

Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand

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Abstract: Fire has been a major driver of forest loss in New Zealand. A conceptual model has been proposed in which positive feedbacks between vegetation, fire and soils can arrest regeneration of recurrently burned wet forest landscapes. We used vegetation data collected across three topographically similar landscapes – Awana, Glenfern and Windy Hill – on Great Barrier Island to (1) describe current vegetation composition and structure and predict future change in composition and (2) assess evidence for interactions between fire and soils slowing regeneration in these landscapes. Compositional data were analysed via classification and ordination, and we used transition matrix models to explore how vegetation composition may change in the future. The vegetation in the three landscapes spans repeatedly burned scrubland dominated by mānuka (*Leptospermum scoparium*) and exotic fire-dependent woody species such as *Hakea sericea*, to intact mature forest. Scrubland vegetation tends to be found on north-facing upper slopes and ridges – drier sites where fire has been more frequent and rendered soil conditions (e.g. organic matter and moisture) poor for plant growth. There is a slow reinvasion of forest species into the *Leptospermum* and *Kunzea* scrubland from gullies and other remnant patches, with wind-dispersed species preceding fleshy-fruited bird-dispersed ones. In the absence of fire in the next few decades the landscapes will continue to move back towards forest. More fires, however, will further degrade these landscapes by removing remaining fertile topsoils from ridges and slopes and by favouring exotic species adapted to recruit from seed and/or resprout vegetatively after fire.

Keywords: disturbance history; fire; multivariate analysis; transition matrix model; vegetation dynamics

Introduction

The nature of post-fire regeneration has been described a number of times for New Zealand forests (e.g. Druce 1957; Esler & Astridge 1974; Payton et al. 1984; Bray et al. 1999; Atkinson 2004). Secondary regrowth after fire, such as *Leptospermum scoparium*¹ (mānuka) and *Kunzea ericoides* (kānuka) scrubland, is susceptible to repeated burning (Druce 1957; Esler & Astridge 1974), and the persistence of mānuka, in particular, is favoured by recurrent fire (Esler 1983). On recurrently burned sites in northern forests, ‘hard site’ species such as *Olearia furfuracea* (akepiro) and exotic woody species (e.g. *Hakea sericea*) may dominate alongside mānuka (Esler & Astridge 1974; Esler 1983). In the absence of fire, kānuka will replace mānuka before in turn being replaced by a range of conifer (e.g. *Agathis australis* – kauri, and *Dacrydium cupressinum* – rimu) and hardwood (e.g. *Coprosma arborea* – māmāngi, *Knightia excelsa* – rewarewa, *Beilschmiedia tawa* – tawa, and *B. tarairi* – taraire) species. Based on regeneration sequences on northern offshore islands, Atkinson (2004) argues that kānuka will usually be overtopped within 100 years, but successional patterns will be spatially heterogeneous, with regeneration quicker, and mānuka and kānuka possibly less significant, in gullies than on slopes and ridges (Esler & Astridge 1974).

The rate of post-fire secondary succession is controlled by a combination of abiotic conditions, propagule availability and patterns of disturbance in time and space (Standish et al. 2009). Repeated fire tends to result in negative effects on soils (e.g. loss of organic matter; McIntosh et al. 2005) and an increase in mānuka and kānuka and (in northern New Zealand) exotic woody species, including *Erica lusitanica* (Spanish heath) and *Hakea sericea* (Druce 1957; Enright 1989; Williams 1992b), which are adapted both to fire and to low-nutrient soils. Conversely, if fire does not return, soil conditions may slowly recover; for example, McQueen (1991) describes increases in soil organic matter along a post-fire chronosequence. Thus, there is a positive feedback between disturbance by fire, soil deterioration

and the presence of a suite of species adapted to these conditions and that tend to promote fire (Druce 1957; McIntosh et al. 2005; Standish et al. 2009). Under such conditions secondary successions are likely to be very slow, if not halted altogether (i.e. inhibition *sensu* Connell & Slatyer 1977).

Most New Zealand forest tree species are either wind or bird dispersed with wind-dispersed species tending to colonise disturbed sites before bird-dispersed species, and with smaller-seeded bird-dispersed species appearing before larger-seeded ones (Bray et al. 1999; Atkinson 2004). Thus, the rate of succession will be influenced by the distance to seed sources, in the case of wind-dispersed species, and by the availability of bird dispersers, such as tūi (*Prosthemadera novaeseelandiae*) and kererū (*Hemiphaga novaeseelandiae*). Conversely, soil seed banks are generally unimportant in New Zealand forest ecosystems with woody forest species notably absent (Sem & Enright 1995, 1996; Standish et al. 2009).

Although post-fire regeneration has been described before in northern New Zealand, quantitative studies on the scale we present are less common. For example, Esler’s (Esler & Astridge 1974; Esler 1983) interpretation of regeneration via *Leptospermum* communities in the Waitakere Ranges (west Auckland) was based on profile drawings from subjectively selected sites; remeasurement plots have been established in regenerating kānuka forest on Little Barrier Island but are small (often less than 10 × 10 m) and the data difficult to interpret (Smale 1993). Here we present a comprehensive landscape-level, quantitative consideration of the dynamics of fire-induced scrubland. Great Barrier Island is currently more than 50% scrubland (Land Cover Database 2) and has been subjected to anthropogenic disturbances in parallel with those on the mainland (Armitage 2001) making it particularly suitable for this purpose. Using vegetation data collected from three landscapes on the island, the aims of this research were to:

- Quantitatively describe (1) the structure and composition of the vegetation in landscapes undergoing succession on Great

¹ Nomenclature follows the Landcare Research online database Ngā Tipu Aotearoa – New Zealand Plants (<http://nzflora.landcareresearch.co.nz/>).

Barrier Island and (2) how the spatial pattern of vegetation in these landscapes may relate to disturbance histories and/or biophysical controls

- Explore, using transition matrix models, trajectories of change in two of these landscapes
- Relate the patterns and dynamics that we describe to models that describe how vegetation and soils respond to disturbance by fire.

Methods

Study site

Great Barrier Island, on the outer edge of the Hauraki Gulf in the North Island (Fig. 1), is the largest of New Zealand’s offshore islands, being approximately 40 km long by 20 km wide. Mountains of volcanic origin run down the centre of the island, with the highest point, Hiramata (Mt Hobson), at 627 m a.s.l. The west coast drops steeply into the sea, while the east coast comprises a series of infilled marine embayments and wetlands (Moore 2001). Fire frequency has risen dramatically since settlement of the island. Māori burned extensive areas of Great Barrier Island c. 750–650 years ago (AD 1250–1350) with associated loss of forest and increases in sediment flux from hillslopes to estuaries and lowland wetlands (Horrocks et al. 2001; Ogden et al. 2006). Subsequently, fire remained frequent, but was probably less extensive and was associated with bracken (*Pteridium esculentum*) cultivation (Ogden et al. 2006). In the period of European settlement fire was used for landscape clearance (AD 1840–1940), but since World War II many previously cleared areas have been abandoned to revert to mānuka and kānuka scrubland. Dramatic declines in the abundance of keystone bird dispersers (Clout & Hay 1989) such as kererū would have accompanied this loss of forest, with flow-on effects to the fleshy-fruited tree species they disperse (Campbell & Atkinson 2002). Surprisingly little has been published on the vegetation ecology of Great Barrier Island, except for some government agency internal reports (e.g. Eadie & Broome 1990) and popular accounts (e.g. Ogden 2001).

Data describing vegetation composition and structure were collected across three landscapes on Great Barrier Island over the period 2005–2008. The Awana study area (Fig. 1) was cleared for farming early in the 20th century, and burned ‘every year’ until the 1940s, when it was covered in ‘Danthonia grass’ (A. Gray, son of original landowner, pers. comm.). It comprises c. 30 ha covering three roughly parallel ridges with intervening gullies running north-west at elevations between 30 and 100 m a.s.l. The area now carries mānuka–kānuka scrubland, with exotic woody weeds such as *Pinus* spp. on the ridges and a few broadleaved native shrubs in the gullies.

Glenfern Sanctuary, on the Kotuku Peninsula (Fig. 1), encompasses c. 150 ha and was established as a restoration area, including intensive predator control, in the late 1990s. Much of Glenfern Sanctuary was cleared for agriculture in the European settlement period, but since the 1950s it has begun to revert to forest. Vegetation at Glenfern ranges from mānuka scrubland with exotic woody species such as *Hakea sericea* on drier north-facing slopes to small patches of remnant forest in some gullies. *Agathis australis* pole stands (rickers) are common on ridges.

Windy Hill, on the southern part of the island (Fig. 1), is also the site of a significant community-based restoration project (established in 2000). The project involves restoration over an area of some 750 ha with intensive predator control over around 300 ha (Ogden & Gilbert 2009). The Windy Hill landscape was also partially cleared in the past but has been allowed to revert back to forest. Vegetation at Windy Hill includes areas of mānuka and kānuka scrubland, gully forest, and *Meterosideros excelsa* (pohutukawa) forest on cliffs.

At both Glenfern and Windy Hill, areas currently in tall kānuka scrubland were cleared by fire during the first few decades of the 20th century. Some areas were reburned at various times since then, although this mostly stopped c. 1940 at Windy Hill and 1965 at Glenfern. Thus, much of all three scrub-covered landscapes can be regarded as relatively young scrubland and forest, with remnant patches of older mature forest. The former presence of this forest over the whole of all areas is indicated by the occasional large tree or stump, and by soil charcoal.

