

Pioneer tree ferns influence community assembly in northern New Zealand forests

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Abstract: *Cyathea medullaris* (Cyatheaceae) is a frequent pioneer of disturbed areas (e.g. landslides) or edge environments, sometimes forming near continuous canopies. We test the hypothesis that colonisation by this species as a pioneer alters the seedling assemblage to favour more shade-tolerant broadleaved trees than that beneath another common native pioneer (*Kunzea robusta*, Myrtaceae) in the same landscapes. We compared vegetation and abiotic characteristics of 166 sites across the Auckland region where *C. medullaris* or *K. robusta* were abundant ($\geq 20\%$ basal area) along successional gradients. Using hierarchical classification and ordination, we identified distinct communities associated with the different pioneers. In the forests we consider, *C. dealbata* is another common understorey tree fern, which sometimes, but not always, co-occurs with *C. medullaris*. *Cyathea medullaris* / *C. dealbata* successions occurred on steep sites with lower annual water deficit whereas *K. robusta* / *C. dealbata* successions were located on flatter, drier sites. The prevalence of macro-charcoal in *K. robusta* / *C. dealbata* forest suggests the prominence of that community is in part an outcome of the increased importance of fire disturbance in New Zealand. Dominance of *C. medullaris*, with *C. dealbata* understoreys, influences community assembly of tree species towards dominance by shade-tolerant species, whereas seedlings of less shade-tolerant small-leaved species are more prevalent in *K. robusta* / *C. dealbata* forests. We provide evidence to suggest that, where present in early forest communities, high tree fern abundance influences the assembly of seedling communities, supporting our hypothesis. Contrary to previous suggestions, a high abundance or basal area of tree ferns on sites not historically affected by fire did not limit the establishment and growth of canopy trees including fleshy-fruited broadleaf species.

Keywords: biotic filter; Cyatheaceae; fire; multivariate analysis; succession; vegetation dynamics

Introduction

The distinctive traits of different pioneer species can influence community assembly and natural succession processes after disturbance (HilleRisLambers et al. 2012; Paterno et al. 2016). For example, the biotic influence of pioneers is evident in the different forest successions occurring beneath *Kunzea* spp.¹ (Myrtaceae), a group of New Zealand native pioneers, compared with those beneath *Ulex europaeus* (Fabaceae), a non-native invasive nitrogen-fixing shrub in the same landscapes in New Zealand (Sullivan et al. 2007). However, abiotic filters (e.g. topography, soil conditions) initially underpin heterogeneous spatial patterns of pioneer taxa across the landscape, based on the tolerances of different pioneer species to disturbance type, abiotic characteristics and competition (Poff 1997; Ejrnæs et al. 2006; Perry et al. 2014). Community assembly will thus reflect historic disturbances, the abiotic conditions influencing pioneer establishment, and the subsequent biotic influence of the dominant pioneer (Connell & Slatyer 1977; Weiher & Keddy 1995; Sullivan et al. 2007; Burton et al. 2011).

The prevailing view of secondary successions initiated by fire and/or other stand destroying disturbances in New Zealand's temperate forest ecosystems is one where pioneer communities

are commonly dominated by Myrtaceae, in particular *Kunzea* spp.² (de Lange 2014) and *Leptospermum scoparium* (Cameron 1960; Esler & Astridge 1974; Wardle 1991; Smale et al. 1997; Richardson et al. 2014). These species arrived in New Zealand from Australia between 2–3 Ma, moving from a landscape where fire is a major determinant of plant traits and communities to New Zealand where natural fire pre-human was relatively infrequent (Thompson 1989; Battersby et al. 2017). However, since human arrival in New Zealand c. 1280 AD (Wilmshurst et al. 2008), fire frequency has dramatically increased in New Zealand's terrestrial ecosystems (Perry et al. 2012a), likely favouring *Kunzea* spp. and *L. scoparium* as pioneer species. The increased likelihood of occurrence of these Myrtaceae pioneers may influence the potential for other pioneers to establish (Esler 1967; Esler & Astridge 1974; Smale 1994; Atkinson 2004; Perry et al. 2010).

² Previously recognised as *Kunzea ericoides* (A. Rich) Joy Thomps., *Kunzea* has recently been revised to recognise 10 species within New Zealand (de Lange 2014) with three commonly occurring in our study area: *K. robusta*, *K. linearis* and *K. amathicola*. The data used in this study, other than that which were collected by the authors, were obtained prior to this taxonomic revision and therefore all records refer to *K. ericoides*. Of the three species of *Kunzea* now present in the Auckland region, the most common forest associated species is *K. robusta*. *Kunzea amathicola* is strongly coastal and *K. linearis* is also restricted to coastal habitat around Auckland's Waitematā Harbour. Therefore, we assign all *Kunzea* records to *K. robusta* in the historic non-coastal forest plots compiled for this study.

¹ Following revision of *Kunzea* de Lange (2014), *K. ericoides* is likely to be at the Nelson sites and *K. robusta* around Wellington in the sites studied in Sullivan et al. (2007).

In *Agathis australis* (kauri) and conifer-broadleaved forest in the North Island, early successional communities dominated by tree ferns can often be a prominent feature of landscapes (Pope 1924; Silvester 1964; Beveridge 1973; Richardson et al. 2014; Fig. 1). Near-continuous canopies of pioneering *Cyathea medullaris* with dense understories including *C. dealbata* have been described (Pope 1924; Ritchie et al. 2003; Brock et al. 2016), but rarely studied. Early successional vegetation communities dominated by tree ferns are rare globally; however, *Cyathea* tree ferns acting as pioneers have been described in tropical ecosystems from Colombia (*C. caracasana*; Arens & Sánchez Baracaldo 2000), Puerto Rico (*C. bryophila* and *C. arborea*; Shiels 2006; Weaver 2008; Walker et al. 2010), and on Trinidad Island off the coast of Brazil (*C. copelandii*; R. Alves & N. Silva pers. comm.). Other early successional communities, developing on retired pasture and agricultural land or after fire, roadworks and landslides, may feature tree ferns as a prominent component, even if not as the dominant pioneers (Wardlaw 1931; Arens & Sánchez Baracaldo 1998; Restrepo & Vitousek 2001; Chacón-Labela et al. 2014). In New Zealand, succession through tree fern dominated stages has been described for *Dicksonia squarrosa* (Dicksoniaceae) and *Cyathea smithii* (Silvester 1964; Blaschke et al. 1992; Walker & Sharpe 2010) where these establish approximately 25 years after the commencement of natural regeneration on landslides and in retired pastures; although none of these reported tree fern dominated stages are pioneering. We are unaware of any published studies of secondary succession involving tree fern pioneer dominated phases for any temperate forest ecosystem.

The two North Island pioneer species we focus on, *K. robusta* and *C. medullaris*, have many similar traits, including rapid height growth (c. 30 cm yr⁻¹), prolific production of wind-dispersed propagules, and relatively short life-spans (approx. 150 yrs; 120 years respectively) (Burrows 1973; Esler & Astridge 1974; Esler 1976; Allen et al. 1992; Smale 1994; Brock et al 2016). Unlike New Zealand's other native tree ferns, *C. medullaris* will regenerate immediately after both gap-phase and landscape-level disturbances and is associated

with high light environments (Wardle 1991; Large & Braggins 2004). *Cyathea medullaris* is shade-intolerant (Bystriakova et al. 2011) and often occupies habitats such as edges and canopy gaps (Pope 1924; Cockayne 1958; Large & Braggins 2004). *Kunzea robusta* is similarly shade-intolerant and associated with open habitats (Burrows 1973; Wardle 1991).

