two regions, Wellington and Nelson. Sites were classified into one of four predefined categories – young gorse, young kānuka, old gorse, old kānuka – based on canopy height of the succession and the dominant early-successional woody species. Few characteristics of the sites and surrounding landscapes differed significantly among site categories, and none consistently across regions. The vegetation composition of gorse and kānuka and their immediate successors differed in both regions, mainly in native woody species. Species richness was often lower in gorse and there were fewer small-leaved shrubs and orchids in gorse. Persistent differences at the older sites suggest the successional trajectories will not converge in the immediate future; gorse leads to different forest from that developed through kānuka. Gorse-dominated succession is therefore not a direct substitute for native successions. We suggest areas of early native succession should be preserved, and initiated in landscapes where successions are dominated by gorse or other naturalised shrubs.

**Keywords:** forest restoration; invasive plants; successional pathways; weed impacts

## Introduction

It is well established that the identity of early-successional species can influence subsequent natural vegetation succession (e.g. Egler 1954; Connell & Slatyer 1977; Chapin et al. 1994). Research is now producing examples of how some early-successional invasive plant species can similarly alter subsequent succession (e.g. Adair & Groves 1998; Titus & Tsuyuzaki 2002; Yoshida & Oka 2004; Bellingham et al. 2005). Leguminous woody weeds are often involved because they fix nitrogen and alter soil fertility (Waterhouse 1986; Yoshida & Oka 2000). Large and long-term impacts on native species will result if early-successional invasive species can alter the trajectory of native successions sufficiently enough to strongly disadvantage certain later-successional native species

(Walker & Vitousek 1991) or facilitate invasion of later-successional invasive plants (Yoshida & Oka 2004). Even in the absence of such long-term effects, the dominance of early succession by one or more invasive plant species will be to the detriment of native species through simple biomass substitution. Gorse (*Ulex europaeus*, Fabaceae) is an invasive species in New Zealand that now dominates early forest succession in many lowland landscapes, with largely unknown long-term consequences.

Before European settlement, the dominant native woody species forming early-successional vegetation in lowland New Zealand on formerly forested sites were Myrtaceae: *Kunzea ericoides* (kānuka) and *Leptospermum scoparium* (mānuka). These have since been replaced over large areas by naturalised Fabaceae, particularly gorse, which covered 53 000 ha by the 1970s

(Blaschke et al. 1981). The role of mānuka and kānuka as common precursors to forest was noted by early writers (Cockayne 1919). For 50 years, it has also been observed that if fire is excluded from gorse, and where a seed source is available, native broadleaved species (e.g. species of *Coprosma, Melicytus, Pseudopanax*) dominate in about 30 years (Druce 1957; McQueen 1993). Kānuka and mānuka, and now gorse, are thus alternative post-disturbance systems for large areas of the New Zealand landscape. Which species dominates is determined largely by the history of fire, grazing, and the proximity of propagules.

By apparently facilitating the restoration of the landscape from failed agriculture to native forest, gorse has been considered beneficial, even to the extent that it 'encourages forest succession *better* than the native pioneering plants' (Esler 1988 p. 597, our emphasis). Thus gorse has come to be viewed as a 'nurse crop' and often managed by 'benign neglect' (Porteous 1993). The unstated assumption among land managers in New Zealand generally is that these widespread vegetation types – naturalised gorse and native mānuka or kānuka scrub – have similar successional trajectories and values for conservation of native biodiversity. This assumption may be false, as there is growing evidence that gorse and kānuka or mānuka scrub differ ecologically at several trophic levels (Yeates & Williams 2001; Williams & Karl 2002; Harris et al. 2004) and some studies show or suggest differences in the composition of vegetation regenerating under gorse and kānuka or mānuka (Druce 1957; Lee et al. 1986; Allen et al. 1992; Wilson 1994).

Any such differences would be unimportant for nature conservation if the large areas of lowland early-successional native vegetation that existed 50 years ago remained, or were being formed in the absence of woody weeds. Instead, over much of lowland New Zealand, the cover of such vegetation is severely diminished, for the following reasons: (1) in the absence of disturbance, native shrublands progress naturally towards later-successional vegetation; (2) 'marginal land' is being converted to pasture or exotic forestry plantations rather than being allowed to revert to secondary vegetation (Wardle 1991); and (3) disturbed areas are increasingly being colonised by woody weeds rather than native species. In addition, mature forests that regenerate through early-successional woody weeds like gorse may differ in their plant species composition, and their ability to support native bird and invertebrate species, from those that would have occupied the site after early-successional native species.

We determined whether or not gorse scrub and kānuka had similar botanical biodiversity values and successional trajectories. We chose Wellington and Nelson regions, where gorse and kānuka stands co-occur as alternative systems on sites with similar physical characteristics, to test the following hypotheses derived from the literature and from extensive observations in New Zealand scrub successions:

(1) Kānuka stands have a different composition and greater richness of understorey broadleaved species than gorse stands at a comparable stage (i.e. when regenerating broadleaved species are of similar height).

(2) Gorse and kānuka scrub do not exhibit convergent successional trajectories, i.e. differences between gorse and kānuka stands are either maintained or accentuated over time.

(3) Several groups of plants are absent from gorse stands, or substantially less abundant in gorse than in kānuka stands, specifically ground orchids (Druce 1957; Lee et al. 1986); two small-leaved, subcanopy shrubs (*Leucopogon fasciculatus* and *Leptecophylla juniperina*, Lee et al. 1986 cf. Allen et al. 1992); podocarp seedlings (Lee et al. 1986 cf. Allen et al. 1992); *Nothofagus* species (if present; Wilson 1994), and *Weinmannia racemosa* (kāmahi). While we expected less *Nothofagus* in gorse than in kānuka (Wilson 1994), *Nothofagus* was unlikely to occur frequently at any of our sites due to its limited dispersal ability (Wardle 1984). We therefore also selected *Weinmannia racemosa*, as a woody precursor closely associated with *Nothofagus* forest (Druce 1957).

## Methods

### Study sites

In Nelson, sites were north-east of Nelson City in the adjacent Wakapuaka and Whangamoa catchments within Bryant, Pelorus, and D'Urville ecological districts. They were distributed over 100 km$^2$ centred on approximately 41º10'S, 173º28'E. Sites in Wellington were north-east of Wellington City, scattered over 400 km$^2$ centered on 40º20'S, 174º55'E. They were principally in the Hutt catchment and inland from the Kapiti Coast, in the Tararua and Wellington ecological districts. The climate of both areas is similar, with a mean annual temperature of approximately 12ºC and 1000–1500 mm of precipitation evenly distributed throughout the year. Soils are derived mostly from acidic sedimentary rocks in both regions. Pre-European vegetation was mostly beech or podocarp-beech forest, and the gorse or kānuka stands have developed since, largely as a result of historical forest clearance for European farming.

### Field sampling

We used a space-for-time sampling design, as has been commonly and successfully used for constructing and comparing vegetation succession both in New Zealand

(Druce 1957; Williams 1983; Lee et al. 1986) and elsewhere (e.g. Adair & Groves 1998). Gorse and kānuka stands of similar age have a very different canopy structure (Williams & Karl 2002). The shorter statured and shorter lived gorse collapses and is replaced by broadleaved native tree species after 35–40 years (Druce 1957), whereas kānuka grows taller and dominates the canopy for at least 60 years (Molloy 1975). Because of this, we compared sites of comparable stage rather than age. We defined stages using the height of the tallest layer of associated regenerating native and naturalised trees.

Sampling was done in January–February 2003. Stands were selected initially on the basis of their canopy composition as viewed from the outside: predominately gorse or predominately kānuka. Stands were then selected for sampling if they represented one of four predefined successional stages:

1. *Young gorse*. Gorse 2–4 m tall dominated the canopy but with broadleaved tree species recently emergent, e.g. the native *Melicytus ramiflorus* (māhoe) or the naturalised *Berberis glaucophyllus* (barberry).

2. *Old gorse*. Scattered live or dead gorse stems, indicating the stand had probably developed through dense gorse, but now dominated by broadleaved tree species > 4 m tall. For old gorse sites we usually had to enter the stand to find the gorse remnants (dead or alive) to confirm that the site had been gorse-covered in the past.

3. *Young kānuka*. Kānuka, sometimes with mānuka, dominated the canopy, with broadleaved tree saplings, 2–4 m tall, in the understorey.

4. *Old kānuka*. Kānuka still occupied >80% of the canopy, above broadleaved tree species > 4 m tall but not yet emergent.