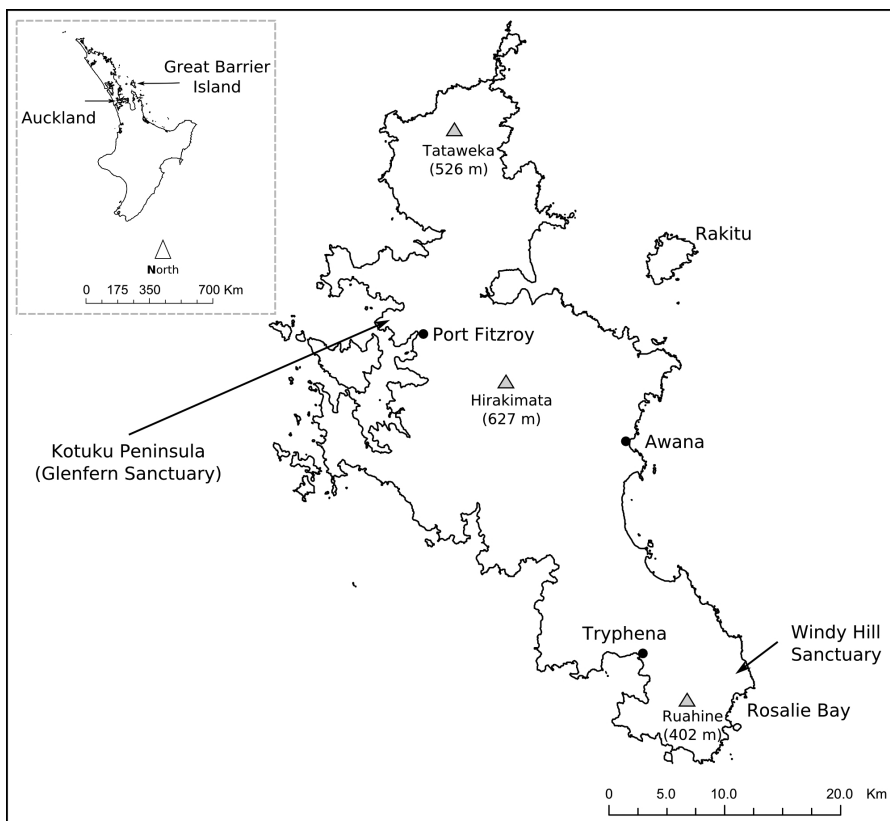


Figure 1. Map showing location of Great Barrier Island (Aotea) in relation to the North Island of New Zealand and the three study sites (Awana, Glenfern Sanctuary and Windy Hill Sanctuary).

Data collection

We collected vegetation data at three sites: Awana, Glenfern and Windy Hill. The vegetation at Glenfern and Windy Hill encompasses scrubland and forest, while that at Awana is entirely scrubland. Thus, we used different sampling methods at Awana than at Glenfern and Windy Hill.

Awana

A transect (100 × 20 m) was located along each of two parallel adjacent ridges in abandoned farmland ($n = 2$). Six further transects were located systematically in relation to these ridge transects: mid-slope on the northern and southern sides of each ridge ($n = 4$) and along the small, ephemeral streams draining the valleys on the northern side of each ridge ($n = 2$). Ten quadrats (5 × 5 m) were located along each transect using a stratified random procedure such that quadrats were located in randomly chosen quarters of cells (10 × 10 m) alternately to the left and right of the transect centre line. In this way, a total of 80 quadrats were enumerated over eight transects. Cover for each plant species was estimated using the Braun-Blanquet cover-abundance score. The average and maximum height of the woody species canopy within the quadrat was measured, and the overall percentages of vegetation cover and bare ground were estimated visually.

A soil sample was collected from each plot ($n = 80$) by scraping off loose litter and digging a hole (c. 10 cm) in each of four quarters of the 10 × 10 m cell. A trowel full of soil was collected from each hole and these were mixed on a sheet of polythene and resampled. This composite sample (mean: 147 g) was placed in a sealed zip-lock bag to retain moisture; all sampling was done over a rainless period. Subsequently the sample was weighed and dried at 100°C for 24 h to determine percentage soil moisture. Weighed subsamples of the dry soil were then mixed with distilled water for pH determination using a standard electrode, or subjected to heating in a furnace at 550°C for 4 h, cooled and reweighed to estimate percentage loss on ignition (LOI) as a measure of soil carbon.

Windy Hill and Glenfern

We used a modified point-centred quarter (PCQ) method (Bryant et al. 2004) to assess vegetation composition and structure across the landscape. While the PCQ method has been criticised, White et al. (2008) suggest that angle-ordered methods, of which PCQ is an example, are robust to departures from their assumptions. A series of transects cross the Glenfern Sanctuary, following a constant bearing and upon which rodent bait-stations are placed at 50-m intervals. We centred PCQ points on pre-existing, mapped bait-stations. At Windy Hill, PCQ points were also 50 m apart, centred on pre-existing mapped stations established for bird surveys.

Conventional PCQ methods randomly locate a centre point and divide the area around that point into quarters. In each quarter, the distance from the point to the nearest woody individual with diameter at breast height (dbh) > 5 cm, including standing dead individuals, was recorded, as was the individual's size (dbh) and identity. This individual was the 'focal tree' for that quarter. The distance measurement provides an estimate of density. In addition to the 'focal tree' in each quarter, we also recorded the identity (only) of the next nearest woody individual with dbh > 5 cm. This modification doubles the sample size for species composition with little added effort. Where individuals had multiple stems with dbh > 5 cm we measured all such stems. If, in a given quarter, a tree fern was closer to the centre point than the focal individual was, then that tree fern's identity, height and distance to the centre point were also recorded. At each point the 'replacement' species (i.e. the species of the individual interpreted as most likely to capture the available canopy space upon death of the current occupant) was recorded for the focal tree in each quarter and any tree ferns measured. The replacement species was assessed subjectively following the methods described in Perry & Enright (2007). Finally, any vascular ground flora within a circle centred on the focal point and with a radius of 3 m were recorded. At each PCQ point we also recorded slope (°), aspect (°), canopy height (m) and landscape position (1–5: 1 = top of slope to 5 = gully).

Stem ages

Basal and sequential (50-cm or 100-cm height intervals) stem cross-sections were cut from 23 kākūka and 21 mānuka stems from Awana (but outside of measured quadrats) on the ridges and gullies for estimation of plant ages, and examination of the plant age-height relationship. Two cores were taken from large *Agathis australis* at Glenfern. Stem sections and cores were dried at room temperature, mounted, and sanded using coarse to fine grades of sandpaper, and rings counted under magnification using a binocular microscope (Olympus SZ61). At Glenfern, rings on cut kākūka stumps were counted in the field.

Quantitative analysis

Vegetation analysis

We used classification to identify discrete vegetation assemblages, and ordination to assess how well defined these assemblages are in the landscape. Similarities between sites were calculated using the Bray–Curtis dissimilarity measure (Faith et al. 1987). The data matrices for Glenfern and Windy Hill were weighted by giving the two individuals nearest to the centre point and any tree ferns present in each quarter a value of two; all other species were given a value of one. Thus we gave more emphasis to larger individuals (i.e. dbh > 5 cm) than to the understorey and forest floor tiers. To compare the three sites alongside each other we used unweighted presence/absence data only.

We used hierarchical cluster analysis to aggregate the sites into discrete groups ('units'), using averaged linkages (Quinn & Keough 2002). At all three sites we used a similar 'community level' cut-off point of between 0.7 and 0.8 Bray–Curtis dissimilarity. This threshold provided broadly interpretable groupings compatible with the small size of the individual samples and the overall continuity visible in the ordinations. We used non-metric multidimensional scaling (nMDS) to ordinate and graphically represent the data (Clarke 1993; Quinn & Keough 2002). All nMDS plots were centred and rotated so that variance was maximised on Axis 1, with axes scaled to half-change units. We used a test of multivariate homogeneity of group dispersions (Anderson 2006) to evaluate differences in the compositional variability of the different vegetation units; permutation was used to evaluate pairwise differences in unit means. To identify those species most responsible for any observed clustering in the data we used SIMPER ('similarity percentage') analysis (Clarke & Warwick 2001). SIMPER quantifies (1) the contribution of each species to the average dissimilarity between groups of samples and (2) the contribution to similarity within a single group. For each vegetation unit identified in the classifications for Windy Hill and Glenfern median basal area (m² ha⁻¹), stem density (stems ha⁻¹) and canopy height (m) were calculated and percentile limits estimated on the basis of 1000 bootstrap samples of 25% of the PCQ points in each unit. All analyses were conducted using R-2.8.0 and the vegan library (R Development Core Team 2009), except for the SIMPER analyses, which were performed in PRIMER 5.