In association with both of these pioneers, *C. dealbata* is a common component of the understory. However, in contrast to *C. medullaris*, *C. dealbata* is a relatively drought and shade-tolerant tree fern species (Bystriakova et al. 2011; Brock et al. 2016). Also, *C. dealbata* is a relatively long-lived, slow-growing tree fern, persisting in forests for up to 250 years (Wardle 1991; Bystriakova et al. 2011; Brock et al. 2016).

Tree ferns are likely to have an important influence on the regeneration niche of potentially dominant tree species in forests through macro-litterfall, shading, influences on nutrient cycling and provision of substrates for epiphytic woody seedlings (Gillman et al. 2004; Gaxiola et al. 2008; Brock et al. 2016). Tree ferns have been described as 'inhibiting' and 'slowing' forest succession (Connell & Slatyer 1977; Walker et al. 2010). For example, Walker et al. (2010) describe the inhibitory influence of tree ferns on the establishment of woody forest canopy species in Puerto Rico, when compared to an area artificially cleared of tree ferns, over a 7 year period. On the other hand, Walker and Aplet (1994) suggest that, over the long-term, tree ferns act as a biotic filter on canopy species composition through their influence on nutrient cycling and soil moisture retention. In regenerating *Agathis australis* forest in New Zealand, Burns and Smale (1990) observed a lack of woody plant regeneration beneath *C. dealbata* (Cyatheaceae) and Norton (1991) recorded an absence of podocarp seedlings around tree ferns. More specifically, Richardson et al. (2014) suggested a causal link between high tree fern basal area (BA), concomitant with the browsing effect of invasive ungulates, and a significant reduction in the establishment success of fleshy-fruited canopy tree species in the Te Urewera area.

We hypothesise that *C. medullaris* will influence the communities developing beneath it in a way different to other



Figure 1. A near continuous canopy of *C. medullaris* across a slope on the north-eastern Hūnua Ranges.

pioneer species such that they show distinct assemblages indicative of subsequent forest types. Furthermore, we hypothesise that these differences in species composition are not related to differences in geographic distance from seed sources, which is an alternative possible explanation for variation in early successional vegetation communities at landscape scales.

This study aims to identify whether: (1) successional communities dominated by either *C. medullaris* or *K. robusta* are associated with different abiotic conditions or disturbance types; (2) tree ferns influence community assembly and resultant forest composition; and (3) any differences in successional communities are determined by spatial separation of the plots in the landscape (i.e. dispersal failure) and not by abiotic conditions.

Methods

Data collection

Vegetation community data

To characterise early successional communities, we obtained a dataset from Auckland Council comprising 154 20 m × 20 m permanent vegetation plots (data collected between 2009 and 2013; Fig. 2). These plots were a subset from a total of approximately 400 permanent plots established systematically across Auckland (Auckland Council 2014; Ruffell et al. 2015), with this subset targeting forest plots that support either *C. medullaris* and/or *K. robusta* with relative BAs of at least 20% of total BA. To improve representation of plots with a high abundance of *C. medullaris*, we supplemented the database with a further 12 plots across the Auckland region. These supplemental survey sites with dense tree fern canopies were identified using aerial photography accessed through the Auckland Council GIS map viewer (<http://maps.aucklandcouncil.govt.nz/aucklandcouncilviewer>). The survey methodology for the Auckland Council and supplemental plots followed permanent plot protocols established by Hurst and Allen (2007). Vegetation plots (20 m × 20 m) were installed in areas of homogenous vegetation. For vascular plants, we recorded species and diameter at breast height of all trees (and tree ferns) >2.5 cm DBH; counted saplings (<2.5 cm DBH but >1.35 m tall) over the entire plot; and subsampled seedlings

(0–1.35 m tall) in 24 0.49 m radius circular plots (=0.75 m² area each) in the plot (Hurst & Allen 2007). For each of the additional *C. medullaris* plots (12) and a comparable number of *K. robusta* plots (12) from the Auckland Council database, we collected data on a subset of biophysical conditions.

Abiotic factors

To obtain general abiotic data for each of the 166 plots, we downloaded spatial data comprising modelled abiotic values and geological data for the Auckland region from the LRIS portal (see <https://lris.scinfo.org.nz> and Table 1). We derived a topographic position index (TPI) layer from elevation data using the raster package (Hijmans 2015) in R version 3.2.3 (R Core Team 2015). These data were loaded into a GIS programme (ArcMap™ 10.3.1) with the physical locations of the vegetation plots used to extract site specific values for these variables. Aspect data for each plot were converted from a bearing (0–360°) into partitioned values of ‘northness’ and ‘eastness’ (Zar 1999).

Biophysical conditions

We used sub-canopy photography using a hemispheric fish-eye lens (Canon 450D, Sigma 4.5mm f/2.8 EX DC HSM) to quantify the understorey light environment in a subset of 24 plots, with photos taken at the northeast and southwest corners and the centre of the plot. Topography around the location of each photo was mapped using a compass and clinometer, and accounted for in the subsequent digital analysis. These photos were processed using Gap Light Analyzer 2.0 (Frazer et al. 1999) to estimate canopy openness as a proxy for understorey light environment.

Soil samples were collected from three random locations in each of the 24 plots using a coring ring of 10 cm diameter. Loose litter was removed, then a 5 cm deep sample was extracted from the organic soil layer. Soil samples were returned to the lab and dried at 35°C for 24 hours, root tissue removed, and the soil passed through a 2 mm sieve; samples for each plot were then combined. Samples were ground and analysed for total C and N concentration using an elemental analyser (TruSpec, LECO Corporation, St. Joseph, Michigan, USA). Soil standards (LECO Lot 1016, 1007) were used for calibration. Ten percent of samples were replicated and results were within the range of variation given for the standards. Analysis of pH was undertaken using the water method (#106i). The remaining material was sent to the Landcare Research Environmental Chemistry Laboratory (Palmerston North) for analysis of available nitrogen (nitrate and ammonium by 2 M KCl extraction, method #118) and phosphorus (Olsen-available Phosphorus, method #124), respectively (Blakemore et al. 1981). Descriptions of methods 106i, 118 and 124 are available from www.landcareresearch.co.nz/resources/laboratories/environmental-chemistry-laboratory. A second 5 cm deep sample (using a cylindrical ring 10 cm in diameter) was taken at each location to derive bulk density; the samples were dried at 105°C for 24 hours and then weighed (Gradwell & Birrell 1979).

Separate small samples (approx. 1 cm³) of soils from the organic soil layer were collected to estimate charcoal abundance as a proxy for recent fire history. These samples were prepared as described by Whitlock and Larsen (2001) and macro-charcoal fragments (>2 mm) counted under a dissecting microscope.