This produced a full-factorial design with two treatments, gorse cf. kānuka and young cf. old. Six stands from each stage were sampled in each of Nelson and Wellington, giving a total of 48 stands (Appendix 1). Stands were selected in a haphazard manner to approximate random as closely as possible, given difficulties such as access to private property and the scarcity of sites complying with our selection criteria. Each sample of the same successional stage was taken from a different landscape unit (hillside, aspect), although occasionally samples of different stages, e.g. old gorse and young kānuka, were co-located in the same landscape unit. Sampling was confined to hillsides below 500 m a.s.l. Within each stand, we placed one 50-m transect, beginning at a random point 20 m in from the edge, and running along a random bearing into the stand. Five circular quadrats, 5 m in diameter, were located at random intervals along each transect. In young gorse stands, transects involved cutting tracks through the otherwise impenetrable vegetation.

We recorded the following within quadrats: the presence of all woody species (native and naturalised), all species considered weeds by the Department of Conservation (2003; 'DOC weeds'), all ferns, all orchids, and pre-selected herbaceous plants to generic level (*Carex*, *Dianella*, *Gahnia*, *Libertia*, *Uncinia*; *Drosera* and *Haloragis* were also pre-selected but never encountered). For simplicity, these few herbaceous genera are considered at the same taxonomic level as species in the analysis and text. Woody species > 30 cm tall were recorded as established juveniles+adults and those ≤ 30 cm as seedlings.

We recorded the following three groups of environmental variables likely to influence species composition and richness either directly through site conditions or by supplying propagules:

*Abiotic landscape variables*. Site topography (gully, toe slope, hill slope, ridge) and elevation (m); site average slope and aspect; distance (km) to the nearest town on NZMS 260 topomaps, as towns are the entry point of many naturalised species into landscapes (Timmins & Williams 1991).

*Biotic landscape variables*. Distance (km) to the nearest native woody vegetation, and the nearest known or possible podocarps; number of DOC weed species observed within 250 m of the site; evidence of herbivorous mammals (yes, no); estimated cover of wild woody vegetation within 250 m of the site, and between 250 m and 1 km from the site (using four categories: ≤5%, 6–25%, 26–50%, >50%).

*Site vegetation structure variables*. Within the five quadrats per site we visually estimated the following: mean canopy height; maximum height of native woody species; maximum height of gorse or kānuka; maximum height of naturalised woody species; canopy cover of gorse or kānuka; canopy cover of native woody species; and canopy cover of naturalised woody species, including vines. Stands were named from canopy cover (Atkinson 1962).

## Data analysis

Multivariate ordination analyses were performed on PRIMER 5 with Windows 98 (Clarke & Gorley 2001). Other analyses were performed as generalized linear models (GLMs) in R version 1.8.1 (R Development Core Team 2003) with Mac OS X.

### Hypothesis 1: Kānuka stands have a different composition and greater richness of understorey broadleaved species than gorse stands at a comparable stage

Unconstrained ordinations using multi-dimensional scaling (MDS) were used to display graphically the similarity between sites in their species composition. Bray–Curtis similarity matrices were used throughout, except when one or more sites contained none of a

group of species being analysed (no woody naturalised plants and no DOC weeds at some sites). In these cases, Euclidean distance similarity matrices were used. When applied to the all-species analysis, both similarity methods produced qualitatively identical and quantitatively similar results.

The ordinations used the presence or absence of species per site, combining the data from the five circular quadrats per transect. Ordinations were created using all taxa (except gorse and kānuka), as well as selected groups of species: native woody juveniles+adults, native woody seedlings, naturalised woody juveniles+adults, naturalised woody seedlings, and ferns. Too few naturalised herbs were present and too few native herbs recorded, to justify separate herb ordinations. An additional ordination was performed using just DOC weeds.

The statistical significance of the effects of the gorse cf. kānuka and young cf. old treatments in these ordinations were assessed by analysis of similarity (ANOSIM), a non-parametric analogue of ANOVA, using 999 random permutations of the observed data. We also tested for differences among treatments in per-site species richness using two-way ANOVAS (as Gaussian GLMs).

The Similarity Percentages (SIMPER) routine in Primer 5 was used to identify the species that characterise the sites with each treatment combination (e.g. those species most consistently present in young kānuka sites). SIMPER was also used to identify which species best characterise the dissimilarities between sites with different treatment combinations (e.g. those species most consistently present in young gorse and absent from young kānuka sites, or vice versa). The similarity–dissimilarity results from SIMPER are derived from species presence or absence data per-site. These results were compared with Morisita–Horn dissimilarity, a robust method of calculating site dissimilarity using abundance data (e.g. Wolda 1981; Krebs 1999). A Morisita–Horn dissimilarity matrix for sites was calculated for the 'abundance' values of each species per site (i.e. how many of the five random quadrats per site contained a species), using the VEGAN vegetation analysis package in R (Oksanen et al. 2004). The within- and between-treatment mean dissimilarity values of Morisita–Horn closely matched the corresponding SIMPER values (linear regression, $R^2 = 0.896$).

### Hypothesis 2: Gorse and kānuka scrub do not exhibit convergent successional trajectories

ANOSIM does not include interactions between treatments. To assess these, we used two additional analyses. Post hoc pairwise tests in a one-way ANOSIM were used to test for significant differences between young gorse and kānuka sites, and between old gorse and kānuka sites.

If young gorse sites differed significantly from young kānuka sites, but there was no difference between old gorse and kānuka sites, this would indicate convergence. We also quantified the dissimilarity between old gorse and young kānuka sites. If these did not differ, it could indicate that time rather than stage of succession was important, with comparably aged old gorse and young kānuka sites having similar vegetation.

### Hypothesis 3: Several groups of plants are absent from gorse stands, or substantially less abundant in gorse than in kānuka stands

Binomial GLMs were used to assess the significance of the treatments on the distribution of selected species. These analyses used as a response variable the proportion of the five quadrats at a site containing a species. The GLM was fitted with a binomial distribution, or a quasi-binomial distribution when the residual deviance was greater than the residual degrees of freedom. The distance to the nearest native vegetation was used as a covariate for all species except the podocarps, for which distance to the nearest podocarp was used instead.

### Testing the independence of treatments from recorded landscape variables

Since we did not experimentally manipulate our study system, it remains possible that significant treatment effects could be caused by historical differences among sites consistent with our treatments. This possibility is partially accounted for by including selected covariates in our GLM analyses (but not ANOSIM). We used GLMs and the BVSTEP routine (for Biota and Environment Matching) of Primer 5 (Clarke & Gorley 2001) to further assess how our treatments were related to all 11 recorded landscape variables and two of the site vegetation structure variables (the maximum height of non-kānuka native trees and shrubs and of gorse or kānuka averaged across quadrats per transect). BVSTEP identifies the combination of variables best correlating with the similarity among sites in species composition. BVSTEP was run with and without our main treatments, always including our landscape and vegetation structure variables, to assess how much our treatments added to the explanation of site differences in species composition.

## Results

### Gorse sites differ from kānuka sites in species composition and richness

In both regions (Table 1, Fig. 1), gorse and kānuka sites differed in their plant species composition (excluding gorse and kānuka). These differences, and all others mentioned in this section, were significant at $P < 0.05$
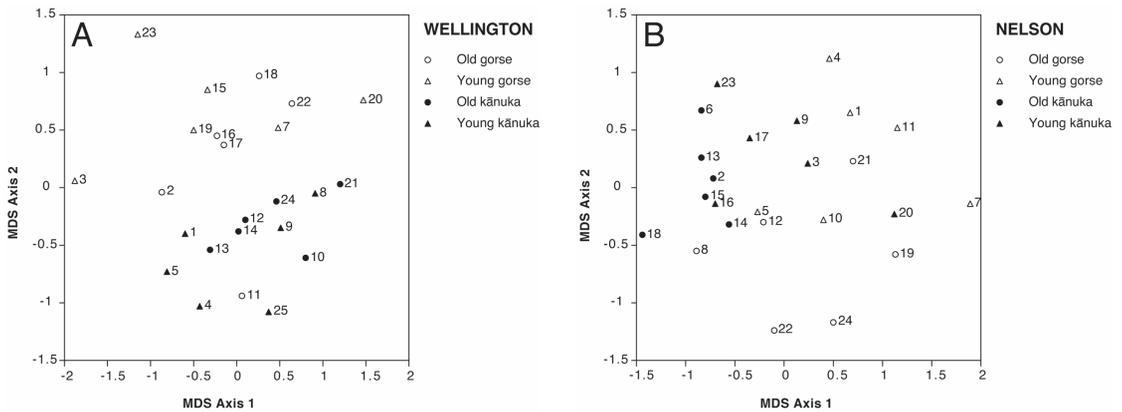
**Figure 1.** Two-dimensional multi-dimensional scaling (MDS) ordinations, plotting sites based on the similarity of their species compositions, for Wellington (A) and Nelson (B). Closer sites are more similar. Stress values on the MDS plots were 0.19 (Wellington) and 0.17 (Nelson). The ordinations are based on the same Bray–Curtis similarity matrices as the ANOSIM statistics in Table 1.