Transition matrix projections

To explore the trajectories of change at Glenfern and at Windy Hill we used a transition matrix model similar to that described by Horn (1975), and used by Ogden (1983) to describe change in forest composition elsewhere in northern New Zealand. At each PCQ point we recorded the identity of a focal species and a replacement species, as well as tree ferns and their replacement if present. These data were used to construct a transition matrix, **A**, which describes the probability of species *i* being replaced by species *j* on its death. We constructed an initial-state-composition (ISC) vector (x_t), which describes the current relative abundance of each species in the landscape, using the abundances of the focal and next nearest individuals. We considered only those species observed in at least 25 transitions; other species were lumped into aggregate categories based on their life-form (shrub, conifer tree, hardwood tree, tree fern). Repeatedly multiplying the matrix **A** by the state vector x_t yields a projection of the abundance of each species in the future (Enright &

Ogden 1979); x_t will eventually stabilise giving an idea of the steady-state composition of the community and the number of generations it will take to achieve this. We projected the transition matrix for each site until a steady-state composition was reached, and examined the predicted change in abundance for each species. The abundances are weighted by species relative longevities as described by Ogden (1983); complete transition matrices, ISCs and species longevities are given in Appendix 1.

Although some of the species we recorded are capable of vegetative resprouting following disturbance we do not consider this. We did not have sufficient data to distinguish between the different successional pathways that may occur under different edaphic conditions (e.g. ridges vs gullies) although it is likely that such differences occur. Despite the assumptions the method carries with it (in particular, that transition rates are constant in time and space; Perry & Enright 2007), such transition matrix projections provide a general picture of the trajectory of change in the composition of the vegetation into the future.

Results

Classification and ordination

In total we collected compositional data for 69 species across 80 samples at Awana, 118 species across 133 samples at Glenfern, and 135 species across 120 samples at Windy Hill, yielding a combined (pooled) matrix of 188 species across 333 samples.

Awana

Classification of the vegetation at Awana (Fig. 2) suggests three clearly defined units: (1) sparse scrubland dominated by mānuka, *Leucopogon fasciculatus* (mingimingi), *Hakea sericea*, and *Erica bacans*, (2) denser scrubland dominated by mānuka, *Olearia furfuracea* (akepiro), and *L. fasciculatus* with *Lepidosperma laterale* and *Schoenus tendo* also present, and (3) regenerating valley forest with kānuka, *Cyathea dealbata* and *C. medullaris* above an understorey including *Geniostoma rupestre* var. *ligustrifolium* (hangehange), *Brachyglottis*

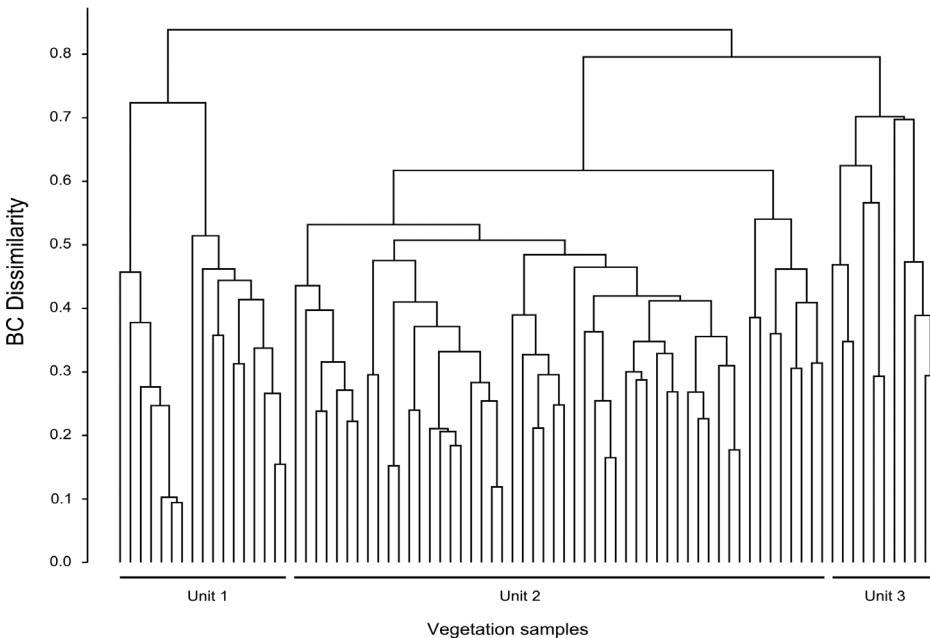


Figure 2. Hierarchical classification of sites at Awana; the classification suggests there are three distinct vegetation units.

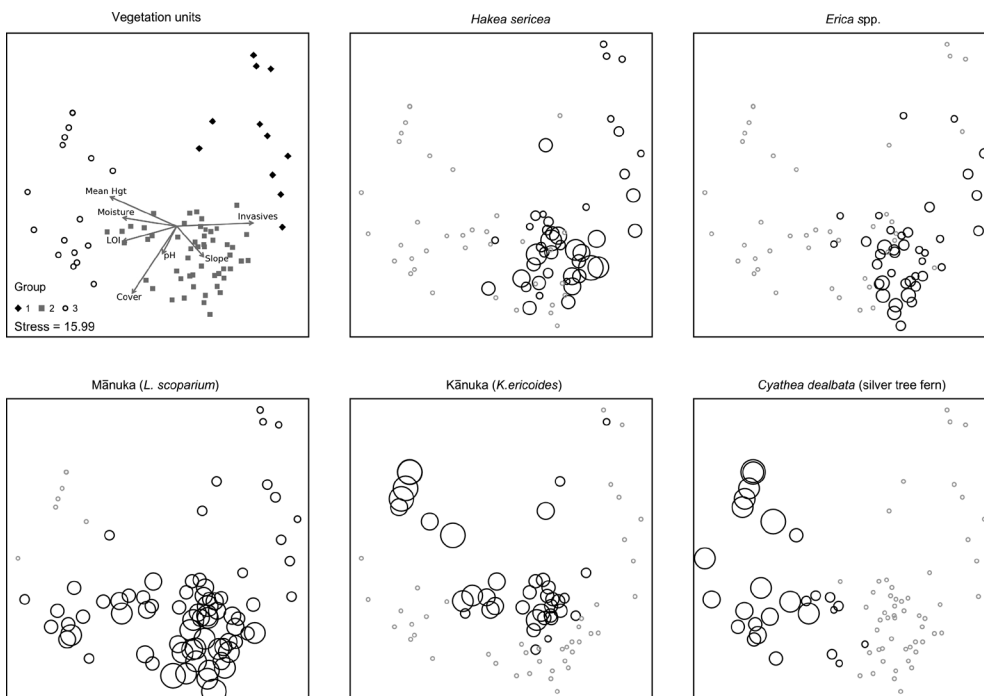


Figure 3. nMDS ordinations for Awana. In the plots highlighting the occurrence of individual species, the size of the circles is proportional to the species' weighted score; *Erica* spp. includes *E. baccans* and *E. lusitanica*. Greyed circles indicate samples where species was absent. Arrows indicate vector fits for environmental variables with correlation significant ($P < 0.05$); length of arrow indicates strength of correlation. Stress for the ordination plot in two dimensions is 15.99.

repanda (rangiora) and *Blechnum novae-zelandiae*. Units 1 and 2 are compositionally similar, but summed cover (i.e. Braun-Blanquet scores summed over all species present) is on average three times greater in Unit 2 than in Unit 1.

The nMDS ordination for the Awana site (Fig. 3) shows a clear separation of the vegetation units. Few sites fall between vegetation units, suggesting that the units are compositionally distinct. The distribution of species in ordination space (Fig. 3) shows exotic woody species (e.g. *Erica* spp. and *Hakea sericea*), along with mānuka and kānuka, associated with sparse scrubland (Unit 1); these exotic woody species are less common in Unit 2 and are absent from Unit 3. Mānuka is common across the two scrub units (1 and 2). Kānuka has highest cover in Unit 3 and *Cyathea dealbata* (silver tree fern) is also found in this unit. Compositional variability is lower in Unit 2 than in Units 1 and 3 ($P = 0.015$ and $P = 0.037$, respectively). Environmental vector fits superimposed on the nMDS plot show soil organic matter (LOI), soil moisture, vegetation cover and vegetation height increasing significantly from Units 1 to 2 and 3 along Axis 1; conversely, the proportion of invasive species increases towards Unit 1 (Fig. 3).

Glenfern

Hierarchical classification suggests that there are four vegetation assemblages at Glenfern Sanctuary (Fig. 4): (1) mānuka-dominated scrubland, (2) kānuka-dominated scrubland, including small shrub/tree species such as *Myrsine australis* (māpau) and *Geniostoma rupestre* var. *ligustrifolium*, and the tree fern *Cyathea dealbata*, (3) older forest with a mixture of tree species including *Agathis australis*, old kānuka, *Knightia excelsa*, *Nestegis lanceolata* (maire) and *Pseudopanax arboreus*, with *C. dealbata* also present, and (4) mature 'gully' forest with dominant species including *Dysoxylum spectabile* (kohekohe), *Vitex lucens* (pūriri), *Beilschmiedia tarairi*, *B. tawa*, and the tree-ferns (*C. dealbata* and *C. medullaris*).

The nMDS ordination for the Glenfern site (Fig. 5) shows discernible clusters in the ordination space; these units do, however, intergrade, with some sites falling between units. Figure 5 also illustrates the distributions of some significant species across the ordination space: mānuka and kānuka were chosen to represent their dominance in the scrubland stages, associated with Units 1 and 2. *Agathis australis* is a potential canopy dominant, associated with Unit 2, and *Dysoxylum spectabile* is the characteristic broadleaved canopy

tree in gullies (Unit 4). *Cyathea dealbata* is the most widespread understorey plant, occurring in all forest types, but predominating in Unit 4. Compositional variability is significantly lower in Units 1 and 2 than in Units 3 and 4 ($P << 0.01$; permutation-based test of multivariate dispersion).