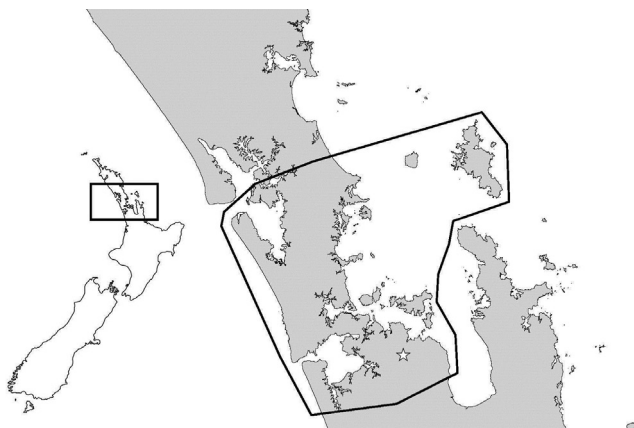


Figure 2. Survey sites were situated throughout the Auckland region, the extent of the sites is delineated by the black outline (latitudinal range of polygon: 36°02.85'S to 37°14.80'S). Approximate location of Figure 1 indicated by star.

Analysis

Vegetation community data

We analysed our data in four stages: (1) discrete vegetation assemblages were identified and their distinctiveness tested; (2) correlative relationships between these vegetation assemblages and environment were identified; (3) the potential influence of tree fern abundance on community assemblage was examined; and (4) the relative contributions of location and environment to variation in species composition were estimated.

Identification of discrete vegetation assemblages

For each plot, the BA of each species (combining trees and saplings) were calculated. The BA contribution of saplings (individuals <2.5 cm DBH) was calculated using 1 cm DBH as a standard for each sapling. We used BA values as an index of relative abundance of each of the species per plot to calculate dissimilarities among plots using the Bray-Curtis dissimilarity measure (Faith et al. 1987). This dissimilarity matrix was used to classify the plots using hierarchical agglomerative clustering with the complete linkage method (Quinn & Keough 2002). Non-metric multidimensional scaling (nMDS) was used to ordinate and graphically represent the data (Clarke 1993; Quinn & Keough 2002).

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to assess whether the groups identified by hierarchical classification were compositionally distinct. As *K. robusta* is more prevalent in the landscape than *C. medullaris*, the number of plots representing these pioneers is potentially unequal. PERMANOVA is sensitive to the relative dispersion of groups in unbalanced designs (Anderson & Walsh 2013); therefore, to assess whether any groups differed in their dispersion we used multivariate homogeneity of variance tests (PERMDISP2; Anderson 2006). To ensure the robustness of the analysis of any unbalanced groups, multiple permutations of PERMANOVA were undertaken using all plots (n) from the smaller group against the same number of plots (n) randomly sampled, without replacement, from the larger group, as suggested by Alekseyenko (2016). Previously only weak relationships have been derived between tree fern BA and height / crown size (although allometric equations have been produced; Beets et al. 2012), casting doubt on the use

of BA as an index of tree fern biomass. Therefore, multiple PERMANOVA analyses were undertaken on the groupings using density (species stems plot⁻¹) and presence/absence data, and finally with the *C. medullaris* and *K. robusta* species data values entirely removed. The latter analysis was designed to avoid potential circularity in our arguments, i.e. are the statistical assemblages produced by hierarchical classification defined by more than simply the presence of the dominant pioneer species? Non-metric multidimensional scaling (nMDS) was used to ordinate and graphically represent the data and the groupings produced by the presence/absence and density data. We used similarity percentage (SIMPER) analysis on the complete vegetation dataset to identify the species that contributed most to dissimilarities between groups. The groups were then named using the approach established by Atkinson (1985) based on the structural and compositional features characterising the vegetation communities in each group. To assess whether there was any consistency in the community composition of the groups, indicator value analysis for species combinations (De Cáceres et al. 2012) was applied to the forest stand and seedling data to identify any species that were faithful to the groups identified by the classification, irrespective of abundance.

Abiotic factors

Data were extracted from the GIS using the spatial analyst package to produce a matrix of abiotic and topographic conditions present at each of the 166 vegetation plots (Table 1). Collinear variables were identified using multiple pairwise correlations using a standard threshold of $r = |0.7|$, and removed from further analysis (Dormann et al. 2013). The data were standardised with a covariance matrix, and a principal components analysis (PCA) of the abiotic data then undertaken. Vectors representing the components explaining greater than 5% of variance were then fitted to the nMDS ordination of the floristic data; those components that had a statistically significant ($P < 0.05$) association with the distribution of plots in ordination space were plotted.

Regeneration niche

An index of seedling height-abundances for each species per plot was derived by multiplying their density by their height

Table 1. LENZ modelled environmental variables used to analyse vegetation community data. All layers are at a spatial resolution of 25 × 25 m.

Data layer	Units	Range (5% – median – 95%)
Acid soluble phosphorus	Index	1 – 1 – 4
Annual water deficit	mm	0 – 38 – 119
Exchangeable calcium	Index	1 – 1 – 2
Induration soil hardness	Index	1 – 4 – 4
Mean annual solar radiation	MJ.m ⁻² .day ⁻¹	149 – 152 – 155
Mean annual temperature	°C	11.3 – 14.4 – 15.8
Mean minimum temperature of the coldest month	°C	3.9 – 6.2 – 8.9
Monthly water balance ratio	Index	20 – 27 – 45
October vapour pressure deficit	kPa	25 – 36 – 41
Slope	° (degrees inclination)	0 – 11 – 33
Soil age	Index	1 – 2 – 2
Soil drainage	Index	2 – 4 – 5
Soil particle size	Index	1 – 2 – 5
Winter solar radiation	MJ.m ⁻² .day ⁻¹	5.8 – 6.0 – 6.5
Fundamental soil layer (North Island)	Various	Various
Topographic Position Index	Index	71 – 471 – 34 970

class (height class 1: 0–15 cm; 2: 16–45 cm; 3: 46–75 cm; 4: 76–105 cm; 5: 106–135 cm; Hurst & Allen 2007), then summing across the plot. Index values per species per plot were ordinated (nMDS with Bray-Curtis dissimilarity). PERMANOVA was used to assess separation in ordination space of plots on the basis of the previous groupings from the tree and sapling data. The abiotic data matrix had a new parameter ‘tree fern BA’ added, and another PCA and the analysis workflow described above repeated.

We used linear regressions between the total BA of tree ferns per plot and the numbers of woody species with BAs of $>0.5 \text{ m}^2 \text{ ha}^{-1}$ per plot to provide a comparison with the woody species richness vs. tree fern BA data presented by Richardson et al. (2014).

Influence of space versus environment on composition

Geographic (Euclidean) distances between all plots were calculated as was the Euclidean distances between sites based on the abiotic data matrix used in the PCA analysis. These abiotic and geographic dissimilarity matrices were, along with the original vegetation dissimilarity matrix, subjected to simple and partial permutational Mantel tests (Mantel & Valand 1970).

All analyses were conducted using R version 3.2.3 (R Core Team 2015) and the *vegan* 2.3-2 and *indicspecies* 1.7.5 libraries (De Cáceres et al. 2012; Oksanen et al. 2015).