**Table 1.** Magnitude and statistical significance of differences in species composition, seedlings (≤30 cm) and 'adults' (>30 cm), among sites associated with the combinations of site treatments: gorse (*Ulex europaeus*) (G) and kānuka (*Kunzea ericoides*) (K), young (Y) or old (O) at two sites, Wellington and Nelson. The main effects (K cf. G and Y cf. O) are from a two-way analysis of similarity, and the comparisons of treatment combinations are from post hoc pairwise comparisons (see Methods). The symbols correspond to the probability (*P*) values (* = $P < 0.05$; ** = $P < 0.01$; note that $P < 0.001$ is impossible with the 999 random permutations in the ANOSIM; '-' = not significant ($P > 0.05$)) and the value is the R statistic (an estimate of the strength of the relationship). ANOSIM results are based on Bray–Curtis similarity matrices except naturalised woody and DOC weed species, where Euclidean similarity matrices had to be used (see Methods).

| Comparison | Species group | | | | | | |
|---|---|---|---|---|---|---|---|
| | All | Native woody Seedlings | Adults | Naturalised woody Seedlings | Adults | Ferns | DOC weeds |
| **A. Wellington** | | | | | | | |
| G cf. K | ** 0.50 | ** 0.36 | ** 0.54 | * 0.07 | * 0.12 | * 0.22 | * 0.12 |
| Y cf. O | - | - | * 0.19 | * 0.13 | - | - | - |
| GY cf. KY | ** 0.47 | * 0.34 | ** 0.45 | * 0.15 | * 0.24 | * 0.27 | ** 0.21 |
| GO cf. KO | ** 0.53 | ** 0.37 | ** 0.62 | - | - | * 0.18 | - |
| GO cf. KY | ** 0.39 | ** 0.35 | ** 0.49 | - | - | - | * 0.13 |
| **B. Nelson** | | | | | | | |
| G cf. K | ** 0.26 | * 0.23 | ** 0.29 | - | - | - | - |
| GY cf. KY | - | - | ** 0.30 | - | - | - | - |
| GO cf. KO | ** 0.38 | * 0.25 | * 0.27 | - | - | - | - |
| GO cf. KY | - | * 0.31 | - | - | - | - | - |

or higher (see Tables 1 & 2). In Wellington, gorse and kānuka sites differed in species composition (Table 1A, Fig. 1A), and kānuka sites were more species-rich than were gorse sites (Table 2A). In Nelson, gorse and kānuka sites again differed in their species composition (Table 1B, Fig. 1B), although not in overall species richness (Table 2B).

The species most responsible for differences in composition between young and old gorse and kānuka sites are listed in Table 3. Species consistently favouring kānuka in both Wellington and Nelson included the native woody plants *Coprosma rhamnoides* (found in 21 kānuka sites and five gorse sites), *Weinmannia racemosa* (12 kānuka sites, one gorse site), and *Olearia*

**Table 2.** Species richness at young and old, gorse and kānuka sites at Wellington and Nelson as the mean number ± SE of species per site (from five quadrats of 5 × 5 m) ($N = 6$ sites per treatment combination). The P-values are from two-way ANOVAs (* = $P < 0.05$; ** = $P < 0.01$; '-' = not significant ($P > 0.05$)).

| Site treatment | Number of species per site | | | |
| --- | --- | --- | --- | --- |
| | All species | Native woody | Naturalised woody | Ferns |
| **A. Wellington** | | | | |
| Young gorse | 19.2 ± 2.9 | 9.2 ± 1.3 | 2.5 ± 0.4 | 6.7 ± 1.6 |
| Old gorse | 23.2 ± 3.1 | 12.7 ± 1.7 | 1.7 ± 0.4 | 8.0 ± 1.6 |
| Young kānuka | 31.3 ± 2.8 | 17.7 ± 1.1 | 2.5 ± 0.8 | 9.3 ± 1.7 |
| Old kānuka | 29.5 ± 2.0 | 17.3 ± 0.8 | 1.0 ± 0.4 | 9.0 ± 1.1 |
| ANOVA results: | | | | |
| Gorse cf. kānuka | ** | *** | - | - |
| Young cf. old | - | - | * | - |
| Interaction | - | - | - | - |
| **B. Nelson** | | | | |
| Young gorse | 17.3 ± 2.5 | 7.7 ± 1.5 | 2.5 ± 0.2 | 5.2 ± 0.8 |
| Old gorse | 20.0 ± 3.9 | 9.3 ± 2.1 | 1.2 ± 0.5 | 8.2 ± 1.6 |
| Young kānuka | 21.8 ± 2.1 | 10.3 ± 1.9 | 2.2 ± 0.7 | 8.3 ± 1.2 |
| Old kānuka | 27.0 ± 2.6 | 17.0 ± 1.8 | 0 ± 0 | 7.7 ± 1.0 |
| ANOVA results: | | | | |
| Gorse cf. kānuka | - | * | - | - |
| Young cf. old | - | * | *** | - |
| Interaction | - | - | - | - |

**Table 3.** Species most characteristic of the sites of each treatment combination, and most distinguishing among treatment combinations. Species are listed in decreasing order of importance, followed in brackets by the number of sites they occurred at (including observations both inside and outside of plots along the site transect). Listed are those species with a (contribution/ standard deviation) >1 for the similarity or dissimilarity within or between treatment combinations. This cut-off was selected because, for similarity measures, it is equivalent here to a species being present in ≥5 of the six sites of a treatment combination. The average similarity and dissimilarity values, and the species contributions to these, were calculated with Similarity Percentage analysis (see Methods). The sixth treatment comparison, between young gorse sites and old kānuka sites, is omitted, as it is not relevant to the aims of the study.

**A. Wellington**

| Young gorse sites (35.8% average similarity) | Young kānuka sites (44.5% average similarity) | Young gorse cf. young kānuka (69% average dissimilarity) |
| --- | --- | --- |
| *Pteridium esculentum* (6/6 sites) | *Parsonsia* sp. (6) | *Parsonsia* sp. (6,0) |
| *Rubus fruticosus** (6) | *Asplenium flaccidum* (6) | *Coprosma rhamnoides* (1,6) |
| *Melicytus ramiflorus* (5) | *Melicytus ramiflorus* (6) | *Rubus fruticosus** (6,1) |
| | *Geniostoma ligustrifolium* (6) | *Asplenium flaccidum* (1,6) |
| | *Coprosma rhamnoides* (6) | *Polystichum richardii* agg. (0,5) |
| | *Brachyglottis repanda* (6) | *Uncinia* spp. (0,4) |
| | *Cyathea dealbata* (5) | *Pseudopanax crassifolius* (0,4) |
| | *Polystichum richardii* agg. (5) | *Pteridium esculentum* (6,3) |
| | | *Coprosma propinqua* (0,4) |
| | | *Prunus* sp. * (1,4) |
| | | *Pittosporum crassifolium* (1,4) |
| | | *Blechnum novaezelandiae* (2,4) |
| | | *Coprosma lucida* (2,4) |

| Old gorse sites (47.4% average similarity) | Old kānuka sites (48.1% average similarity) | Old gorse cf. old kānuka (61.3% average dissimilarity) |
| --- | --- | --- |
| *Macropiper excelsum* (6) | *Uncinia* spp. (6) | *Uncinia* spp. (1,6) |
| *Melicytus ramiflorus* (6) | *Cyathea dealbata* (6) | *Parsonsia* sp. (0,5) |
| *Geniostoma ligustrifolium* (6) | *Melicytus ramiflorus* (6) | *Ripogonum scandens* (1,5) |
| *Brachyglottis repanda* (6) | *Geniostoma ligustrifolium* (6) | *Asplenium oblongifolium* (1,5) |
| *Hedycarya arborea* (5) | *Brachyglottis repanda* (6) | *Olearia rani* (1,5) |