Windy Hill

Classification (not shown) of the vegetation at the Windy Hill site suggests two poorly defined groups. On the corresponding nMDS plot these groups intergrade (Fig. 6), but, based on the SIMPER analyses, are separated on the basis of the abundance of kānuka, *Beilschmiedia tawa*, *Rhopalostylis sapida* (nikau) and *B. tarairi*. The two units are not significantly differently dispersed. *Coprosma arborea* is abundant across Windy Hill and bridges the two vegetation units. The successional trend is clearly demonstrated (diagonally from top left to bottom right) in the ordination: mānuka is replaced by kānuka, then by *Coprosma arborea*, and finally by the broadleaved forest species – represented here by *Beilschmiedia tarairi* (Fig. 6). As at Glenfern, the tree fern *Cyathea dealbata* is found throughout.

Vegetation structure, composition and context

Awana

The three units identified at Awana differ in their vegetation structure and soils (Fig. 7). There are significant differences in cover ($F_{2,77} = 53.28$, $P << 0.01$), mean height ($F_{2,77} = 28.96$, $P << 0.01$) and proportion of invasive species ($F_{2,77} = 52.12$, $P << 0.01$) between the three units. Cover and mean height are lowest in Unit 1 ($23.5 \pm 34.9\%$ and 0.91 ± 1.02 m, respectively) and highest in Unit 3 ($100.0 \pm 0.0\%$ and 4.92 ± 2.28 m, respectively), and the average proportion of invasive species per sample declines from Unit 1 (0.25 ± 0.09) to Unit 3 (0.0 ± 0.0). Mean species richness peaks in Unit 2 (13.3 ± 2.3 species), and is lowest in Unit 1 (8.7 ± 1.6 species). Of the dominant woody exotics, *Hakea sericea* is found at 90%, 65% and 0% and *Erica baccans* at 45%, 34% and 0% of Unit 1, 2 and 3 sites, respectively.

Kānuka can achieve heights of at least 16 m while mānuka rarely exceeds 10 m. Sequential stem cross-sections for mānuka and kānuka from ridge and gully sites reveal a strong difference in growth rate on ridges vs lower slopes and gullies that is consistent across the two species. Based on regressions, mānuka height growth rates on ridges and lower slopes are 5.3 ± 0.6 (mean ± 1 SE; $n = 29$) and

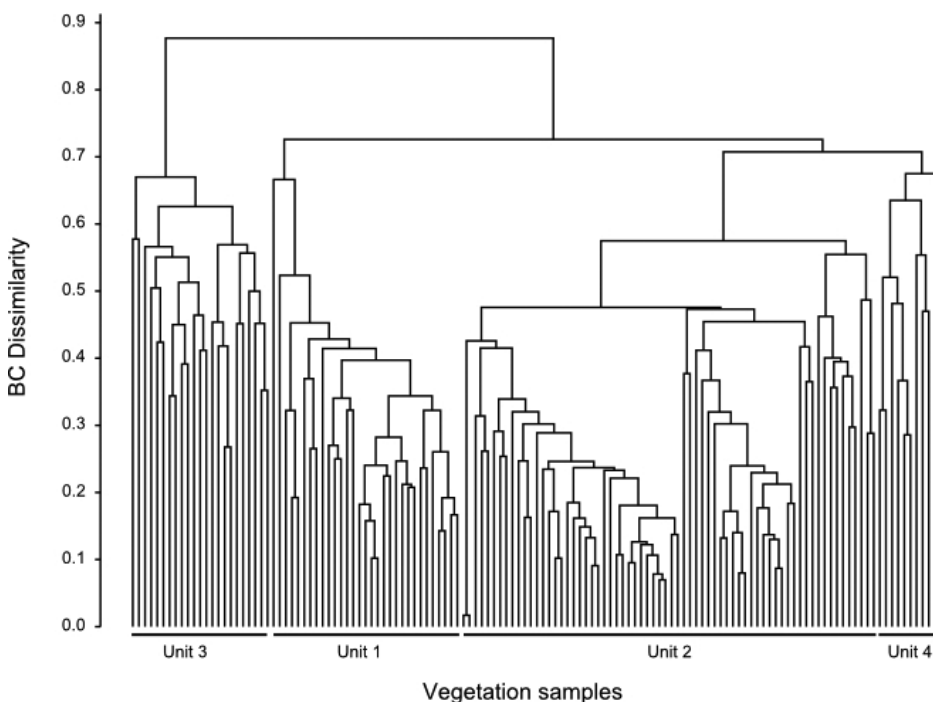


Figure 4. Hierarchical classification of sites at Glenfern Sanctuary; the classification suggests there are four distinct vegetation units.

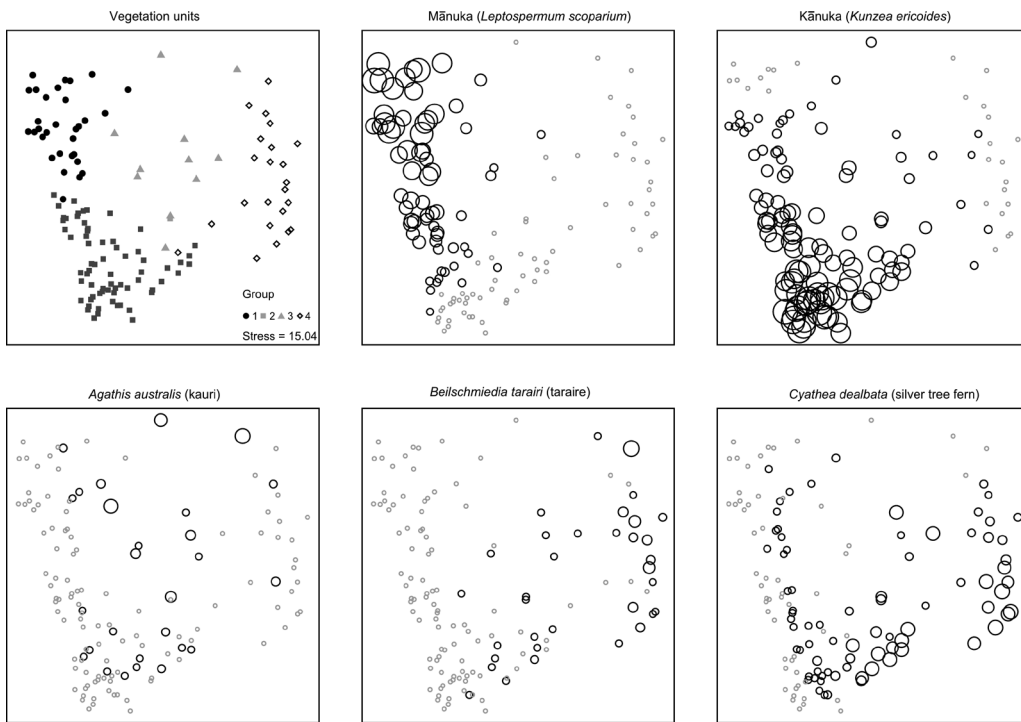
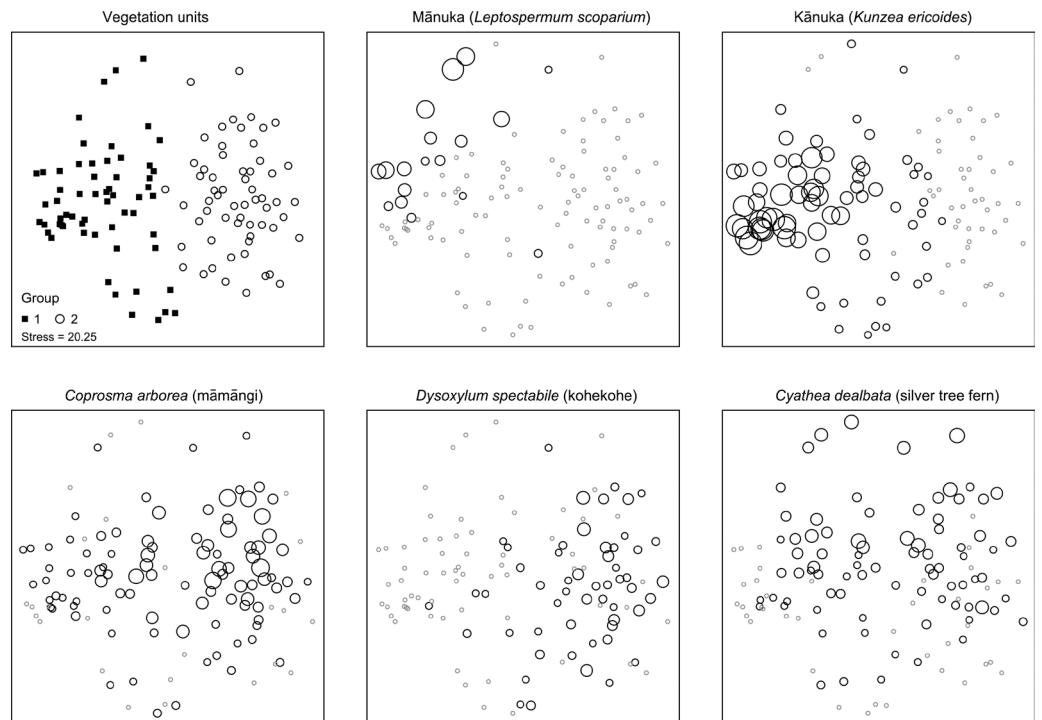


Figure 5. nMDS ordinations for the Glenfern site. In the plots highlighting the occurrence of individual species, the size of the circles is proportional to the species weighted score. Greyed circles indicate samples where the species was absent. Stress for the ordination plot in two dimensions is 15.04.