Results

Community analysis

Hierarchical classification and ordination suggest that the 166 plots fell into two groups (Fig. 3). SIMPER analyses show that the dissimilarities between these two groups are based on the relative contributions of three species: *K. robusta* (17.1% contribution) in one group, and the tree ferns, *C. medullaris* (11.6%) and *C. dealbata* (13.4%) in the other. Resampled PERMANOVA analyses showed that these groups were distinct in ordination space ($F_{1,116} = 27.06\text{--}35.86$; $P < 0.001$), and PERMDISP2 analysis indicated that the two groups differ in their dispersion ($F_{1,116} = 0.04\text{--}5.95$; $P < 0.05$), with the *C. medullaris* pioneer-associated group more compact than the *K. robusta* pioneer-associated group in ordination space. Analysis of the tree and sapling density data produced two groups largely consistent with the BA analysis: 93% of plots remained in the *C. medullaris* group, and 71% of the *K. robusta* plots remained in the same group. Multiple PERMANOVA analyses on these density data also showed that the distinction between the groups remained ($F_{1,116} = 16.60\text{--}24.14$; $P < 0.001$). The hierarchical classification of the presence/absence data suggested three groups; 75% of the plots previously associated with the *C. medullaris* pioneer-associated communities remained distinct, while the *K. robusta* pioneer-associated plots were now represented by two groups. PERMANOVA

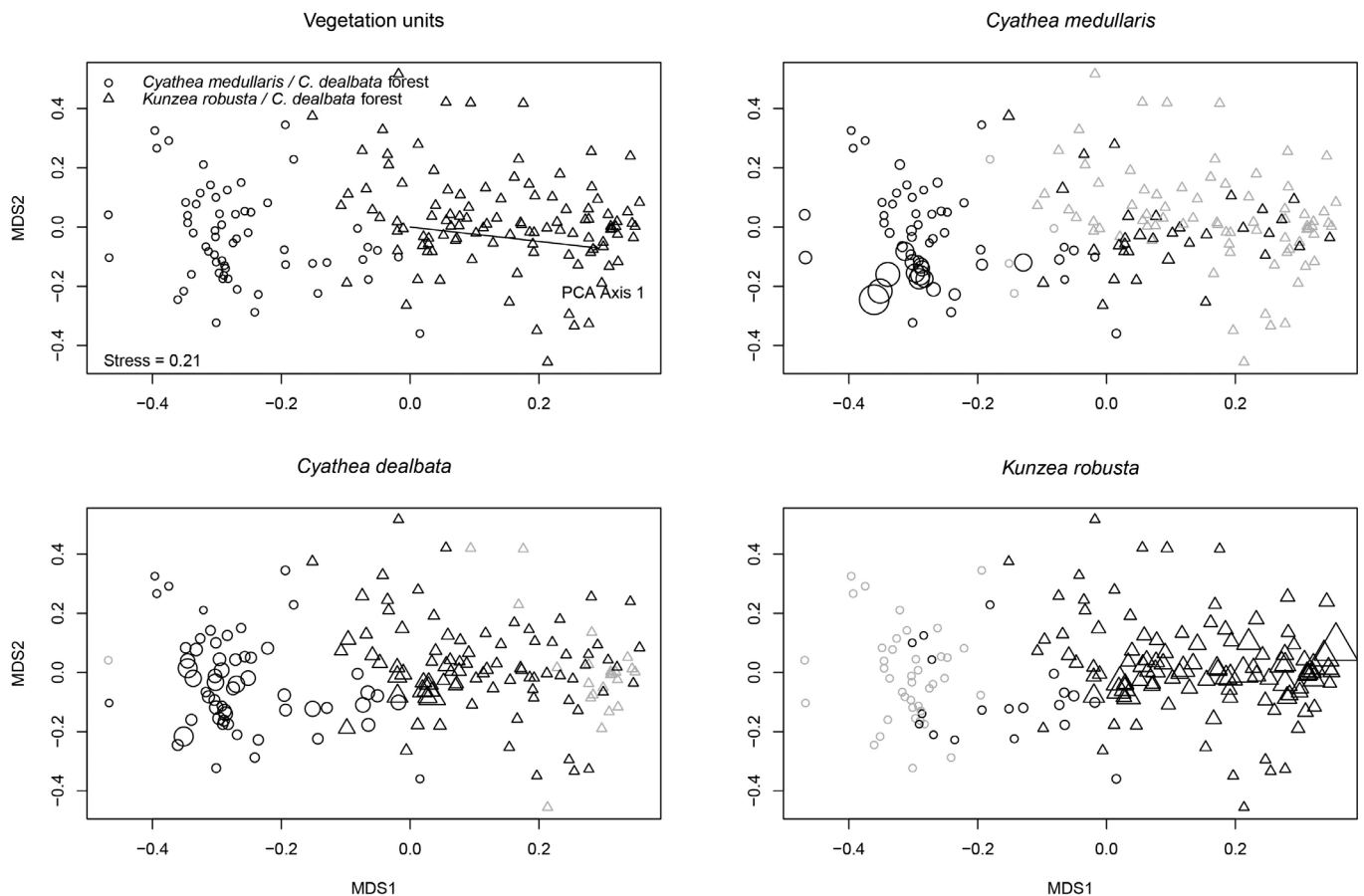


Figure 3. nMDS ordination of the vegetation data; stress for the ordination in two dimensions is 0.21. The size of the symbols is proportional to the BA of *C. medullaris*, *C. dealbata* or *K. robusta* recorded in each plot. Grey symbols indicate plots where species were absent. The arrow indicates vector fits for the principal component factor associated with increasingly dry and flat sites that was significantly correlated ($P = 0.0001$) with axis 1 of the nMDS.

of the groupings of the presence/absence data confirmed that they were compositionally distinct ($F_{1,116} = 16.66\text{--}22.48$; $P < 0.001$). In the final tree and sapling vegetation analysis, in which the BA values of the pioneer species *C. medullaris* and *K. robusta* were removed, the *K. robusta* group fragmented further into six separate groups (ordinations of these datasets are in Appendix S1, see supplementary material). The communities were named, following Atkinson (1985), on the basis of their composition and structure as *C. medullaris* / *C. dealbata* forest, and *K. robusta* / *C. dealbata* forest. *Cyathea dealbata* was common to both groups; however, it had significantly greater basal area in the *C. medullaris* pioneer-associated communities ($13.4 \pm 9.2 \text{ m}^2 \text{ ha}^{-1}$) than the *K. robusta* pioneer-associated communities ($4.9 \pm 7.5 \text{ m}^2 \text{ ha}^{-1}$).

Indicator value analysis (using the complete BA dataset) recognised 14 species as 'faithful' (where $P \leq 0.001$ after Bonferonni correction) to *C. medullaris* / *C. dealbata* forest and 10 species to *K. robusta* / *C. dealbata* forest (Table 2; Appendix S1). Shade-tolerant forest canopy species with large fleshy fruits such as *Beilschmiedia tawa* (Lauraceae) were faithful to *C. medullaris* / *C. dealbata* forest in the tree and sapling data, with broadleaved canopy species such as *Hedycarya arborea* (Monimiaceae) faithful in both tree, sapling and seedling data. Species such as *Leucopogon fasciculatus* (Ericaceae) and *Phyllocladus trichomanoides* (Podocarpaceae) were most commonly associated with *K. robusta* / *C. dealbata* forest (Table 2; see Appendix S2 in supplementary material).