| | | |
|---|---|---|
| *Coprosma grandifolia* (5) | *Ripogonum scandens* (5) | *Coprosma robusta* (1,4) |
| *Polystichum richardii* agg. (5) | *Coprosma grandifolia* (5) | *Macropiper excelsum* (6,2) |
| *Asplenium oblongifolium* (5) | *Pseudopanax arboreus* (5) | *Schefflera digitata* (4,0) |
| | *Parsonsia* sp. (5) | *Weinmannia racemosa* (0,4) |
| | *Olearia rani* (5) | *Asplenium flaccidum* (0,4) |
| | | *Pseudopanax crassifolius* (1,4) |
| | | *Leucopogon fasciculatus* (1,4) |
| | | *Hedycarya arborea* (5,2) |
| | | *Polystichum richardii* agg. (5,2) |
| | | *Pseudopanax arboreus* (2,5) |
| | | *Blechnum fluviatile* (4,2) |
| | | *Coprosma propinqua* (4,2) |

| Young gorse cf. old gorse (63.1% average dissimilarity) | Young kānuka cf. old kānuka (54.2% average dissimilarity) | Old gorse cf. young kānuka (60.9% average dissimilarity) |
|---|---|---|
| *Macropiper excelsum* (1,6) | *Ripogonum scandens* (1,5) | *Parsonsia* sp. (6,0) |
| *Polystichum richardii* agg. (0,5) | *Olearia rani* (1,5) | *Asplenium flaccidum* (6,0) |
| *Schefflera digitata* (1,4) | *Prunus* sp.* (4,0) | *Coprosma rhamnoides* (1,6) |
| *Coprosma lucida* (4,1) | *Polystichum richardii* agg. (5,2) | *Prunus* sp.* (0,4) |
| *Coprosma propinqua* (0,4) | *Weinmannia racemosa* (1,4) | *Uncinia* spp. (1,4) |
| | *Pittosporum crassifolium* (4,1) | *Pseudopanax crassifolius* (1,4) |
| | *Asplenium bulbiferum* (2,4) | *Hedycarya arborea* (5,2) |
| | *Blechnum capense* agg. (4,2) | *Blechnum novaezelandiae* (1,4) |
| | *Leucopogon fasciculatus* (2,4) | *Pittosporum crassifolium* (1,4) |
| | *Coprosma propinqua* (4,2) | *Pseudopanax arboreus* (2,4) |
| | *Pteridium esculentum* (2,4) | *Schefflera digitata* (4,2) |
| | | *Blechnum fluviatile* (4,2) |

**B. Nelson**

| Young gorse sites (32.5% average similarity) | Young kānuka sites (36.2% average similarity) | Young gorse cf. young kānuka (68.0% average dissimilarity) |
|---|---|---|
| *Pteridium esculentum* (6) | *Pteridium esculentum* (6/6 sites) | *Coprosma rhamnoides* (0,6) |
| *Clematis vitalba** (6) | *Coprosma rhamnoides* (6) | *Weinmannia racemosa* (1,4) |
| *Melicytus ramiflorus* (5) | *Melicytus ramiflorus* (5) | *Myrsine australis* (2,4) |
| | *Carpodetus serratus* (5) | *Cyathea dealbata* (2,4) |

| Old gorse sites (31.6% average similarity) | Old kānuka sites (44.4% average similarity) | Old gorse cf. old kānuka (69.5% average dissimilarity) |
|---|---|---|
| *Pteridium esculentum* (6) | *Coprosma rhamnoides* (6) | *Weinmannia racemosa* (0,5) |
| *Melicytus ramiflorus* (6) | *Brachyglottis repanda* (6) | *Olearia rani* (0,5) |
| | *Weinmannia racemosa* (5) | *Brachyglottis repanda* (2,6) |
| | *Olearia rani* (5) | *Carpodetus serratus* (1,5) |
| | *Cyathea dealbata* (5) | *Asplenium flabellifolium* (4,0) |
| | *Melicytus ramiflorus* (5) | *Pittosporum tenuifolium* (0,4) |
| | *Carpodetus serratus* (5) | *Blechnum discolor* (0,4) |
| | *Asplenium flaccidum* (5) | *Uncinia* spp. (1,4) |
| | | *Pseudopanax arboreus* (1,4) |
| | | *Leucopogon fasciculatus* (2,4) |
| | | *Myrsine australis* (2,4) |

| Young gorse cf. old gorse (68.8% average dissimilarity) | Young kānuka cf. old kānuka (61.6% average dissimilarity) | Old gorse cf. young kānuka (68.6% average dissimilarity) |
|---|---|---|
| *Clematis vitalba** (6,1) | *Olearia rani* (1,5) | *Carpodetus serratus* (1,5) |
| *Asplenium flabellifolium* (0,4) | *Rubus fruticosus** (4,0) | *Weinmannia racemosa* (1,4) |
| *Asplenium flaccidum* (1,4) | *Brachyglottis repanda* (2,6) | *Asplenium flabellifolium* (4,1) |
| | *Coprosma grandifolia* (1,4) | *Myrsine australis* (2,4) |
| | *Blechnum discolor* (1,4) | *Coprosma robusta* (4,2) |
| | *Coprosma robusta* (2,4) | |
| | *Pittosporum tenuifolium* (2,4) | |
| | *Hedycarya arborea* (2,4) | |

* Naturalised species.

*rani* (11 kānuka sites, one gorse site), and the native herbs *Uncinia* spp. (17 kānuka sites, four gorse sites) (Appendix 2).

There were more native woody species at kānuka than at gorse sites, across young and old sites and in both regions (Table 2). Similarly, the composition of native woody species (juveniles+adults and seedlings) differed between gorse and kānuka sites in both regions (Table 1A, B). We found fewer naturalised woody species than native woody species overall, and fewer sites with one or more naturalised woody species. There were 17 naturalised cf. 50 native woody species at Wellington sites, and 7 naturalised cf. 46 native species at Nelson sites. All sampled sites contained native woody species, and 83% of Wellington sites and 63% of Nelson sites contained one or more naturalised woody species, other than gorse (Table 2).

There were differences between gorse and kānuka sites in their naturalised woody species composition in Wellington (Table 1), but not Nelson, where there were fewer such species. There were no differences between gorse and kānuka sites in the number of naturalised woody species per site, although in both Wellington and Nelson there was a strong age effect, with old sites having fewer naturalised species (Table 2) and a different species composition (Table 1) than young sites. This site age effect was typically stronger for naturalised woody species than native woody species (Tables 1 & 2). Of the naturalised woody species, *Rubus fruticosus* (blackberry) and *Prunus* sp. (wild cherry) best distinguished gorse from kānuka sites (Table 3), but only young gorse from young kānuka sites, and only in Wellington.

In Wellington, fern species composition differed between gorse and kānuka sites (Table 1A) although there were no differences in fern species richness (Table 2A). At young Wellington sites, kānuka sites were more likely to contain *Asplenium flaccidum*, *Polystichum richardii* agg. and *Blechnum novaezelandiae* agg., while more gorse sites had *Pteridium esculentum* (bracken) (Table 3). At old Wellington sites, kānuka sites were again more likely to contain *Asplenium flaccidum*, while more gorse sites had *Asplenium oblongifolium*, *Polystichum richardii* agg. and *Blechnum fluviatile* (Table 3). These species occurred also at Nelson sites, but they did not show such strong patterns and there were no differences in the number or composition of fern species between gorse and kānuka sites of either age (Tables 1B & 2B).

### Succession trajectories through gorse and kānuka do not converge

If the succession trajectories tended to converge, we would expect fewer differences in species composition between old gorse and old kānuka than between young gorse and young kānuka sites. However, this was not the

case. In Wellington, differences in species composition (Table 1A) and species richness (no interaction in Table 2A) were found between gorse and kānuka at both young and old sites. Notably, these differences in species composition included native woody seedlings (Table 1A). The dissimilarity between old kānuka and old gorse sites was less than the dissimilarity between young kānuka and young gorse sites, for both SIMPER dissimilarity using species presence–absence (61.3% and 69.0% respectively, Table 3B), and Morisita–Horn dissimilarity using species 'abundance' (63.2% and 69.4% respectively.