Figure 6. nMDS ordinations for the Windy Hill site. In the plots highlighting the occurrence of individual species, the size of the circles is proportional to the species weighted score. Greyed circles indicate samples where the species was absent. Stress for the ordination plot in two dimensions is 20.25.



26.0 ± 1.2 (n = 88) cm yr⁻¹, respectively, and for kānuka are 8.9 ± 0.6 (n = 53) and 26.3 ± 1.0 (n = 44) cm yr⁻¹, respectively. Mānuka and kānuka height growth rates are not statistically different on lower slopes, but kānuka grows significantly faster than mānuka on ridges (F = 19.11, P << 0.001).

Near-surface soil organic matter (LOI), pH and moisture vary significantly between the units (F_{2,77} = 19.48, 11.58 and 8.08, Units 1, 2 and 3 respectively; P << 0.001 for all), with organic matter content and moisture increasing from Unit 1 to Unit 3 and pH lower in Unit 1 than in Units 2 and 3 (Fig. 7). Most of the composite (<10 cm) samples represented A-horizon soils, but some from Unit 1 included soil from exposed B or C horizons.

Glenfern

There are clear structural differences in the four vegetation units identified at Glenfern, with stem density decreasing and basal area and canopy height increasing from Unit 1 to Unit 4 (Fig. 8a). Basal areas range from 20 to 60 m² ha⁻¹; stem densities fall from 2400 stems ha⁻¹ in Unit 1 to 700 stems ha⁻¹ in Unit 4. Mean species richness increases from 10.5 ± 3.1 in Unit 1 to 15.2 ± 3.6 species in Unit 4. Mānuka is the canopy dominant at 71% of Unit 1 points, with mean (± SE) dbh of 6.6 ± 0.3 cm, while kānuka is dominant in Unit 2 (dominant at 77% of Unit 2 sites, with mean dbh of 13.8 ± 0.6 cm). Based on kānuka ring counts Unit 1 is less than 30 years old and Units 2 and 3 are 30–40 and 40–60 years old, respectively. Ring

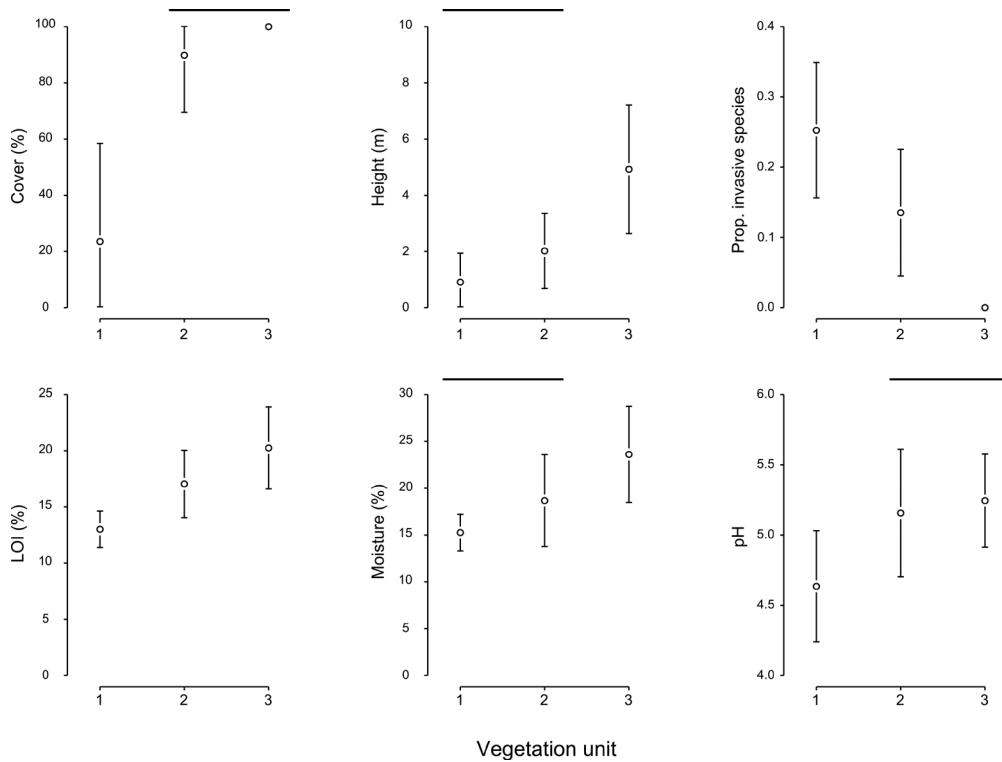
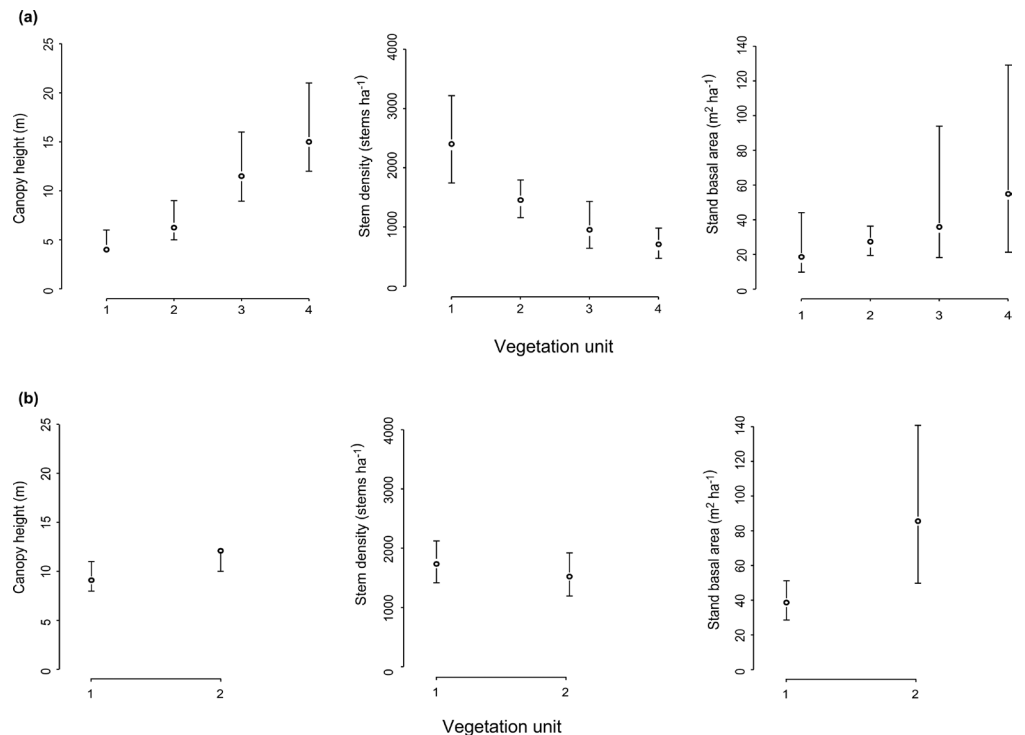


Figure 7. Vegetation structure and soil conditions for the three vegetation units identified at Awana; values are means \pm 1SD; horizontal line denotes pairs of means that are not significantly different (Tukey’s HSD; $p > 0.01$).

Figure 8. Stand structure characteristics for the four vegetation units identified at Glenfern (a) and the two vegetation units identified at Windy Hill (b). Values are bootstrapped medians with 95% percentile limits (based on 1000 samples, with replacement, of 25% of PCQ points for each unit).



counts on cut stumps indicate that individual kānuka up to 12 m tall and 35 cm dbh are c. 100 years old. Mānuka is absent from Units 3 and 4, and kānuka is present in these units only as scattered large and senescing individuals (27% of Unit 3 samples with mean dbh 19.8 ± 2.3 cm and 3% of Unit 4 samples with mean dbh 23.2 ± 6.9 cm). *Agathis australis* is co-dominant with kānuka in Unit 3 sites (23% as canopy dominant with mean dbh 22.6 ± 4.0 cm); *A. australis* and kānuka frequently co-occur in regenerating kauri pole stands. The larger kauri pole stands at Glenfern may date from much earlier fires associated with Māori activity. Increment cores extracted from the largest *Agathis australis* at Glenfern (129 cm in diameter) yielded an establishment date of 1771, pre-dating European arrival. In Unit

4 the dominant canopy species are *Dysoxylum spectabile* (canopy dominant at 32.6% of sites; mean dbh = 19.9 ± 4.5 cm), *Beilschmiedia tawa* (21%; 29.3 ± 5.2 cm) and *B. tarairi* (12%; 17.6 ± 2.1 cm). Some individuals of a size much larger than these means occur in Unit 4 including an *Agathis australis* with dbh of 88 cm and a *Vitex lucens* with dbh of 168 cm.