Abiotic factors

The first PCA component was significantly correlated with Axis 1 ($P < 0.05$) of the vegetation ordination, highlighted a gradient from steep ($13.4 \pm 6.5^\circ$; mean ± 1 SD), moist (annual

water deficit = 30.5 ± 27.5 mm) slopes towards lower elevation sites with increased annual water deficit (53.2 ± 25.9 mm) and flatter topography ($10 \pm 5.6^\circ$) (Fig. 3).

The organic soil layer showed significant differences in pH (*C. medullaris* / *C. dealbata* forest $\bar{x} = 5.83 \pm 0.25$, *K. robusta* / *C. dealbata* forest $\bar{x} = 4.96 \pm 0.26$) and ammonium concentrations (*C. medullaris* / *C. dealbata* forest $\bar{x} = 130.65 \pm 80.38 \text{ mg kg}^{-1}$, *K. robusta* / *C. dealbata* forest $\bar{x} = 76.74 \pm 23.81 \text{ mg kg}^{-1}$) between *C. medullaris* and *K. robusta* pioneer-associated communities, although the differing soil depths and densities at the sites meant little difference in ammonium pools (Table 3). The abundance of particulate macro-charcoal in the topsoil differed between the two communities (Table 3). Several *K. robusta* / *C. dealbata* forest sites had macro-charcoal amounts ($\bar{x} = 185.82 \pm 221.86 \text{ pieces cm}^{-3}$) indicative of recent, local fire(s), whereas there was little evidence for local fire events in the *C. medullaris* / *C. dealbata* forest sites ($\bar{x} = 6.24 \pm 3.88$).

Regeneration niche

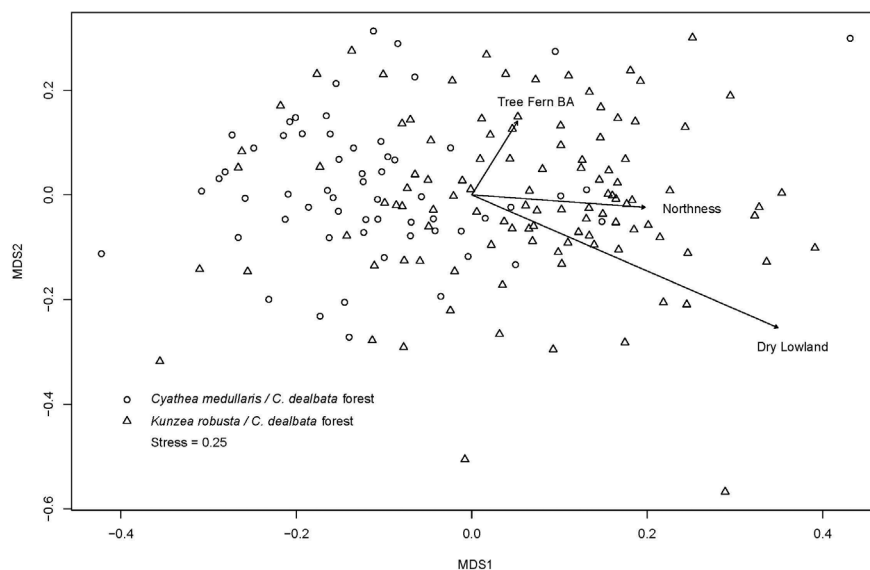
The seedling communities of the *C. medullaris* / *C. dealbata* forest and *K. robusta* / *C. dealbata* forest were separated in ordination space (PERMANOVA: $F_{1,116} = 4.99\text{--}8.02$; $P < 0.001$; Fig. 4), consistent with the separation of the tree/sapling communities. Three factors had significant correlations ($P < 0.05$) with the ordination axes, and indicated that nMDS Axis 1 described a gradient of decreasing elevation, increasing temperature and annual water deficit ($P = 0.0001$), and increasingly northerly-facing aspects on well-drained soils ($P = 0.0036$). The gradient most associated with Axis 2 of the ordination was increasing tree fern BA (62% of BA values represented by *C. dealbata*) ($P = 0.036$).

Table 2. A summary of the canopy tree, understorey and tree fern species (tree, sapling and seedlings) that are identified as faithful to either *C. medullaris* / *C. dealbata* forest or *K. robusta* / *C. dealbata* forest; species presented here were faithful to a highly significant ($P < 0.001$) degree. The complete list of faithful species is in Appendix S2.

<i>Cyathea medullaris</i> / <i>Cyathea dealbata</i>		<i>Kunzea robusta</i> / <i>Cyathea dealbata</i>	
Tree and sapling data			
Species	Family	Species	Family
<i>Hedycarya arborea</i>	Monimiaceae	<i>Phyllocladus trichomanoides</i>	Podocarpaceae
<i>Olearia rani</i>	Asteraceae	<i>Kunzea robusta</i>	Myrtaceae
<i>Beilschmiedia tawa</i>	Lauraceae	<i>Leucopogon fasciculatus</i>	Ericaceae
<i>Dysoxylum spectabile</i>	Meliaceae	<i>Coprosma rhamnoides</i>	Rubiaceae
<i>Knightia excelsa</i>	Proteaceae	<i>Leptospermum scoparium</i>	Myrtaceae
<i>Meliccytus ramiflorus</i>	Violaceae	<i>Olearia furfuracea</i>	Asteraceae
<i>Rhopalostylis sapida</i>	Areaceae		
<i>Coprosma grandifolia</i>	Rubiaceae		
<i>Schefflera digitata</i>	Araliaceae		
<i>Brachyglottis repanda</i>	Asteraceae		
<i>Cyathea medullaris</i>	Cyatheaceae		
<i>Cyathea dealbata</i>	Cyatheaceae		
<i>Dicksonia squarrosa</i>	Dicksoniaceae		
<i>Cyathea smithii</i>	Cyatheaceae		
Seedling data			
<i>Hedycarya arborea</i>	Monimiaceae	<i>Phyllocladus trichomanoides</i>	Podocarpaceae
<i>Laurelia novae-zelandiae</i>	Atherospermataceae	<i>Coprosma arborea</i>	Rubiaceae
<i>Rhopalostylis sapida</i>	Areaceae	<i>Kunzea robusta</i>	Myrtaceae
<i>Coprosma grandifolia</i>	Rubiaceae	<i>Coprosma rhamnoides</i>	Rubiaceae
<i>Schefflera digitata</i>	Araliaceae	<i>Leucopogon fasciculatus</i>	Ericaceae
		<i>Olearia furfuracea</i>	Asteraceae

Table 3. Ranges of biophysical conditions (5% – median – 95%) present in the organic soil layer in the *C. medullaris* / *C. dealbata* and *K. robusta* / *C. dealbata* forest communities (no multiple P-value corrections applied).