In Nelson, young gorse sites did not differ in species composition from young kānuka sites, but old gorse sites differed from old kānuka sites (Table 1B). As in Wellington, old gorse and old kānuka sites also differed in their native woody seedling composition (Table 1B). While the SIMPER dissimilarity between old kānuka and old gorse sites (69.5%) was close to that between young kānuka and young gorse sites (68%) (Table 3B), the Morisita–Horn values showed the same pattern as in Wellington (60.9% and 75.7% respectively). While the dissimilarity between old gorse and kānuka sites tended to be less than for young sites, this decreasing heterogeneity among sites was also seen within old gorse and kānuka sites (Table 3B).

Our selection of sites on the basis of height of regenerating natives, rather than age, meant old gorse sites were likely younger than old kānuka sites. This was not to the extent that old gorse sites resembled young kānuka. In Wellington, these two differed in their overall species composition, native woody species, and DOC weeds (Table 1A). They also showed a site-dissimilarity (60.9% SIMPER, 65.4% Morisita–Horn) comparable to that between old gorse and old kānuka sites (61.3% SIMPER, 69.0% Morisita–Horn). In Nelson, old gorse and young kānuka sites differed significantly only in the composition of native woody seedlings (Table 1B), but also showed a comparable site-dissimilarity (68.6% SIMPER, 73.1% Morisita–Horn) to that for old gorse cf. old kānuka sites (69.5% SIMPER, 75.7% Morisita–Horn).

### Individual species respond differently to gorse and kānuka

Overall there were no treatment effects on the distribution of podocarp species among sites. In Wellington, only a single *Podocarps hallii* (Hall's totara) seedling was found at one young kānuka site (Appendix 2). Three species of podocarp were recorded at Nelson sites, *Dacrycarpus dacrydioides* (kahikatea), *Podocarpus hallii* and *Prumnopitys taxifolia* (mataī). There were no significant treatment effects on podocarp distribution in Nelson, even after taking into account the significant effect of distance from each site to the nearest adult podocarp (range 0.2–5 km, $P < 0.05$, minimum

adequate GLM contained only source distance, total d.f. = 23). In Nelson, *Dacrycarpus dacrydioides* was found at one old gorse site, and seedlings of *Podocarpus hallii* at three young kānuka sites and one old gorse site, and *Prumnopitys taxifolia* at one young gorse site, one young kānuka sites, and one old kānuka site (another *Prumnopitys taxifolia* seedling was found outside the plots along the transect at a second old kanuka site)(Appendix 2).

The single native orchid species found, *Pterostylis banksii*, occurred more often in kānuka than in gorse sites, and in old kānuka rather than young kānuka sites in Nelson (gorse cf. kānuka, $F = 23.0$, residual d.f. = 22, $P < 0.001$; young cf. old, $F = 24.0$, $P < 0.001$). It was not found in Wellington.

*Leucopogon fasciculatus* and *Leptecophylla juniperina* (mingimingi) were more frequent in kānuka than in gorse sites, both in Wellington and Nelson (all $P < 0.01$ and residual d.f. = 22; *Leucopogon fasiculatus* Nelson $F = 9.5$, Wellington $F = 9.0$; *Leptecophylla juniperina* Nelson $F = 9.1$, Wellington $F = 11.2$). *Leucopogon fasiculatus* was found in some gorse sites in both Wellington and Nelson, but fewer than kānuka sites (Appendix 2). *Leptecophylla juniperina* was confined to kānuka sites in both Wellington and Nelson, and only old kānuka sites in Wellington (Appendix 2).

*Weinmannia racemosa* was found less often in gorse than kānuka sites, and in old rather than young sites in Nelson (gorse cf. kānuka, $F = 22.4$, residual d.f. = 22, $P < 0.001$; young cf. old, $F = 11.2$, $P < 0.01$), but no significant relationships were found in Wellington. In Nelson, *W. racemosa* was present at all old kānuka sites and two young kānuka sites, but at no gorse sites. In Wellington, *W. racemosa* was found at five kānuka sites and in only one gorse site, but at that site it occurred in three of the five quadrats (where it may have established at a similar time to gorse).

**Sampled gorse and kānuka sites are random with respect to most landscape characteristics**

In both regions, no abiotic landscape variables were associated with the treatments. In Wellington and Nelson, the same one biotic landscape variable was associated with gorse–kānuka treatments, but the direction of its effect differed between regions. In Wellington, the mean (±SE) percentage woody vegetation cover between 250 m and 1 km from sites was higher on average surrounding gorse (72.8% ± 3.2%) than kānuka (53.3% ± 7.2%) (the only explanatory variable in the minimum adequate binomial GLM, $z$-value $-2.0$, residual deviance 27.3 from 22 d.f., $P < 0.05$). In contrast, in Nelson this percentage woody cover was lower on average surrounding gorse (50.1% ± 7.0%) than kānuka (69.7% ± 4.3%) (minimum adequate binomial GLM, $z$-value 2.1, residual deviance 28.0 from 22 d.f., $P < 0.05$).

In Wellington, but not Nelson, the maximum height of native vegetation tended to be lower in gorse than kānuka sites (mean $4.0 ± 0.4$ m cf. $5.0 ± 0.4$ m, respectively; ANOVA $F = 5.0$, total d.f. = 23, $P < 0.05$). Wellington sites were closer to the nearest town than were Nelson sites (mean $1.45 ± 0.33$ km cf. $8.43 ± 1.14$ km; Welch $t$-test, $t = -2.2$, d.f. = 43.2, $P < 0.05$) and twice as far from the nearest native vegetation (mean $1.48 ± 0.27$ km cf. $0.73 ± 0.21$ km; Welch $t$-test, $t = -2.3$, d.f. = 41.5, $P < 0.05$); Wellington sites were scattered more widely.

The best model for explaining the vegetative similarity of Wellington sites, as revealed by BVSTEP from our treatments and all environmental variables, contained the following variables (in order of decreasing contribution): gorse cf. kānuka, maximum height of native vegetation, canopy cover of natives and exotics, distance to the nearest native vegetation, and number of DOC weeds within 250 m. These together had a correlation coefficient ($R$) of 0.43. In comparison, a model with just the two treatments is almost as good ($R = 0.41$). Notably absent from the best model was site age, although this was closely correlated with height and canopy-cover variables.

The best model for the Nelson data contained gorse cf. kānuka, young cf. old, maximum height of the gorse or kānuka, maximum height and canopy cover of naturalised woody species, site elevation, presence or absence of mammalian browsing, and distance to the nearest town. These together had a correlation coefficient ($R$) of 0.47. A model including only the treatment variables had a correlation coefficient of 0.29. So, unlike Wellington, the additional variables explain substantially more of the variation among Nelson sites than our treatments alone.

# Discussion

### Gorse ≠ kānuka

We found gorse stands have a different species composition and lesser species richness than kānuka stands at comparable successional stages, that these differences are maintained over time, and that several groups of plants are absent from or less common in gorse than in kānuka stands. This supports early age-based comparisons that can be made between gorse and kānuka – in Dunedin, comparing gorse scrub up to 30 years of age (Lee et al. 1986) with similar-aged nearby kānuka forest (Allen et al. 1992), and 14-year-old gorse and kānuka stands compared in Nelson (Williams & Karl 2002).

Our findings are consistent with recent evidence showing that gorse and kānuka scrub in Nelson differ at several trophic levels: they have different soil microfauna (Yeates & Williams 2001), invertebrates

(Harris et al. 2004), and bird communities (Williams & Karl 2002). On the basis of the seed rain and seedling survival, Williams and Karl (2002) anticipated our results by suggesting that successions through gorse or kānuka have different pathways leading to different forest types. Strong evidence for different pathways also comes from Banks Peninsula in Canterbury, where kānuka scrub returns to its original cover of beech forest (*Nothofagus*), whereas on similar sites, succession through gorse leads to native broadleaved forest (Wilson 1994).

Studies near Dunedin in Otago show richness of native woody species, including lianes, was lower under gorse scrub up to 30 years of age (14 species with >5% frequency) (Lee et al. 1986) than under similar-aged kānuka forest (up to 26 species) slightly further north (Allen et al. 1992). Podocarp seedlings were absent from gorse plots while a few were present in the kānuka, suggesting gorse may be a less favourable nurse crop for podocarps. We found insufficient podocarps in either vegetation type in our study to confirm this. The Dunedin data show also that gorse scrub has fewer small-leaved shrub species (*Coprosma*, *Cyathodes, Leucopogon*) than kānuka scrub (Lee et al. 1986 cf. Allen et al. 1992), a finding we confirm. Ground species also differ; there were three forest herb and fern species with a frequency of >5% under gorse compared with up to 20 under kānuka (Lee et al. 1986 cf. Allen et al. 1992). Native orchids such as *Pterostylis* spp. were absent from gorse but common beneath similar-aged kānuka at Dunedin (Lee et al. 1986; cf. Allen et al. 1992) and within one catchment in the Hutt Valley (Druce 1957).