There are differences between the topographic units ($G = 46.21$, d.f. = 12, $P \ll 0.01$ using Williams correction) and aspects ($G = 20.19$, d.f. = 9, $P = 0.016$ using Williams correction) that the vegetation units occupy in the landscape (Fig. 9a). Mānuka-dominated scrubland (Unit 1) tends to occur on steeper, north-facing (dry) ridges and upper slopes, whereas Vegetation Unit 4, which is dominated by forest tree species

such as *Dysoxylum spectabile* and *Vitex lucens*, is restricted to wetter parts of the landscape (e.g. gullies and south-facing slopes).

Windy Hill

The two vegetation units identified at Windy Hill differ in their structure, but not as clearly as the four units that were identified at Glenfern. Unit 1 contains more kānuka and less *Beilschmiedia tawa*, *Rhopalostylis sapida* and *B. tarairi* than Unit 2, suggesting that it is younger; *Coprosma arborea* is found across both units. Stem density decreases and canopy cover increases from Units 1 to 2, and canopy height increases; the largest change is in basal area, which increases from around 40 m² ha⁻¹ in Unit 1 to 90 m² ha⁻¹ in Unit 2 (Fig. 8b). Mean species richness in the two units is very similar (17.4 ± 5.1 vs 18.1 ± 4.3 species in Units 1 and 2, respectively). Species richness (per 10 m²) was 6.3 ± 1.7 at Windy Hill, which is higher than at either Awana (4.9 ± 1.2) or Glenfern (4.2 ± 1.6). Mānuka and kānuka are most frequent in Unit 1 (occurring as a canopy dominant at 13% and 55% of Unit 1 sites, respectively, with mean (±SE) dbh of 10.2 ± 1.1 cm and 14.9 ± 0.7 cm, respectively). Mānuka is uncommon in Unit 2 (one canopy-dominant individual of dbh 36 cm), and kānuka appears as scattered large individuals (canopy dominant at just 3% of Unit 2 samples, with mean dbh 30.2 ± 3.4 cm). Unit 2 is dominated by *Coprosma arborea* (canopy dominant at 25% of sites; mean dbh = 19.3 ± 0.8 cm), *Beilschmiedia tarairi* (19% of sites; mean dbh = 20.2 ± 1.8 cm) and *Rhopalostylis sapida* (15% of sites; no dbh, as a monocot); as at Glenfern, there are some much larger individuals scattered across the Windy Hill landscape (the largest individual measured was a *Vitex lucens* with dbh of 153 cm).

While the relationships between vegetation composition and slope, aspect, and topographic position are not as clear at Windy Hill as they are at Awana or Glenfern (Fig. 9), there are significant differences in the topography and aspects of the two units. More Unit 1 samples occurred on upper slopes than did Unit 2 samples ($G = 20.66$, d.f. = 4, $P < 0.01$ using Williams correction). There is a weak trend for Unit 1 samples to occur on south- and west-facing slopes whereas Unit 2 samples tended to occur on north- and east-facing ones ($G = 7.93$, d.f. = 3, $P = 0.048$ using Williams correction). There were no statistical differences in the steepness of slope between the two classes.

Transition matrix projections

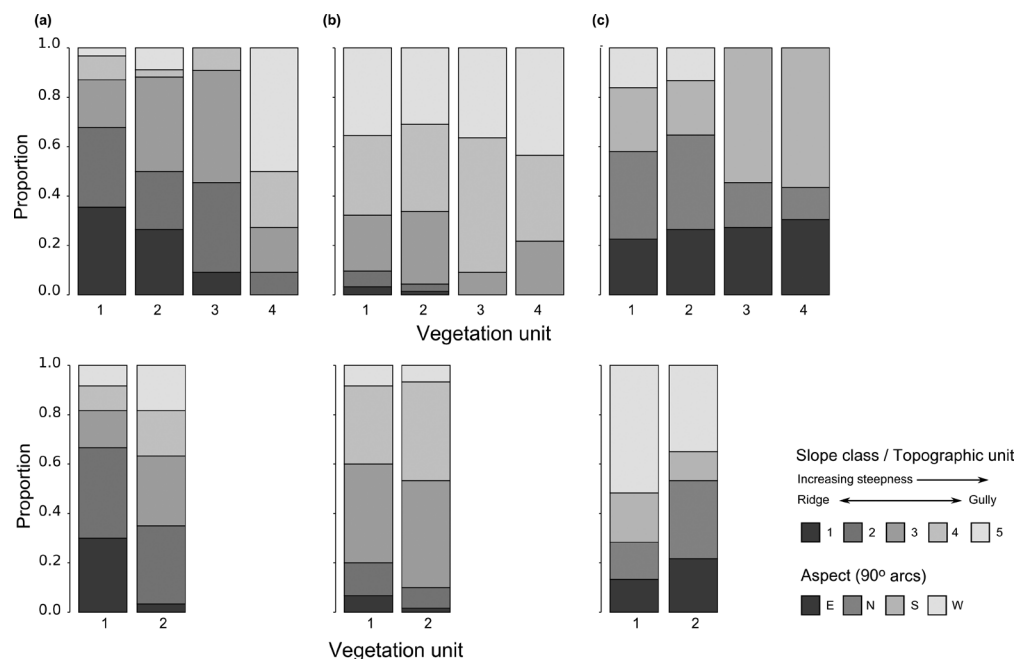
Despite current differences in composition between Glenfern and Windy Hill, and ignoring the possibility that succession may proceed

differently under different edaphic conditions (e.g. ridges vs gullies), the projection matrices suggest they will converge in the absence of disturbance such as fire or clearing (Fig. 10). The Glenfern projection stabilises (i.e. reaches a steady-state composition that does not change after further projection) after 9–10 generations and the Windy Hill projection after 5–6 generations. At both Glenfern and Windy Hill the stable final composition includes more broadleaved (in particular, *Beilschmiedia tawa*, *B. tarairi* and *Dysoxylum spectabile*) and conifer tree species, with commensurate declines in mānuka and kānuka and other shrub species, including the exotic *Hakea sericea* at Glenfern. Although the final composition at both sites is similar, there are some subtle differences: *B. tarairi* dominates at both sites, but *B. tawa* and tree ferns are predicted to be more dominant at Glenfern than Windy Hill, with *Rhopalostylis sapida* more important at Windy Hill than at Glenfern.

Discussion

Despite being compositionally distinct (PERMANOVA; $F_{2,330} = 54.11$, $P < 0.001$), the three sites represent a continuum from highly degraded (Awana) to more intact (Windy Hill) vegetation (Fig. 11a). The vegetation units identified at Awana, Glenfern and Windy Hill broadly mirror stages described for secondary successions elsewhere in New Zealand (e.g. Druce 1957; Esler & Astridge 1974; Esler 1983; Smale 1993). Awana represents the earliest phase of the regeneration sequence, and is the site most affected by the positive feedback between fire, changes to soil, and invasion by exotic woody species (Fig. 11b). North-facing ridges at Awana have poor soils (low organic-matter levels, moisture levels and pH) and are associated with the types of ‘hard site’ vegetation that Esler and Astridge (1974) found on steep, north-facing slopes in the Waitakere Ranges (west Auckland). Mānuka and kānuka growth rates are five and three times slower, respectively, on ridges than in gullies; at 20–25 years old, individuals of these species are 1–1.5 m tall on ridges and 5–7 m tall in gullies. Although the two species have similar growth rates on more fertile soils found in gullies and south-facing slopes, kānuka lives longer than mānuka and consequently overtops it. On the less fertile ridges kānuka enters the succession after mānuka has established, but then overtops it within 20–30 years in the absence of fire. On the north-facing ridges at Awana regeneration is ‘inhibited’ (*sensu* Connell & Slatyer 1977) with recurrent fires further deteriorating soils and so favouring flammable species such as mānuka, *Hakea* spp. and *Erica* spp.

Figure 9. Landscape context – (a) topographic unit (1 = ridge, to 5 = gully); (b) slope (1 = 0–5°, 2 = 5–10°, 3 = 10–20°, 4 = 20–30°, 5 = 20–30°+); and (c) aspect – for the four vegetation units identified at Glenfern (top) and the two vegetation units identified at Windy Hill (bottom).