Variable	<i>Cyathea medullaris</i> / <i>Cyathea dealbata</i>	<i>Kunzea robusta</i> / <i>Cyathea dealbata</i>	ANOVA/ Wilcoxon Test p
Total Carbon			
Conc. (%)	7.07 – 36.45 – 42.29	3.34 – 9.68 – 21.62	0.001 **
Pool (kg.m ⁻²)	0.39 – 4.97 – 9.09	0.31 – 2.07 – 4.77	0.022 *
Total Nitrogen			
Conc. (%)	0.15 – 0.24 – 0.51	0.01 – 0.11 – 0.16	0.007 **
Pool (kg.m ⁻²)	0.39 – 1.32 – 2.24	0.22 – 0.49 – 1.00	7.5 × 10⁻⁴ ***
C:N	13.89 – 19.05 – 29.77	11.27 – 20.39 – 37.82	0.598 ns
Nitrate NO ₃			
Conc. (mg.kg ⁻¹)	0.34 – 1.15 – 4.69	0.45 – 2.33 – 59.29	0.498 ns
Pool (g.m ⁻²)	0.00 – 0.02 – 0.07	0.00 – 0.42 – 1.27	0.264 ns
Ammonium NH ₄			
Conc. (mg.kg ⁻¹)	17.05 – 126.47 – 238.90	43.83 – 74.42 – 113.67	0.039 *
Pool (g.m ⁻²)	0.33 – 1.54 – 4.56	0.28 – 1.49 – 2.90	0.458 ns
NH ₄ :NO ₃	30.14 – 111.02 – 203.66	4.17 – 43.88 – 192.60	0.917 ns
Phosphorus			
Conc. (mg.kg ⁻¹)	6.13 – 20.21 – 36.20	4.41 – 6.51 – 60.21	0.130 ns
Pool (g.m ⁻²)	0.03 – 0.32 – 0.53	0.03 – 0.14 – 1.74	0.682 ns
pH	5.52 – 5.79 – 6.17	4.57 – 5.01 – 5.27	2 × 10⁻⁸ ***
Charcoal (pieces)	2.50 – 4.33 – 12.72	37.01 – 58.42 – 589.27	3 × 10⁻⁵ ***
Canopy openness (%)	1.07 – 2.62 – 4.05	1.58 – 3.79 – 11.67	0.104 ns
Litter depth (cm)	1.00 – 12.00 – 52.45	0.00 – 3.50 – 14.18	2 × 10⁻¹⁶ ***
Soil depth (cm)	8.14 – 13.60 – 26.11	1.30 – 4.20 – 10.39	2 × 10⁻¹⁶ ***
Tree fern BA (m ² .ha ⁻¹)	3.96 – 21.28 – 57.99	0.00 – 2.14 – 22.39	2.2 × 10⁻¹⁶ ***
Bulk density g.cm ⁻³	0.09 – 0.21 – 0.84	0.34 – 0.47 – 0.82	0.043 *

**Figure 4.** nMDS ordination of the height-weighted seedling abundance data; stress for the ordination plot is 0.25. Arrows indicate vector fits for environmental variables with significant correlations ($P < 0.05$); length of arrows indicates strength of correlation.

Woody species richness (only those with BAs $> 0.5 \text{ m}^2 \text{ ha}^{-1}$ counted) was not correlated with the total tree fern BA in either the entire vegetation dataset (slope \pm SE = 0.05 ± 0.03 , $P = 0.15$, adjusted $R^2 = 0.01$; total tree fern BA range: $0.00\text{--}42.76$, $\bar{x} = 5.54$), or in the *C. medullaris* / *C. dealbata* forest (slope \pm SE = -0.02 ± 0.04 , $P = 0.59$, adjusted $R^2 = 0.01$; total tree fern BA range: $0.00\text{--}38.94$, $\bar{x} = 15.56$).

Influence of spatial vs. abiotic effects on composition

Analysis of the vegetation, abiotic and geographic dissimilarity matrices suggested a strong abiotic influence on the presence of *C. medullaris* / *C. dealbata* forest in the landscape (Table 4). There was no correlation between the abiotic variables and the

distribution of *K. robusta* / *C. dealbata* forest in the landscape when these were considered independently of the *C. medullaris* / *C. dealbata* forest. Nor did we detect any dispersal limitation for successional species between the plots, with both simple and partial Mantel tests being non-significant.

Discussion

Our results identified two distinct pioneer vegetation communities in northern New Zealand forests; the switch that determines which trajectory is followed is initially determined on the basis of abiotic filters (Fig. 3). Pioneer establishment

Table 4. Partial Mantel test values for all tree and sapling data across the Auckland region, and values for separate regeneration pathways under *C. medullaris* / *C. dealbata* forest and *K. robusta* / *C. dealbata* forest.

Vegetation communities (n)	Distance	Mantel <i>r</i>
Combined pioneer communities (n = 166)	Geographic: environmental partialled out	-0.007 <i>ns</i>
	Environmental: geographic partialled out	0.212**
<i>Cyathea medullaris</i> / <i>Cyathea dealbata</i> forest (n = 59)	Geographic: environmental partialled out	-0.109 <i>ns</i>
	Environmental: geographic partialled out	0.251**
<i>Kunzea robusta</i> / <i>Cyathea dealbata</i> forest (n = 107)	Geographic: environmental partialled out	0.049 <i>ns</i>
	Environmental: geographic partialled out	0.011 <i>ns</i>

differentiates along a gradient dominated by changes in annual water deficit and slope. We identified a distinct pioneer community associated with the pioneer species *C. medullaris*, which promotes a seedling community modulated by the presence of *C. medullaris* and the presence of understorey *C. dealbata*, thus supporting our first hypothesis. This pathway is different to the successional trajectory associated with sites with *K. robusta* as a pioneer; even with *C. dealbata* present in the understorey of this forest type (though at lower abundance than the *C. medullaris* associated type). Seedling community composition was associated with tree fern BA and this suggests a response in the regeneration niche to the presence of abundant tree ferns. Although it is not possible to evince independent biotic and abiotic filters (Cadotte & Tucker 2017), we suggest that, in line with the studies of Richardson et al. (2014), Coomes et al. (2005), Gillman et al. (2004) and Walker et al. (2010), tree ferns mediate the regeneration niche beneath them when in sufficient abundance.

In considering early successional communities, one of the key questions is how different compositions are influenced by the original local site conditions or by the dominant pioneer. The influence of dominant pioneer species on the availability of seedling sites may have long-term effects on the composition of vegetation communities (Sullivan et al. 2007; Burton et al. 2011; Paterno et al. 2016). We suggest that New Zealand pioneers, both native and exotic, do influence the regeneration niche of potential forest dominants, by layering a biotic filter on the original heterogeneity in the landscape (Grubb 1977; HilleRisLambers et al. 2012). Therefore, the relative abundance of these pioneers in the landscape is likely to influence the trajectory, timeline and climax vegetation of succession.