Successional studies must consider the context of surrounding biota, landscape processes, and the history of human disturbance, including fire (Debussche et al. 1980; Cook et al. 2005). Comparing successions with and without weeds can be complicated by many factors. Naturalised shrub species facilitate (*sensu* Connell & Slatyer 1977) the establishment of taller native vegetation in one region, but they may inhibit establishment in another. For example, *Cytisus scoparius* (broom) facilitates the regeneration of taller broadleaved species on hill slopes in the South Island of New Zealand (Williams 1983), but inhibits taller native species in Australian uplands (Waterhouse 1986; Smith 1994). Local site factors, for example topography, may also confound comparisons of succession, with and without weeds (Adair and Groves 1998). In the Hutt Valley, gorse successions on valley floors differed from those through native or naturalised shrubs on hill slopes (Druce 1957).

Seed dispersal may greatly influence vegetation succession over quite short distances. Most seed deposited by small birds such as silvereyes in New Zealand is likely to fall within 100 m from source (Burrows 1994; Bray et al. 1999; Stansbury 2001). This contributed to the differences in seed fall measured in gorse and kānuka scrub within the same catchment in Nelson (Williams & Karl 2002). The absence of native species from gorse stands within 100 m of native vegetation in Dunedin was attributed to properties of the gorse stands (Lee et al. 1986), although grazing is also a factor (Wilson 1994).

In our comparisons of gorse and kānuka, we minimised geographical and environmental factors influencing propagule pressure and current grazing by sampling over a wide area, and recording potential seed source proximity. As a result, no abiotic landscape variables were significantly related to our treatments; the two significant biotic landscape variables showed opposite trends in the two regions yet their gorse cf. kānuka effects were consistent; and models considering all variables consistently identified gorse cf. kānuka as the most significant explanatory variable. For these three reasons we consider it likely that vegetation differences between gorse and kānuka sites are determined primarily by these species, although there may be additional historical factors differentiating our gorse and kānuka stands.

## Species most affected by gorse–kānuka differences

A few native species, typified by *Melicytus ramiflorus*, are common in young stands of both gorse and kānuka (Table 3), as they are in early forest successions throughout much of New Zealand (Wardle 1991). Other species differentiate the four successional stages in the two regions (Table 3). The small-leaved shrub *Coprosma rhamnoides* is abundant under kānuka throughout New Zealand (e.g. Wardle 1971; Esler & Astridge 1974) and is particularly important in differentiating young kānuka from young gorse. Similarly, the significantly greater frequency of the small-leaved *Leucopogon fasciculatus* and *Leptecophylla juniperina* in kānuka suggests kānuka provides habitat for small-leaved shrubs that are perhaps less able to exist in gorse (Lee et al. 1986; cf. Allen et al. 1992). *Olearia rani* also ranked highly as a species differentiating old kānuka and gorse in Wellington and Nelson (Appendix 2). This species, and species of *Leucopogon* and *Leptecophylla*, are characteristic of *Nothofagus truncata* (hard beech) subseres [sic] in the Wellington region (Druce 1957); differences between gorse and kānuka may still partly reflect differences in the soils of our sites, if more kānuka than gorse sites are located on sites of past *N. truncata* forests. We found no orchids in gorse scrub, mirroring results from Dunedin (Lee et al. 1986; cf. Allen et al. 1992). Native orchids have been observed in gorse (Johns & Molloy 1983) but kānuka must be considered a favoured habitat.

Our hypothesis that gorse was less favourable than kānuka for podocarp establishment could not

be adequately tested, because podocarp seedlings or juveniles were scarce at all sites. While gorse facilitates establishment of *Podocarpus totara* var. *waihoensis* in Westland, primarily by suppressing grass growth (Miller & Wells 2003), no comparisons with kānuka or mānuka are available. Podocarp seedlings were rare in our study even where there were isolated podocarp trees within a few hundered metres and the gorse or kānuka scrub had adequate stature (Bray et al. 1999). In Nelson, *Weinmannia racemosa* was common in kānuka sites but absent from all gorse sites. A similar trend in Wellington was not significant, perhaps partly because Wellington sites were further from older native vegetation. Isolation from sources of native species, especially those on alluvial soils (Park & Walls 1978), is affecting the composition of gorse and kānuka stands in Wellington and Nelson, and probably most of lowland New Zealand.

Significant differences in naturalised woody species and DOC weeds between gorse and kānuka in Wellington, and not Nelson, likely resulted in part, from their greater species richness in Wellington. All species we recorded only in Wellington are horticultural escapes, e.g. *Tradescantia fluminensis* and *Selaginella kraussiana*, and all, except *Senecio glastifolius,* grow nearer Nelson City than our quadrats (PAW, pers. obs.). Our Wellington sites are richer in naturalised species because they are closer to urban propagule sources than our Nelson sites (Timmins & Williams 1991; Sullivan et al. 2005), illustrating the effects of context on vegetation successions (Debussche et al. 1980).

Naturalised species that have reached sufficient abundance in the landscape differentiate the quadrat groups: *Rubus fruticosus* distinguished young gorse sites from young kānuka sites in Wellington but not Nelson. This difference is probably because we used frequency as a measure rather than cover; *R. fruticosus* was a canopy component of gorse scrub in Nelson but only a minor understorey plant in young kānuka. *Prunus* sp*.,* present mainly as seedlings in young kānuka stands and not at all in old kānuka (Table 3), strongly distinguished young kānuka from young gorse in Wellington, but not in Nelson. Wild *Prunus* species are rare in the Nelson catchments sampled, whereas closer to cultivated trees fringing Nelson City they regenerate through gorse scrub (PAW, pers. obs.). *Berberis glaucocarpa* did not differentiate gorse from kānuka in either region, despite being a canopy component (e.g. *Coprosma* spp.–barberry–gorse scrub). We found only seedling *B. glaucocarpa* in kānuka, although pure *B. glaucocarpa* scrub develops from gorse in parts of rural Nelson (PAW, pers. obs.). The relative paucity of naturalised woody species like *B. glaucocarpa* and *Prunus* species in the sampled sites of Wellington and Nelson regions likely reflects their early invasion stage; their potential to invade either native or exotic

successional vegetation remains to be seen.

There are a great many differences between gorse and kānuka, both above and below ground, that may account for these species patterns. Gorse stands appear to be dominated to a greater extent by naturalised bird species (Williams & Karl 2002), which may alter the dispersal of plant species into sites. Stand structural dynamics differ, with old gorse sites having a densely shaded understorey unlike old kānuka sites, which have an open, evenly shaded understorey below a tall, open canopy (Williams & Karl 2002; see also Grime & Jeffrey 1965). This may explain the rarity of small-leaved understorey shrubs like *Coprosma rhamnoides*, *Leucopogon fasciculatus*, and *Leptecophylla juniperina* in gorse successions. Gorse has a greater litter depth than kānuka (Lee et al. 1986), which may affect seedling establishment. Differences below ground may influence the abundance of some plant species, including the great nitrogen-fixing capacity of gorse (Egunjobi 1969), the competition for moisture from leguminous shrubs like gorse when grown with other trees (Watt et al. 2003), the mycorrhizal associations of Myrtaceae (McNabb 1968) and thus phosphorus nutrition (Baylis 1971), and differences in soil microfauna (Yeates & Williams 2001). Experiments will be required to explore these effects and their interactions (e.g. Monk & Gabrielson 1985).

## Future of gorse and kānuka scrub

The decreasing dissimilarity between old gorse and kānuka sites relative to young sites, seen in both Wellington and Nelson sites, does not appear to indicate that the succession trajectories are converging. Rather, it likely reflects, in part, reduced heterogeneity among all older sites, associated with the weakening influence of founder effects common in such secondary vegetation (Partridge 1989). This interpretation is supported by the comparably lower within-treatment dissimilarity among old sites compared with young sites.