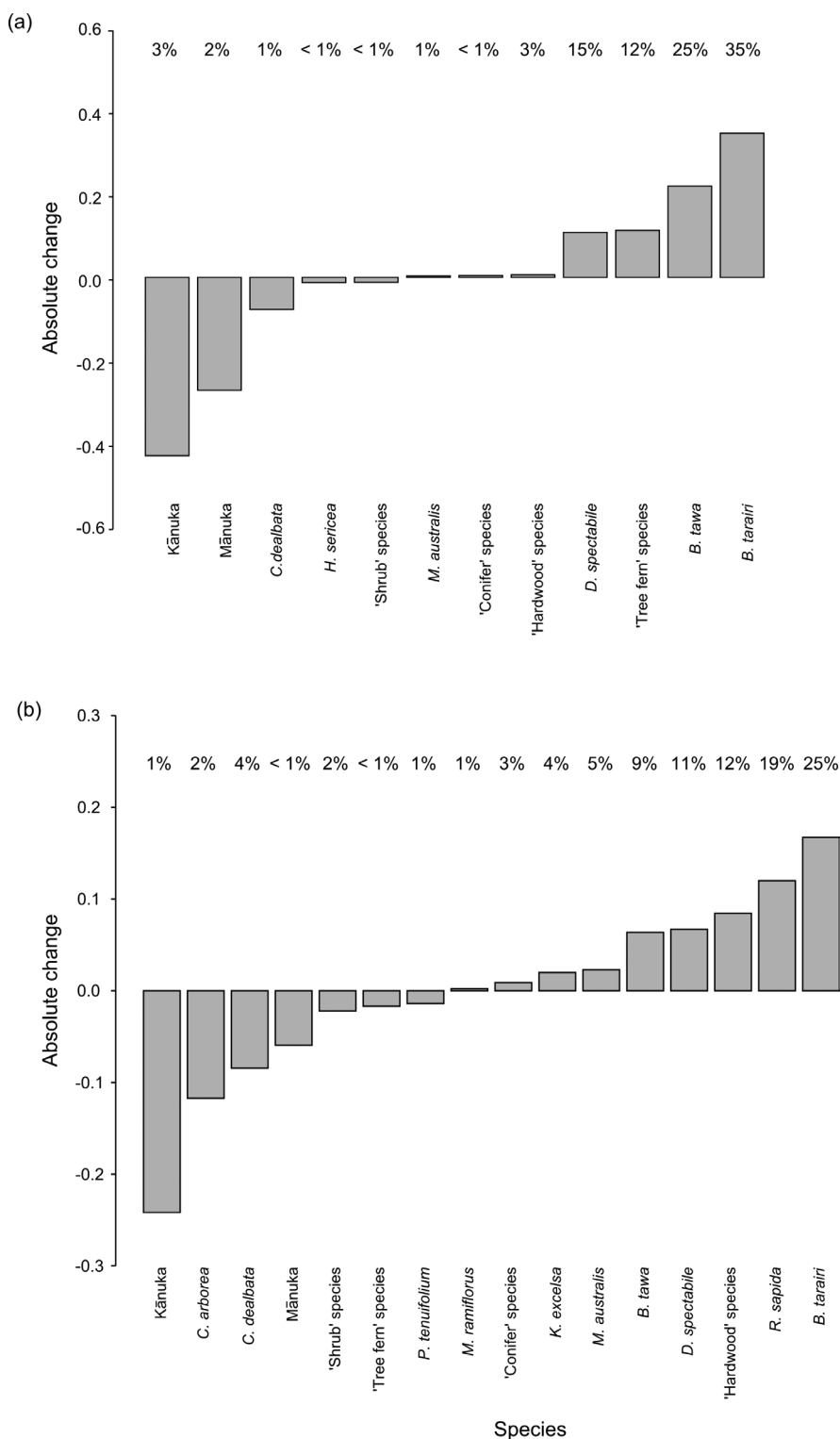
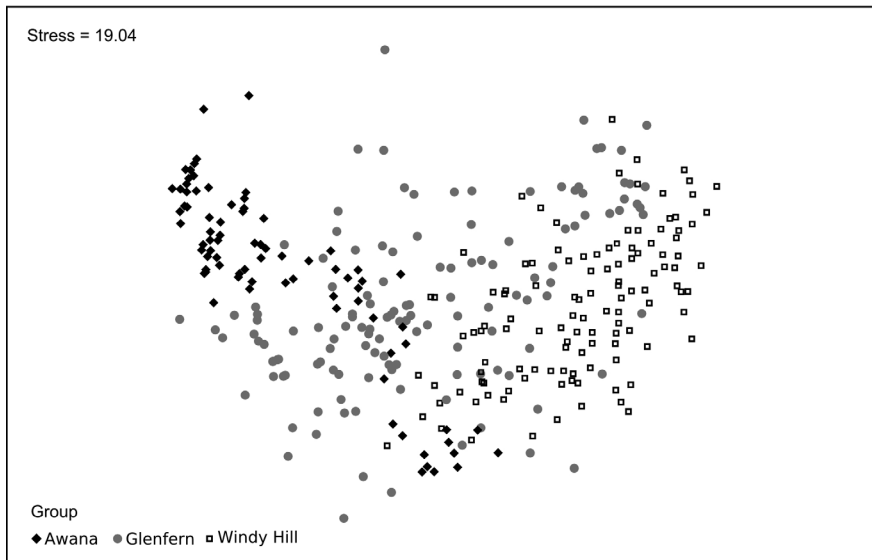


Figure 10. Absolute changes in dominance of the most abundant species based on transition matrix projections for (a) Glenfern and (b) Windy Hill; % values above the bars are the relative abundance of the species once the projections have stabilised.

The vegetation units identified at Glenfern represent a successional sequence from mānuka-dominated scrubland (with exotic woody weeds such as *Hakea sericea*) to remnant patches of gully forest dominated by broadleaved canopy tree species; stem size-frequency for mānuka and kānuka support this interpretation with mānuka absent from 'older' units and kānuka present infrequently as large, senescing individuals. Units 2 and 3 at Glenfern are intermediate between the endpoint units, suggesting that forest is reinvading the ridges and mid-slopes from the gullies. The presence of *Agathis australis* and sclerophyllous species such as *Knightia excelsa* and *Nestegis* spp. in Unit 3, along with the slightly drier positions this unit occupies

in the landscape, suggest that it is a distinct forest type as much as it is a transitional type between Units 2 and 4, and suggests the role of edaphic variation in driving trajectories of secondary succession. The two vegetation units at Windy Hill, while intergrading, also represent successional stages with a shift from regenerating mānuka-kānuka to forest dominated by *Coprosma arborea*, *Rhopalostylis sapida* and *Beilschmiedia tarairi*. The relationship between vegetation composition and aspect is also less marked at Windy Hill, with mānuka-kānuka forest being weakly associated with south-facing slopes, rather than the north-facing slopes such vegetation characterises at Glenfern and Awana. In general, Windy Hill is less

(a)



(b)

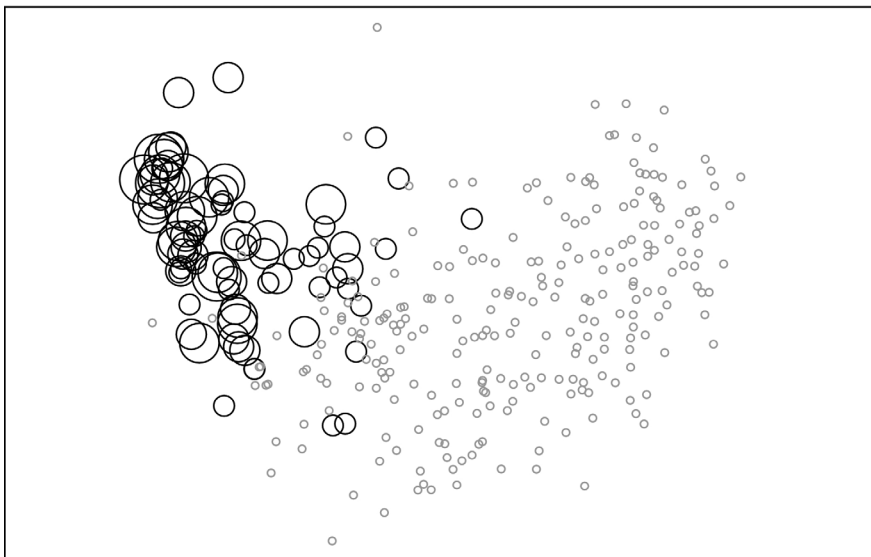


Figure 11. nMDS ordination for the Awana, Glenfern and Windy Hill sites combined using presence/absence data (a) and highlighting the abundance of exotic woody species (b; summed presence of *Hakea* spp., *Pinus* spp., *Erica* spp. and *Ulex europaeus*). Stress for the ordination plot in two dimensions is 19.04.

degraded than Glenfern, with large areas of intact and/or recovering forest and recently disturbed areas dominated by mānuka-scrubland with an absence of woody exotics.

At all three sites there is evidence of a slow reinvasion of the mid- and upper-slopes from the gullies by forest vegetation; this is a general pattern across much of Great Barrier Island (Ogden 2001) and much of New Zealand. The reinvasion process described above will be centred on expansion from fire refugia such as gullies, and will also be driven by the movement of bird-dispersed (i.e. fleshy fruited) species in the landscape. The sequence of regeneration at the three sites is similar to that described by Bray et al. (1999) and Atkinson (2004), with wind-dispersed species preceding small fleshy-fruited species (e.g. *Phyllocladus trichomanoides* – tanekaha, *Pseudopanax* spp. and *Coprosma* spp.), which precede large(r) fleshy-fruited species (e.g. *Podocarpus ferrugineus* – miro, *Beilschmiedia tawa* and *B. tarairi*). This sequence likely reflects how the habitat requirements (e.g. perch and roost sites) and dietary preferences of frugivorous birds are met in different successional communities (Bray et al. 1999; Williams & Karl 2002). For example, kererū are the only bird species capable of dispersing the largest fleshy-fruited species and require large trees, which are absent early in succession, to perch in to support their

weight. Seed predation by invasive mammals (e.g. rats and mice) may further slow regeneration (Campbell & Atkinson 2002; Ogden & Gilbert 2009). In the absence of major disturbance in the near future, the transition matrix models suggest a broad convergence in forest types, ignoring landscape-level edaphic differences (e.g. ridges vs gullies), although some differences in composition will remain (e.g. the difference in the abundance of *Beilschmiedia tawa* and *Rhopalostylis sapida* at Windy Hill compared with Glenfern).

There is little consensus in how species richness and diversity change over successions (Huston 1994; Rosenzweig 1995), with various models predicting richness and diversity peaking at either early (e.g. the initial floristic composition model of Egler (1954)) or intermediate (e.g. the intermediate disturbance hypothesis of Connell (1978)) stages of succession before declining as interspecific competition strengthens. Biodiversity, measured as dispersion in composition, increased from Awana to Glenfern to Windy Hill. Thus, there is a weak trend for richness and diversity to increase with the inferred age of the vegetation as post-fire regeneration proceeds. However, the three sites we consider do not span the entire succession; there is forest on Great Barrier Island more intact than that at Windy Hill (e.g. some of the forest in the 'Te Papanahi' block in the northern

part of the island; Eadie & Broome 1990), but comparable species richness data are not available for it.

Great Barrier Island has experienced two periods of fire: one at the time of Māori settlement and a second at the time of European settlement. While fire frequencies may have peaked at the time of these colonisations fire has remained a recurrent landscape-level disturbance. Much of the island is now covered in early-successional mānuka and kānuka scrubland (i.e. Units 1 and 2 at Awana and Glenfern) – mānuka and kānuka are both killed by fire and are highly flammable (Esler & Astridge 1974), whereas the regenerating later-successional species that establish under it, while killed by fire, are not so highly flammable (Ogden 2001). The most degraded communities (e.g. Unit 1 at Awana and parts of Glenfern; Fig. 11b) occur on north-facing ridges and top slopes – sites where fire might be expected to occur more often and where soil profiles are most degraded (lowest moisture and organic matter; Fig. 7). Such sites are where exotic fire-dependent species (e.g. *Hakea sericea* and *Ulex europaeus*) and 'hard site' (*sensu* Esler & Astridge 1974) species such as *Olearia furfuracea* and *Leucopogon fasciculatus* are most abundant. This vegetation is the most flammable in the landscape.

If there are no major fires for the next few decades, the flammability of the landscape will decrease, and regeneration to forest will continue. If, however, there are fires, then the succession will restart, but will be even slower as soils and nutrients are lost from ridges and upper slopes. Exotic shrubs with serotinous (canopy seed storage) traits (e.g. *Hakea sericea* and *H. gibbosa*) will be favoured by fires as they disperse seed post-fire, and require fire to persist in the longer term. Such exotic shrubs can also affect successional dynamics (Williams 1992a). Much of Great Barrier Island lies in a critical window of high flammability, with the recovering forest being flammable and fire-sensitive now, but in the longer term much less flammable. The small remnant patches of forest scattered across Great Barrier Island represent what McGlone (2001, p. 19) terms 'ecosystems in-waiting'.

Conclusions

Using more than 300 vegetation samples we have quantified many of the assertions made elsewhere about interactions between recurrent fire, vegetation composition and soil conditions. We have demonstrated that repeated fire, by facilitating the invasion of woody exotic species adapted to fire, and by altering soil conditions, can inhibit succession back to forest. The spatial pattern of vegetation in the landscapes of Great Barrier Island represents the interplay between topography and disturbance histories. Young vegetation such as mānuka scrubland tends to occupy drier, north-facing, ridge-top sites – the parts of the landscape that have most often experienced fire. This vegetation is highly flammable. Following recurrent fires during first Māori, then European, colonisation of Great Barrier Island over the last 600–700 years, there is a slow return to forest driven by the reinvasion of the lower and mid-slopes from remnant forest in fire-refugia such as gullies. In the absence of fire in future decades, and assuming sufficient propagule availability, this reinvasion will result in more of the landscape shifting to less flammable forest.

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Appendix 1. Supplementary material

Transition matrices and species longevities (years) for the Glenfern and Windy Hill sites; species are denoted using six-letter codes (first three letters of genus and then first three letters of species), S = small tree/shrub, TA = angiosperm tree, TC = conifer tree, TF = tree fern. ISC = initial state composition (proportional abundance of each species at $t = 0$).

Glenfern landscape

	Beitar	Beitaw	Cyadea	Dysspe	Hakser	Kuneri	Lepsco	Myraus	S	TA	TC	TF	Species	ISC	Longevity (yrs)
Beitar	0.400	0.063	0.218	0.194	0.000	0.018	0.000	0.400	0.083	0.357	1.000	0.200	Beitar	0.008	400
Beitaw	0.200	0.125	0.000	0.194	0.000	0.004	0.000	0.200	0.000	0.071	0.000	0.200	Beitaw	0.026	400
Cyadea	0.000	0.000	0.382	0.161	0.000	0.065	0.006	0.000	0.083	0.286	0.000	0.000	Cyadea	0.090	60
Dysspe	0.000	0.500	0.127	0.097	0.000	0.011	0.000	0.000	0.250	0.071	0.000	0.000	Dysspe	0.051	350
Hakser	0.000	0.000	0.000	0.000	0.250	0.022	0.045	0.000	0.000	0.000	0.000	0.000	Hakser	0.013	30
Kuneri	0.000	0.063	0.000	0.000	0.000	0.462	0.176	0.000	0.167	0.000	0.000	0.000	Kuneri	0.451	120
Lepsco	0.000	0.000	0.000	0.000	0.500	0.183	0.653	0.000	0.167	0.000	0.000	0.000	Lepsco	0.299	60
Myraus	0.000	0.000	0.127	0.065	0.000	0.093	0.023	0.000	0.083	0.071	0.000	0.000	Myraus	0.008	100
S	0.000	0.125	0.055	0.161	0.000	0.093	0.080	0.200	0.083	0.143	0.000	0.000	S	0.020	30
TA	0.000	0.063	0.073	0.000	0.000	0.022	0.000	0.200	0.000	0.000	0.000	0.000	TA	0.023	350
TC	0.000	0.000	0.000	0.000	0.250	0.022	0.000	0.000	0.000	0.000	0.000	0.000	TC	0.002	500
TF	0.400	0.063	0.018	0.129	0.000	0.007	0.017	0.000	0.083	0.000	0.000	0.600	TF	0.008	100

Windy Hill landscape

	Beitar	Beitaw	Coparb	Cyadea	Dysspe	Kniexc	Kuneri	Lepsco	Melram	Myraus	Pitten	Rhosap	S	TA	TC	TF	Species	ISC	Longevity (yrs)
Beitar	0.085	0.067	0.110	0.069	0.080	0.000	0.027	0.029	0.143	0.133	0.000	0.190	0.037	0.053	0.133	0.100	Beitar	0.080	400
Beitaw	0.021	0.267	0.012	0.014	0.040	0.000	0.007	0.000	0.000	0.067	0.000	0.048	0.000	0.053	0.000	0.000	Beitaw	0.026	400
Coparb	0.021	0.000	0.134	0.042	0.000	0.000	0.200	0.400	0.000	0.000	0.000	0.000	0.074	0.105	0.067	0.000	Coparb	0.139	120
Cyadea	0.064	0.067	0.061	0.278	0.040	0.083	0.160	0.171	0.000	0.067	0.000	0.095	0.148	0.053	0.400	0.200	Cyadea	0.122	60
Dysspe	0.085	0.067	0.073	0.056	0.040	0.083	0.020	0.000	0.286	0.000	0.067	0.048	0.000	0.053	0.000	0.000	Dysspe	0.043	350
Kniexc	0.000	0.000	0.049	0.028	0.080	0.083	0.000	0.000	0.000	0.067	0.000	0.000	0.074	0.000	0.067	0.000	Kniexc	0.020	250
Kuneri	0.000	0.000	0.012	0.014	0.000	0.000	0.100	0.086	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.100	Kuneri	0.255	120
Lepsco	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	Lepsco	0.060	60
Melram	0.064	0.067	0.024	0.056	0.000	0.000	0.020	0.000	0.000	0.067	0.333	0.024	0.037	0.000	0.000	0.100	Melram	0.012	60
Myraus	0.085	0.133	0.085	0.069	0.000	0.167	0.253	0.229	0.143	0.200	0.133	0.024	0.074	0.105	0.133	0.200	Myraus	0.026	100
Pitten	0.000	0.000	0.024	0.000	0.000	0.000	0.013	0.000	0.000	0.133	0.067	0.024	0.000	0.000	0.000	0.000	Pitten	0.026	100
Rhosap	0.362	0.267	0.329	0.208	0.440	0.333	0.027	0.000	0.286	0.067	0.200	0.357	0.148	0.316	0.133	0.100	Rhosap	0.071	120
S	0.149	0.000	0.073	0.097	0.200	0.167	0.140	0.057	0.143	0.133	0.067	0.119	0.259	0.053	0.067	0.100	S	0.046	30
TA	0.064	0.067	0.012	0.042	0.080	0.000	0.013	0.000	0.000	0.067	0.067	0.071	0.000	0.211	0.000	0.100	TA	0.032	350
TC	0.000	0.000	0.000	0.028	0.000	0.083	0.007	0.000	0.000	0.000	0.067	0.000	0.037	0.000	0.000	0.000	TC	0.026	500
TF	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	TF	0.017	100