Associations between *C. medullaris* and *K. robusta* pioneer communities, abiotic conditions and disturbance types

The hierarchical classification of the forest community vegetation data indicated two distinct vegetation communities associated with the pioneers *C. medullaris* and *K. robusta*. These pioneer-associated communities arose from preferential establishment under different topographic and edaphic conditions, and after fire (as inferred from soil charcoal) in the case of *K. robusta*. *Cyathea medullaris* has several specific traits that facilitate the role of a pioneer species on vegetation-free disturbed soil, often associated with edge habitats and high light environments. In particular, it can establish on exposed bare soil surfaces (after landslides and anthropic activities that disturb soils e.g. forestry harvesting) in, what are for many tree ferns, high irradiance situations (Bystriakova et al. 2011). *Cyathea medullaris* pioneer-associated communities in the landscape (Fig. 1) lead to a (early) successional pathway supporting more notophyll (leaf length 75–125 mm) canopy species different from the well-described *K. robusta* succession

(Wardle 1991), which supports forest communities dominated by microphyll (leaf length <75 mm) taxa.

Kunzea robusta was more common as a pioneer species in drier, flatter, lower elevation areas (Burrows 1973); Burrell (1965) also observed an absence of *Kunzea* establishment on steep, wet slopes. In general, flat, relatively dry, lowland areas have been the focus of human activity over the last 750 years, particularly in terms of forest clearance of timber, intensive agriculture and susceptibility to anthropogenic fires (Ewers et al. 2006; Perry et al. 2012b). Fire destroys primary forest, maintains some fire-adapted successional communities, and causes soil and nutrient loss from ecosystems (Perry et al. 2012a). Evidence of significant volumes of macro-charcoal in the topsoil under *K. robusta* / *C. dealbata* forest suggests that this community establishes in areas of the contemporary landscape that have experienced recurrent twentieth century anthropogenic fires, particularly in steeper, wetter areas where we have identified conditions that might otherwise be suitable for the establishment of *C. medullaris* (Esler & Astridge 1974). Anthropogenic fire has been frequently connected to the re-establishment of *K. robusta* in early successional communities (Payton et al. 1984; Perry et al. 2014). We suggest that the modern prevalence of *K. robusta* in the landscape, particularly as a pioneer species in regenerating forest, may, in part, represent reinvasion or encroachment in response to historic anthropogenic activities in the landscape, in particular fire and alteration of nutrient cycling (Perry et al. 2010). These *K. robusta* successions may develop where other naturally occurring successional systems would, in the absence of anthropogenic fire, have established.

Whilst it is almost impossible to disentangle the relative influence of fire and environment on the *K. robusta* / *C. dealbata* forest (Perry et al. 2010), the main abiotic drivers correlated with the establishment of the *C. medullaris* / *C. dealbata* forest were increased slope steepness, more neutral soil pH, lower ambient temperatures and lower annual water deficit. A more level topography (for example lowland plains) in association with drier, more acidic soils, will likely facilitate the development of a *K. robusta* / *C. dealbata* forest, responding to soil catena from ridge to gully, and conditions most prone to fire and historic anthropogenic activities (logging, grazing etc.). The *C. medullaris* and *K. robusta* associated community establishment process is initiated by abiotic drivers and subsequently modulated and amplified in part by the traits of the pioneers, and the relative abundance of *Cyathea* tree ferns.

Influence of *C. medullaris* and *K. robusta* on the regeneration niche and compositional trajectory towards conifer-broadleaved forests vs. *A. australis* associated forests

Ordinations of the tree, sapling and seedling composition data suggest that pioneer communities are sorted on the basis of

interactive macro-environmental gradients in temperature, elevation, topography and annual water deficit (Fig. 3). However, the BA of tree ferns, which appears decoupled from the abiotic drivers of pioneer species establishment, also influences the position of seedling communities in ordination space. *Cyathea medullaris* / *C. dealbata* forest supports the regeneration of broadleaved podocarp communities characterised by *Laurelia novae-zelandiae* (Atherospermataceae), *B. tawa*, *Dysoxylum spectabile* (Meliaceae) and *Prumnopitys ferruginea* (Podocarpaceae), whereas species regenerating in *K. robusta* / *C. dealbata* forest (relatively lower tree fern abundance) tend towards *A. australis* associated communities faithfully supporting species characteristic of drier, more acid and nutrient-poor soils such as *Coprosma arborea* (Rubiaceae) and *P. trichomanoides* (Burns & Smale 1990; Wyse et al. 2013; Jager et al. 2015). However, this analysis does not suggest conifer-dominance in post-*K. robusta* / *C. dealbata* forest; the relatively small number of faithful species in this community compared to the *Cyathea* pioneer-associated system rather suggests a less predictable community composition in *Kunzea* pioneer-associated systems.

Studies describing patterns associated with tree fern prominence in forest understoreys suggest a suppression of podocarp regeneration (Wardle 1974; Smale et al. 1987; Coomes et al. 2005), and Norton (1991) suggests that seedling establishment is suppressed within tree fern drip-lines. Many of New Zealand's tall podocarp species are light demanding, hence shaded conditions are not conducive to regeneration (Ebbett & Ogden 1998; Lusk et al. 2009). Our data indicate that complete suppression is not necessarily a trait of ecosystems with abundant tree ferns as a rich suite of species occur in such systems. Species associated with *C. medullaris* / *C. dealbata* forest such as *D. spectabile* and *Beilschmiedia tawa* are likely present in these communities as a result of their shade-tolerant life-history traits (Smale & Kimberley 1983; Lusk et al. 2015). Furthermore, as seedlings, the shade tolerant *P. ferruginea* is a faithful component of the *C. medullaris* / *C. dealbata* forest suggesting that certain traits, in particular shade-tolerance, might be significant in determining community assembly and regeneration of the canopy in these systems. *Prumnopitys ferruginea* is also the most common species recorded in the seedling bank by Norton (1991) in a stand where tree ferns were an abundant component of the understorey.

No negative relationships were identified between total tree fern BA per plot and numbers of woody species in either the entire vegetation dataset, or the *C. medullaris* / *C. dealbata* forest in our study (Table 5); the BAs recorded ranged in excess ($>42.8 \text{ m}^2 \text{ ha}^{-1}$) of those described in Richardson et al. (2014) ($21.2 \text{ m}^2 \text{ ha}^{-1}$). We suggest that high tree fern BA *per se* does not suppress regenerating canopy species richness, and that other factors such as dispersal failure, herbivory and

the long-term disturbance regime are a more significant driver for the recruitment failure and arrested successions observed by Richardson et al. (2014). The mechanisms underpinning the influence of tree ferns on seedling regeneration cannot be established from our data because they lack detailed spatial resolution and the location of the tree ferns in relation to the seedling subplots was not recorded; further experimental work is necessary to determine this relationship.

While nutrient concentrations in the organic layer of the two types of sites that were sampled were similar, they did differ in pH, and total C and N pools; all three variables were higher in the organic layer sampled underneath tree fern dominated communities. Isolating the effect of tree ferns on soil nutrient status is difficult because tree ferns are patchily abundant in the understorey of *K. robusta* / *C. dealbata* forest. Moreover, tree fern impacts may be localised as indicated by Silvester (1964) for *D. squarrosa*. The distinct differences in pH, total N and C across the two sets of communities may be a response to the presence of these distinct vegetation communities. Nevertheless, tree ferns will have a strong direct influence on the establishment of seedlings through a combination of lowering available light levels below the canopy and through macro-litterfall (Gillman et al. 2004) creating deep litter (Table 3).

Distinctive communities assembled under the canopies of *C. medullaris* and *K. robusta* were characterised by a recurring suite of high fidelity species that occurred in multiple tiers (for example, *B. tawa*, *Beilschmiedia tarairi* (Lauraceae), *D. spectabile* and *Vitex lucens* (Lamiaceae) were identified as faithful to the *C. medullaris* / *C. dealbata* forest). This outcome suggests that there is a consistent compositional assembly for the *C. medullaris* community. The *K. robusta* / *C. dealbata* forest, present in a narrower range of abiotic conditions than the *C. medullaris* / *C. dealbata* forest, was more variable in community composition, and had fewer faithful species as it fragmented into six separate groups with the removal of the pioneer species from the analysis. While it is difficult to quantify the extent of the contribution of tree fern presence, the number of species faithful to the *C. medullaris* / *C. dealbata* forest suggests that tree ferns function as a strong biotic filter. Teasing apart the influences of fire from the abiotic conditions of the *K. robusta* / *C. dealbata* forest limits interpretation, however, it is likely that the presence of *C. dealbata* in varying abundance within these systems affects the regeneration niche again through shading, nutrient cycling and macro-litterfall (Grubb 1977; Gillman et al. 2004; Perry et al. 2010; Richardson et al. 2014). The seedling community data available to this study were limited in the full consideration of tree ferns as drivers of community assembly; tree fern trunks provide establishment surfaces for many small-seeded species (Bellingham & Richardson 2006; Gaxiola et al. 2008). Although the relatively

Table 5. Tree fern BAs and numbers of woody species with BAs $> 0.5 \text{ m}^2 \text{ ha}^{-1}$ ($\bar{x} \pm 1 \text{ s.d.}$), in vegetation groups and in plots where tree fern BAs $> 21.2 \text{ m}^2 \text{ ha}^{-1}$; significance values from pairwise t-test with Bonferroni correction.

Vegetation groups	\bar{x} BA of tree ferns	\bar{x} no. woody species
^a <i>Cyathea medullaris</i> / <i>Cyathea dealbata</i> forest (n=59)	15.7 \pm 9.9 ^{b,c***}	9.4 \pm 3.3 <i>ns</i>
^b <i>Kunzea robusta</i> / <i>Cyathea dealbata</i> forest (n=107)	5.5 \pm 8.0 ^{a,c***}	6.6 \pm 2.9 ^{a***}
^c Communities where tree fern BA $> 21.2 \text{ m}^2 \text{ ha}^{-1}$ (n=21)	28.7 \pm 5.9 ^{a,b***}	7.8 \pm 2.9 <i>ns</i>

smooth trunk surface of *C. medullaris* provides relatively few attachment points for higher plants (Beever 1984), the presence of *C. dealbata* is likely to influence assembly as an establishment surface.

Influence of spatial versus abiotic effects on community composition

The lack of a strong distance effect between plots vs. community dissimilarity (low values for Mantel tests of Euclidean distance) across the entire Auckland region (including the islands of the Hauraki Gulf) suggests local abiotic conditions are a stronger filter on community assembly in these ecosystems than is species dispersal. Furthermore, it would appear that the establishment of canopy tree species in regenerating forest is occurring despite seed predation and localised herbivory of seedlings and saplings (Smale et al. 1995; Grant-Hoffman et al. 2010; Morales et al. 2016). Where mammalian seed predators are present in the landscape, they preferentially use warmer, steeper topography, and prefer forest supporting *Beilschmiedia* spp., *D. spectabile* and *V. lucens* over *K. robusta* (King et al. 1996; Ogden & Gilbert 2009). This pattern suggests that if seed predation were a significant determinant of differences between the seedling communities then the *C. medullaris* / *C. dealbata* forest would be more affected, but this was not apparent in our analyses.

A common approach to the restoration of native forest systems in northern New Zealand is to plant *K. robusta* as a pioneer species. We suggest this study should encourage promoters of such regeneration and restoration schemes in the North Island to consider using *C. medullaris* where conditions are appropriate (increased slopes, more neutral soil pH, lower ambient temperatures and lower annual water deficit). Planting, and establishment of tree fern sporophytes post-translocation, may not be successful, as sporophytes are not necessarily tolerant or easily transplanted (Eleuterio & Pérez-Saliciup 2009). Furthermore, little is known of the ecology of the gametophyte life-stage of the tree ferns limiting a 'self-seeding' approach by providing a source of spores. Herbicide spraying of *Cenchrus clandestinum* (kikuyu grass) at Tāwharanui Regional Park (north of Auckland) removed a dense, deep sward of grass from a steep bank on the southern slopes of the peninsula (on which the park is located) creating an opportunity for *C. medullaris* to establish (M. Maitland, pers. comm.). This outcome suggests that in some conditions it will be possible to induce a stand of *C. medullaris* to establish as a precursor to tall coastal broadleaved forest.

Summary

Forest regeneration following stand-level vegetation removal in northern New Zealand can commence with pioneer communities of either *K. robusta* or *C. medullaris*. Tree ferns as pioneers are rare globally, particularly in the temperate biome, and in this study we show that they favour steep slopes, with decreased annual water deficit. Under these conditions shade-tolerant broadleaved and podocarp forest species establish beneath the tree ferns. In contrast, *K. robusta* is more common on flat, dry sites that have often experienced fire, and is associated with less shade-tolerant sclerophyllous small-leaved forest species. The communities that establish with these distinct pioneers are different, although both comprise a *C. dealbata* understorey, and appear to support distinct vegetation associations: *C. medullaris* systems are associated with a broadleaved-podocarp forest community; *K.*

robusta systems are associated with *A. australis* communities.

The presence of a high abundance or biomass of *C. medullaris* and *C. dealbata* on sites not historically affected by fire did not limit the establishment of shade-tolerant canopy trees. Furthermore, the presence of tree ferns was strongly associated with seedling communities in ordination space, which suggests biotic filtering across all communities where tree ferns are recorded, both as pioneers, and in the understorey. We found no evidence of community composition being limited by a lack of seed dispersal agents, nor evidence to suggest that high tree fern density is a limiting factor on succession.

This description of a pioneer community dominated by tree ferns is novel for the southern temperate region. Although it is not possible to clarify landscape-level feedbacks from correlative studies alone, this study serves to demonstrate the likely significant influence of tree ferns in the early development of forest ecosystems. Future studies attempting to disentangle the role of tree ferns as determinants of community assembly should focus along gradients of dominance of *K. robusta* vs. *C. dealbata*. In contrast to *K. robusta* vs. *C. medullaris*, the abiotic controls on these species' establishment are less dichotomous, and hence the influence of tree fern presence on community assembly more detectable. Applied research into how to 'seed' *C. medullaris* into the landscape, coupled with research into the ecology of the gametophyte of this unusual tree fern species would usefully inform future habitat restoration projects.

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Supplementary Material

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

Appendix S1. Ordinations of vegetation data using (i) frequency data (S1.1); (ii) presence / absence data (in place of BA data; S1.2); and (iii) BA data with values for *Cyathea medullaris* and *Kunzea robusta* removed (S1.3).

Appendix S2. Table of complete output from indicator species analysis.

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