The woody species presently characterising the sites and differentiating kānuka and gorse are native lianes, shrubs or small trees to 10 m, except *Pseudopanax crassifolius* (13 m) and *Weinmannia racemosa* (26 m) (Poole & Adams 1990). Within this narrow range of potential canopy species, gorse and kānuka are still differentiated and their present floras will lead to different vegetations c. 10 m tall. The differences between old gorse and kānuka sites in woody seedling composition suggest differences are likely to persist into the next generation of canopy vegetation. Further, our data and observations indicate that in the presence of adequate seed sources, gorse scrub is more likely than kānuka scrub to lead to vegetation dominated by bird-dispersed naturalised woody species, e.g. *Berberis glaucocarpa.* These are preferred foods only of exotic birds or silvereyes (Williams & Karl 1996).

Where the transition from gorse to another naturalised plant does occur, and it is not universal, there may be a compounding influence on native biodiversity, termed 'environmental meltdown' by Simberloff and Von Holle (1999). Such potential long-term effects would be additional to the apparent impacts of gorse scrub itself, on plant species, as we have shown here, and on other trophic levels (Yeates & Williams 2001; Williams & Karl 2002; Harris et al. 2004).

In summary, the associated floras of gorse scrub and kānuka scrub, and their immediate successors, are different. Species richness is often lower in gorse, particularly for small-leaved shrubs, and it has fewer orchids. Although gorse leads to native forest it will be a different forest from that developed through kānuka, and will probably not include beech forest (Wilson 1994). Not only do extant stands of gorse and kānuka differ at several trophic levels, gorse also leaves an imprint on the landscape long after it has disappeared. It cannot therefore simply be a substitute for native successional species. Manually establishing patches of kānuka and mānuka within landscapes dominated by gorse or other naturalised shrubs may be necessary to assist with the preservation of components of native secondary vegetation. Current management by benign neglect will benefit from some benevolent intervention.

# Acknowledgements

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**Appendix1.** Site locations and vegetation canopy composition (Atkinson 1962) for young gorse (GY), old gorse (GO), young kānuka (KY), and old kānuka (KO), at gorse and kānuka sites in Wellington (W) and Nelson (N). Coordinates are from the standard New Zealand Map Series (NZMS 260) topomaps.

| Site no. | Type | Location | NZMS 260 Grid | Altitude (m) | Canopy composition |
|---|---|---|---|---|---|
| W3 | GY | Kenepuru Stm | R27 668 075 | 80 | (māhoe)–gorse scrub |
| W7 | GY | Wainuiomata R. | R27 731 909 | 130 | māhoe–gorse–bracken shrubland |
| W15 | GY | Korokoro Stm | R27 683 009 | 220 | māhoe–gorse–rangiora scrub |
| W19 | GY | Speedys Stm | R27 727 023 | 190 | gorse scrub |
| W20 | GY | Waiwhetu Stm | R27 751 982 | 120 | [kāmahi–kānuka] gorse–bracken scrub |
| W23 | GY | Takapuwahia | R27 637 075 | 40 | [māhoe]–gorse scrub |
| W2 | GO | Korokoro Stm | R27 656 997 | 300 | māhoe–[gorse] forest |
| W11 | GO | Whareroa Stm | R26 789 292 | 60 | māhoe forest |
| W17 | GO | Wainuiomata R. | R27 695 829 | 240 | māhoe forest |
| W18 | GO | Hutt R. | R27 710 945 | 120 | māhoe forest |
| W22 | GO | Hutt R. | R27 743 997 | 60 | māhoe forest |
| W16 | GO | Hutt R. | R27 684 016 | 200 | māhoe–rangiora forest |
| W1 | KY | Porirua Stm | R27 648 001 | 280 | [māhoe]–kānuka forest |
| W4 | KY | Duck Creek | R27 698 088 | 50 | kānuka treeland |
| W5 | KY | Taupo Stm | R26 675 118 | 60 | kānuka treeland |
| W8 | KY | Wainuiomataiti Stm | R27 755 937 | 200 | kānuka–kāmahi forest |
| W9 | KY | Karehana Bay | R26 667 136 | 100 | Kānuka forest |
| W25 | KY | Browns Bay | R27 685 089 | 60 | Kānuka forest |
| W10 | KO | Whareroa Stm | R26 783 263 | 80 | Kānuka forest |
| W12 | KO | Mangaroa R. | R27 811 020 | 200 | Kānuka forest |
| W13 | KO | Mangaroa R. | R27 834 007 | 220 | Kānuka forest |
| W14 | KO | Mangaroa R. | R27 837 005 | 240 | kānuka–rangiora treeland |
| W21 | KO | Waiwhetu Stm | R27 752 983 | 100 | Kānuka forest |
| W24 | KO | Takapuwahia Stm | R27 633 078 | 80 | Kānuka forest |
| N1 | GY | Whangamoa R. | O27 025 507 | 140 | gorse–Himalayan honeysuckle–bracken scrub |
| N10 | GY | Whakapuaka R. | O27 457 001 | 90 | gorse scrub |
| N11 | GY | Whangamoa R. | O27 509 026 | 140 | [*Coprosma* spp.]–gorse–barberry scrub |
| N4 | GY | Lud R. | O27 415 975 | 129 | (hawthorn)– gorse–blackberry–bracken scrub |
| N5 | GY | Collins R. | O27 497 014 | 250 | (barberry–māhoe)–gorse scrub |
| N7 | GY | Whakapuaka R. | O27 453 018 | 17 | gorse scrub |
| N12 | GO | Whangamoa R. | O27 510 028 | 160 | māhoe scrub |
| N19 | GO | Toi Toi Stm. | O26 559 114 | 20 | māhoe–gorse scrub |
| N21 | GO | Whakapuaka R. | O27 437 988 | 80 | māhoe scrub |
| N22 | GO | Collins R. | O26 571 021 | 220 | māhoe–fivefinger scrub |
| N24 | GO | Whakapuaka R. | O27 443 993 | 100 | māhoe forest |
| N8 | GO | Whakapuaka R. | O27 504 996 | 497 | māhoe forest |
| N16 | KY | Whangamoa R. | O27 553 066 | 100 | kānuka scrub |
| N17 | KY | Whangamoa R. | O27 554 074 | 90 | mānuka–kānuka scrub |
| N20 | KY | Whangamoa R. | O26 562 108 | 40 | kānuka scrub |
| N23 | KY | Whangamoa R. | O26 552 099 | 40 | kānuka scrub |
| N3 | KY | Lud R. | O27 425 977 | 200 | kānuka forest |
| N9 | KY | Whakapuaka R. | O27 468 015 | 190 | kānuka scrub |
| N13 | KO | Delaware Bay | O27 530 088 | 200 | kānuka forest |
| N14 | KO | Elizabeth Stm | O27 573 097 | 110 | kānuka scrub |
| N15 | KO | Elizabeth Stm | O27 572 094 | 140 | kānuka scrub |
| N18 | KO | Whakapuaka R. | O27 467 982 | 240 | kānuka scrub |
| N2 | KO | Whangamoa R. | O27 017 502 | 177 | kānuka forest |
| N6 | KO | Whakapuaka R. | O27 482 976 | 342 | kānuka forest |

**Appendix 2.** Species recorded at gorse and kānuka sites in Wellington and Nelson. Listed next to each species is the number of sites of each treatment combination (i.e. young gorse, old gorse, young kānuka, old kānuka) where the species was present in one or more plots along a site transect. Six sites were visited with each treatment combination in each region. All woody species and ferns were recorded at all sites, but not all herbaceous species. All listed ferns are native except *Nephrolepis cordifolia* and *Selaginella kraussiana*. The herbaceous species listed are only those that were consistently recorded at all sites. Department of Conservation listed weeds at the time of the analysis are marked with an asterisk (additional weeds found along transects but not in plots were *Acer pseudoplatanus, Asparagus scandens, Cortaderia selloana,* and *Senecio glastifolius*). Plant names follow the New Zealand Plant Names Database (http://www.landcareresearch.co.nz/databases, cited April 2007). Presence and absence data per site for all taxa identified to species have been added to the publicly available New Zealand Biodiversity Recording Network website (http://www.nzbrn.org.nz).

| Nelson, Wellington | Number of sites (/6) where a species was present |
|---|---|---|---|---|---|---|---|---|
| Nelson, Wellington | N | N | N | N | W | W | W | W |
| Gorse, Kānuka | G | G | K | K | G | G | K | K |
| Young, Old | Y | O | Y | O | Y | O | Y | O |
| **Native woody species** | | | | | | | | |
| *Alectryon excelsus* | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Aristotelia fruticosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Aristotelia serrata* | 3 | 3 | 2 | 2 | 0 | 1 | 1 | 1 |
| *Beilschmiedia tawa* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Brachyglottis repanda* | 1 | 2 | 1 | 6 | 3 | 6 | 6 | 6 |
| *Carpodetus serratus* | 3 | 1 | 4 | 5 | 1 | 1 | 1 | 3 |
| *Clematis forsteri* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Clematis paniculata* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| *Coprosma grandifolia* | 2 | 3 | 0 | 4 | 4 | 5 | 3 | 5 |
| *Coprosma lucida* | 3 | 2 | 0 | 3 | 4 | 1 | 2 | 3 |
| *Coprosma propinqua* | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 2 |
| *Coprosma propinqua × C. robusta* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Coprosma repens* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Coprosma rhamnoides* | 0 | 3 | 6 | 6 | 1 | 1 | 6 | 3 |
| *Coprosma robusta* | 3 | 4 | 1 | 4 | 3 | 0 | 2 | 4 |
| *Coprosma rotundifolia* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Coprosma spathulata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Cordyline australis* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cordyline banksii* | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Coriaria arborea* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Corynocarpus laevigatus* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| *Dacrycarpus dacrydioides* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dodonaea viscosa* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dysoxylum spectabile* | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 |
| *Elaeocarpus dentatus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Fuchsia excorticata* | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Gaultheria antipoda* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Geniostoma ligustrifolium* | 0 | 1 | 0 | 0 | 4 | 6 | 6 | 6 |
| *Griselinia littoralis* | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Hebe stricta* | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Hedycarya arborea* | 0 | 3 | 0 | 4 | 2 | 4 | 2 | 2 |
| *Helichrysum lanceolatum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hoheria populnea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Knightia excelsa* | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 |
| *Leptecophylla juniperina* | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 2 |
| *Leucopogon fasciculatus* | 2 | 1 | 3 | 4 | 1 | 1 | 2 | 4 |
| *Macropiper excelsum* | 0 | 0 | 0 | 0 | 1 | 5 | 3 | 2 |
| *Melicytus lanceolatus* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Melicytus ramiflorus* | 5 | 6 | 5 | 5 | 5 | 6 | 6 | 6 |
| *Metrosideros diffusa* | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 |
| *Metrosideros robusta* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Muehlenbeckia australis* | 2 | 1 | 0 | 1 | 4 | 3 | 1 | 2 |
| *Myrsine australis* | 2 | 2 | 3 | 3 | 3 | 1 | 2 | 2 |
| *Nothofagus fusca* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Nothofagus solandri* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Nothofagus truncata* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

| | Number of sites (/6) where a species was present | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Nelson, Wellington | N | N | N | N | W | W | W | W |
| Gorse, Kānuka | G | G | K | K | G | G | K | K |
| Young, Old | Y | O | Y | O | Y | O | Y | O |
| *Olearia paniculata* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Olearia rani* | 0 | 0 | 0 | 5 | 0 | 1 | 1 | 5 |
| *Parsonsia* spp. | 0 | 0 | 1 | 0 | 0 | 0 | 6 | 5 |
| *Passiflora tetrandra* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pennantia corymbosa* | 0 | 2 | 1 | 0 | 0 | 2 | 3 | 2 |
| *Pittosporum crassifolium* | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 |
| *Pittosporum eugenioides* | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 3 |
| *Pittosporum tenuifolium* | 0 | 0 | 1 | 4 | 2 | 1 | 1 | 2 |
| *Podocarpus hallii* | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 0 |
| *Prumnopitys taxifolia* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Pseudopanax arboreus* | 2 | 1 | 2 | 4 | 3 | 2 | 4 | 5 |
| *Pseudopanax crassifolius* | 0 | 2 | 0 | 1 | 0 | 1 | 4 | 4 |
| *Pseudopanax simplex* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Pseudopanax* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pseudowintera colorata* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rhopalostylis sapida* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 |
| *Ripogonum scandens* | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 5 |
| *Rubus australis* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Rubus cissoides* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Rubus* sp. (unidentified native) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Schefflera digitata* | 0 | 1 | 0 | 0 | 1 | 4 | 2 | 0 |
| *Solanum aviculare* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Streblus heterophyllus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Urtica ferox* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Weinmannia racemosa* | 0 | 0 | 2 | 5 | 1 | 0 | 1 | 4 |
| **Naturalised woody** | | | | | | | | |
| *Berberis glaucocarpa* | 2 | 3 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Chamaecytisus palmensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Clematis vitalba* | 6 | 1 | 3 | 0 | 0 | 1 | 0 | 0 |
| *Cotoneaster glaucophyllus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Crataegus monogyna* | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Erica lusitanica* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *Hedera helix* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Ilex aquifolium* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Jasminum polyanthum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Leycesteria formosa* | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Lonicera japonica* | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| *Passiflora mixta* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Prunus* sp. | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Rubus fruticosus* | 4 | 3 | 4 | 0 | 6 | 2 | 1 | 2 |
| *Senecio mikanioides* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Teline monspessulana* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| **Ferns and allies** | | | | | | | | |
| *Adiantum cunninghamii* | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 |
| *Adiantum* sp. (unidentified) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Asplenium bulbiferum* | 0 | 1 | 1 | 0 | 1 | 3 | 1 | 4 |
| *Asplenium colensoi* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Asplenium flabellifolium* | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Asplenium flaccidum* | 1 | 4 | 3 | 5 | 1 | 0 | 4 | 4 |
| *Asplenium gracillimum* | 1 | 3 | 1 | 1 | 0 | 1 | 3 | 1 |
| *Asplenium hookerianum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Asplenium oblongifolium* | 0 | 3 | 1 | 1 | 3 | 5 | 3 | 1 |
| *Asplenium polyodon* | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 2 |
| *Blechnum discolor* | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 3 |
| *Blechnum filiforme* | 0 | 0 | 1 | 1 | 1 | 2 | 3 | 2 |

| | Number of sites (/6) where a species was present | | | | | | | |
| Nelson, Wellington | N | N | N | N | W | W | W | W |
| Gorse, Kānuka | G | G | K | K | G | G | K | K |
| Young, Old | Y | O | Y | O | Y | O | Y | O |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Blechnum fluviatile* | 1 | 2 | 2 | 0 | 3 | 4 | 2 | 2 |
| *Blechnum novaezelandiae* | 1 | 0 | 0 | 1 | 1 | 0 | 3 | 2 |
| *Blechnum penna-marina* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Blechnum procerum* | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 |
| *Cyathea dealbata* | 2 | 4 | 4 | 5 | 3 | 3 | 5 | 6 |
| *Cyathea medullaris* | 0 | 0 | 0 | 0 | 2 | 2 | 1 | 1 |
| *Dicksonia squarrosa* | 1 | 2 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Diplazium australe* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Histiopteris incisa* | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 |
| *Hymenophyllum demissum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hymenophyllum scabrum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hymenophyllum* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Hypolepis rufobarbata* | 0 | 1 | 1 | 0 | 0 | 3 | 0 | 0 |
| *Leptopteris hymenophylloides* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Lindsaea linearis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Lycopodium scariosum* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| *Nephrolepis cordifolia* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Paesia scaberula* | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 2 |
| *Pellaea rotundifolia* | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Phymatosorus diversifolius* | 1 | 3 | 2 | 3 | 3 | 4 | 4 | 4 |
| *Phymatosorus scandens* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pneumatopteris pennigera* | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 2 |
| *Polystichum richardii* | 1 | 2 | 1 | 1 | 0 | 4 | 4 | 2 |
| *Polystichum vestitum* | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 |
| *Pteris* aff. *macilenta* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pteridium esculentum* | 6 | 6 | 6 | 4 | 6 | 3 | 2 | 4 |
| *Pyrrosia eleagnifolia* | 0 | 2 | 2 | 1 | 1 | 0 | 0 | 0 |
| *Selaginella kraussiana* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Tmesipteris tannensis* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Native herbs** | | | | | | | | |
| *Carex* spp. | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Dianella* spp. | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 |
| *Earina* spp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Gahnia procera* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Gahnia* spp. | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *Libertia* spp. | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Microlaena avenacea* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Pterostylis banksii* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| *Uncinia* spp. | 2 | 1 | 3 | 4 | 0 | 1 | 4 | 6 |
| **Naturalised herbs** | | | | | | | | |
| *\*Hypericum androsaemum* | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *\*Phytolacca octandra* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *\*Tradescantia fluminensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |