Evidence for arrested successional processes after fire in the Waikare River catchment, Te Urewera

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Abstract: Anthropogenic fire has transformed New Zealand's vegetation. Small-scale historical Māori fires in the forests of Te Urewera National Park, North Island, initiated forest successions that were dominated early on by *Kunzea ericoides* (Myrtaceae), and later by *Knightia excelsa* (Proteaceae) and *Weinmannia racemosa* (Cunoniaceae). Previous work in these forests suggested that the more recent of these successions, initiated after the arrival of deer in the late 19th century, have failed to recover to pre-fire composition and structure. This failure was attributed to browsing pressure that prevented palatable canopy tree species such as *Weinmannia racemosa* establishing at adequate densities. We tested this hypothesis by quantifying changes in forest structure, tree species composition and above-ground tree biomass between 1980 and 2010 using permanent forest plots in three successional communities. The three communities were dominated by (1) *Kunzea ericoides* – kanuka, (2) *Knightia excelsa* – rewarewa, and (3) *Weinmannia racemosa* – kamahi. We show that above-ground biomass increased in all communities between 1980 and 2010, and did so most strongly in the first two communities. However, tree species composition changed little over the same time except for a more than three-fold increase in tree fern abundance in the kanuka community where they are now co-dominant with *Kunzea ericoides*. Recruitment of trees of canopy species was very low (≤ 0.06% per year) relative to mortality (1.1–3.9% per year) in all three communities. The proportional increase in above-ground biomass observed in the kanuka community was low relative to the large proportional increase in basal area. This occurred because of the higher abundance of tree ferns in 2010 plots that have low stem tissue density. The minimal compositional change over 30 years in these communities and paucity of recruitment of trees of canopy species point to arrested succession. Without management intervention to increase tree recruitment rates of canopy species, forest successions in this region will be characterised by high tree fern abundance, low biomass at local scales, and limited transitions to tall forest communities.

Keywords: carbon storage; *Cyathea dealbata*; dark diversity; fire ecology; herbivore-mediated arrested succession; New Zealand

Introduction

Anthropogenic fires have made a widespread impact on the extent and composition of woody vegetation around the world (Bowman et al. 2009). New Zealand is distinctive in that human settlement was recent (c. AD 1280; Wilmshurst et al. 2008) and prehuman fires were infrequent (Ogden et al. 1998; McGlone & Wilmshurst 1999; Perry et al. 2013). Few New Zealand tree species are adapted to survive fire (Perry et al. 2013), and fires typically initiate a secondary succession with few living trees from the original community. Young successional stands are often dominated by one or both of two highly flammable myrtaceous tree species (*Leptospermum scoparium* or *Kunzea ericoides*) (Cameron 1960; Wardle 1991; Perry et al. 2010). Transition to tall forest communities under present-day fire regimes is thus contingent on rapid establishment of less flammable rainforest tree species. The pace at which less flammable canopy tree species establish has been slowed throughout many parts of New Zealand by soil erosion following fire (Perry et al. 2010), loss of native avian dispersers (Cameron 1954; Kelly et al. 2010), and browsing pressure from introduced deer (McKelvey 1955; Wardle et al. 2001), possums and rats (Wilson et al. 2003), with greatest consequences in early-successional environments (Mason et al. 2010). Without recruitment of canopy tree species, early-successional communities cannot transition to mature forest and successional change slows to the point that the succession is described as arrested, stalled or inhibited (Connell & Slatyer 1977; Zanne & Chapman 2001).

Mechanisms underpinning transitions between successional states must be understood in order to identify the causes of arrested succession (Standish et al. 2008). Detecting and demonstrating arrested successions relies on proposing expected structural and compositional trajectories for a site, against which observed changes can be assessed (Connell & Slatyer 1977; Zanne & Chapman 2001; Standish et al. 2008). In mixed-species forests, compositional shifts to late-successional species are typically associated with declining stem density, and increasing mean stem diameter, basal area and above-ground biomass (e.g. Christensen 1977; Peet 1981; Saldarriaga et al. 1988). Hypothesised compositional trajectories accompanying those structural changes can be developed using long-term palynological records (e.g. Wilmshurst et al. 1997), historical accounts of succession (e.g. Wassilieff 1986), stand reconstructions (e.g. Payton et al. 1984), and by reviewing the regional species pool and determining which species are absent from any specific site from the pool of possible species – the 'dark diversity' sensu Pärtel et al. (2011).

Te Urewera is the largest area of indigenous forest in the North Island. In contrast to forests elsewhere in New Zealand with similar elevation and climates, Te Urewera has retained its forest cover despite centuries of human settlement and land use activities (Best 1925). In Te Urewera and throughout New Zealand, early Māori used fire to clear forests, primarily to cultivate crops and to encourage bracken fern (*Pteridium esculentum*; Dennstaedtiaceae) for its edible rhizomes, and to clear the land for defence, habitations and transport (Best 1925; McGlone et al. 2005). Frequent fires over the last 700 years have created a mosaic of successional communities throughout Te Urewera ranging in age and extent (McKelvey 1973). Successional communities are often dominated by *Kunzea ericoides* or *Leptospermum scoparium*, initially with other short-statured hardwood species (e.g. *Pittosporum tenuifolium*, Pittosporaceae) and the tree fern *Cyathea dealbata* (Cyatheaceae), later with *Knightia excelsa* (Proteaceae) and *Weinmannia racemosa* (Cunoniaceae) and eventually with young podocarp trees (Cameron 1954, 1960; McKelvey 1955; Beveridge 1973; Payton et al. 1984). However, while this successional pathway is apparent from space-for-time reconstructions across the landscape, and from palynological records (e.g. Wilmshurst et al. 1997), it is rarely observed under present conditions in Te Urewera forests following natural disturbance. This has led to the suggestion that successional processes are arrested in these forests. McKelvey (1955) proposed that compositional change from early- to late-successional communities was not occurring in the region because of ungulate browsing of broadleaved tree species under *Kunzea ericoides*. In particular, he focused on *Weinmannia racemosa* and its critical role in facilitating the establishment of later successional tree species. McKelvey (1955) showed that succession in these forests relies strongly on the establishment of *Weinmannia racemosa*, which acts as a nurse tree for the establishment of podocarps because the spreading canopy architecture appeals to perching birds (Beveridge 1973). *Weinmannia racemosa* also permits a relatively high proportion of light to reach the understorey, which is conducive to the growth and survival of podocarp seedlings (Norton 1991). Deer preferentially browse *Weinmannia racemosa* (Wardle & MacRae 1966; Husheer 2007) and McKelvey (1955) reasoned that significant reductions in the abundance of *W. racemosa* and other hardwood species throughout Te Urewera following the arrival of deer would contribute to arrested succession in *Kunzea ericoides* stands. We further suggest that greatly reduced bird densities (Lyver et al. 2008; Kelly et al. 2010) and consequently diminished avian seed dispersal (Cameron 1960) would slow succession.

In this study, we test McKelvey's hypothesis that post-fire successions in Te Urewera are arrested because canopy tree recruitment is inadequate to yield compositional change. We remeasured 16 permanent vegetation plots in three post-fire successional forest communities in the Waikare River catchment, central Te Urewera, to evaluate evidence for arrested succession over a period of 30 years (1980 to 2010).

Materials and methods

Permanent plots

The study area was the Waikare River catchment, central Te Urewera, New Zealand (38°27′ S, 177°11′ E). Mean annual temperature is 10.0°C (summer mean is 14.5°C, winter mean is 5.6°C) and mean annual rainfall is 1730 mm, distributed equally through the year. Water deficits occur during summer (Leathwick et al. 2003) when the monthly mean number of rain days is just six and solar radiation is high (mean is 19 MJ m^{-2}) (all climate data from the Tarapounamu Climate Station, 2007–2013 inclusive, CliFlo Database, NIWA, 2013). Sixteen permanent plots (20 × 20 m) were established in 1980. Plots were subjectively located in three discrete successional communities dominated by (1) *Kunzea ericoides* (kānuka community; *n* = 7 plots), (2) *Knightia excelsa* (rewarewa community; *n* = 5 plots), and (3) *Weinmannia racemosa* (kāmahi community; *n* = 4 plots) (Beadel 1991) that form a sequence from early to mature post-fire successions (Fig. 1). Communities were defined following extensive reconnaissance of the Waikare region and post-fire stand reconstructions (Payton et al. 1984). The kānuka community had a minor component of *Melicytus ramiflorus* (Violaceae) and *Cyathea dealbata*, beneath a dense monospecific canopy of *Kunzea ericoides*. The rewarewa community was defined by dominant large individuals of *Knightia excelsa* with an understorey of *Kunzea ericoides* and *Cyathea dealbata*, and scattered young individuals of *Weinmannia racemosa*. The kāmahi community was dominated by a canopy of *Weinmannia racemosa* with scattered *Knightia excelsa* individuals, little if any *Kunzea ericoides* and young trees of late-successional species such as *Dacrydium cupressinum* and *Elaeocarpus dentatus* (Elaeocarpaceae) (Beadel 1991). We did not date the time since fire in our communities but, on the basis of diameter–age relationships in Payton et al. (1984), the kānuka community contained a small number of individuals (<10) with a modelled age of 100–170 years, which may approximate the age of

Figure 1. Post-fire successional communities in the Waikare River catchment, Te Urewera, New Zealand: (a) open *Knightia excelsa* community-type with scattered *Kunzea ericoides* and an understorey of *Cyathea dealbata* and ground cover of *Microlaena avenacea*; (b) dense understorey of *Cyathea dealbata* below a senescing canopy of *Kunzea ericoides*.

the community itself. At plot establishment, the diameter at breast height (dbh, cm) was measured on all trees with dbh ≥ 2.5 cm and these were identified to species and tagged with a unique identifier. We remeasured stem diameters (Hurst & Allen 2007) in 2010 and additionally measured tree heights on a subset (between 1 and 206, depending on species) of live individuals.

Compositional change

We assessed compositional change within each plot and across all plots in each community, using stem basal area data. We calculated total basal area of each species on each plot in 1980 and 2010 from stem diameter; assessed change in median basal area for each species within each community, using Mann–Whitney *U* tests; and whole-community change in composition, using ordination. Basal area data were log-transformed while preserving zero values following McCune et al. (2002). We used non-metric multidimensional scaling (NMS) to optimally arrange the compositional data from each plot in 1980 and 2010 in multidimensional space. NMS was performed in the *vegan* library of R (Oksanen et al. 2012). We tested for a statistical difference in composition among the three communities and between the two years, using a non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). This was implemented in R, using *adonis* in the *vegan* library with default settings.

We calculated stem recruitment and mortality rates for all stems of canopy tree species combined across all plots in each community. Canopy tree species were defined as those that could achieve a height of ≥ 15 m and thus contribute to a mature forest canopy (McGlone et al. 2010). We calculated annualised stem recruitment rates (r) as:

r (% per year) = 100 × [(1 + number of recruits / number of stems initially) (1/number of years) – 1]

and annualised stem mortality rates (m) as:

m (% per year) = 100 × {[$\log_e$(number of stems initially) – $\log_e$(number of stems surviving)]/number of years}.

Live stem biomass

We estimated above-ground live stem biomass from allometric equations published in Coomes et al. (2002) and species-specific stem tissue density. We modelled live stem volume on each plot at each measurement, using dbh and tree height. Tree heights were either measured in 2010 or estimated from dbh. The relationship between dbh and height was modelled for each species, using the data collected in 2010 from these plots where sufficient numbers of individuals were available, or, for remaining species, using a dataset collected at a national scale from the New Zealand Land Use and Carbon Accounting System (LUCAS) (Beets et al. 2012). We used a log-log regression (Coomes et al. 2002) to model stem height, using species, elevation and dbh. These regressions were used to estimate stem height of all the individuals in our 16 plots in 1980 and 2010 where height data were not available. Live stem volumes were converted to biomass, using stem-specific tissue density (i.e. oven-dry mass of a whole-stem sample including bark, relative to fresh volume; Table 1) measured on at least three individuals of each species in the study area, or taken from published data for the central North Island (Hinds & Reid 1957; Beets et al. 2008, 2012).

The method for measuring tree ferns differed between 1980 and 2010. In 1980 all individuals with foliage ≥1.35 m tall were counted in each plot. In 2010, all individuals with foliage≥1.35 m tall were counted and adult tree ferns, i.e. those with a stem height ≥1.35 m, were also tagged for measurement of dbh and stem height. Height and diameter data are required to calculate live stem biomass so these data had to be inferred for the 1980 population. For each plot, we calculated the proportion of all tree ferns that were tagged adults in 2010. We assumed that this proportion had remained stable between 1980 and 2010 in each plot and used this to estimate the number of individuals in the 1980 count that would have been adults. As a conservative approach for estimating stem biomass, these individuals were allocated the mean diameter and height for that species on that plot from the 2010 data. Recruitment and mortality rates were not calculated for tree fern species as tagged individuals are essential for these calculations.

We used mixed-effects models to assess whether change in structural measures between 1980 and 2010 differed among communities. Observations were non-independent within plots between years and this was accommodated using a random effect. Models of stem counts and species richness used

Table 1. Stem tissue density and median basal area in 1980 and 2010 for seven species in three communities in the Waikare River catchment, te Urewera, New Zealand. Data are only presented for those species with a median basal area ≥0.5 m^2 ha^{-1} at either measure in a community. Medians are presented, as data violate the assumptions of normality required for parametric statistics. Differences in the medians between 1980 and 2010 were tested for using Mann–Whitney *U* tests.

Species	Stem tissue density	Kānuka Community			Rewarewa Community			Kāmahi Community		
		Basal area			Basal area			Basal area		
	(kg m^{-3})	1980	2010	Change	1980	2010	Change	1980	2010	Change
Tree species										
Kunzea ericoides	638 (13, *n* = 6)*	21.2	24.2	NS	21.5	22.4	NS			
Knightia excelsa	523 (7, *n* = 4)**				7.0	12.0	NS	3.1	0.0	− (*P* = 0.07)
Weinmannia racemosa	523 (19, *n* = 15)**				21.8	26.3	NS	40.2	37.7	NS
Beilschmiedia tawa	508 (13, *n* = 11)**							0.7	2.5	NS
Melicytus ramiflorus	404 (3, *n* = 3)*	3.4	1.9	NS						
Tree fern species										
Cyathea dealbata	260 (11, *n* = 22)**	11.2	21.2	+ (*P* = 0.0006)	0.9	1.9	NS	1.9	3.3	NS
Dicksonia squarrosa	177 (23, *n* = 6)*	0.2	1.8	+ (*P* = 0.08)	0.2	1.8	NS			

* Samples collected near Ruatāhuna for this study; ** Values from Beets et al. (2012).

generalised linear mixed-effects models with Poisson errors. These were implemented in R, using *glmer* in the *lme4* library. Models of basal area, above-ground stem biomass and mean diameter used linear mixed-effects models implemented in R using *lme* in the *nlme* library.

Finally, we evaluated the relationship between community mean basal area and live stem biomass, relative to all New Zealand indigenous forests. Our goal was to provide a wider context for how forest biomass should increase with stand basal area. To examine New Zealand indigenous forests, we calculated basal area and live stem biomass across all LUCAS plots (using the methods described above) measured between 2002 and 2007 and plotted these two attributes against one another. We superimposed the means for our three communities in 1980 and 2010.

Results

Tree species composition changed significantly only in the kānuka community (Table 1; Figs 2 & 3). Stem density of *Cyathea dealbata* increased nearly three-fold between 1980 and 2010 in the kānuka community (Fig. 3), and basal area of *Cyathea dealbata* doubled (Table 1) to the point where it was co-dominant with *Kunzea ericoides* (Table 1; Fig. 2). Stem density (Fig. 3) and basal area (Table 1) of another tree fern – *Dicksonia squarrosa* – also increased in the kānuka community, although this species was much less abundant than *Cyathea dealbata* (Table 1; Fig. 3). Tree fern abundance increased in the rewarewa and kāmahi communities, but not significantly so (Table 1; Fig. 3). Similarly, basal area of *Knightia excelsa* declined significantly in the kāmahi community (Table 1) and basal area of *Beilschmiedia tawa* (Lauraceae) increased non-significantly (Table 1; Fig. 2). Composition scarcely changed in the rewarewa community (Table 1, Figs 2 & 3).

Rates of canopy tree recruitment were very low (<0.06% per year) and substantially less than mortality rates (Table 2). Only 21 trees were recruited over the total of 0.64 ha measured, and most of these were *Kunzea ericoides* ($n = 11$ stems). No *Weinmannia racemosa* stems were recruited into the kānuka community, and only two podocarp stems were recruited – a *Dacrydium cupressinum* stem in the kāmahi community and a *Podocarpus cunninghamii* stem in the kānuka community. Only 9 of the 21 recruits were ≥10 cm dbh. Sapling counts of canopy tree species were low in all communities and declined across all three communities between 1980 and 2010, significantly so in the kānuka community (Table 3). Tree species (including tree ferns) richness was low (richness ranged from 2 to 12 species in a 400-m^2 plot, and mean richness across all plots was just 6.6 species) and did not change between 1980 and 2010 in any community (Table 3).

Mean stem diameter and stem density did not change significantly between 1980 and 2010 in any of the three communities (Table 3). Basal area increased in all three communities but only significantly so in the kānuka community (Table 3). Above-ground biomass increased in all three communities (Table 3) and the increases for each community were examined by plotting basal area against modelled biomass (Fig. 4). Mean basal area and mean above-ground biomass increased in all three communities but the slope of the relationship between these two was shallow in the kānuka community relative to the nationwide dataset (Fig. 4).

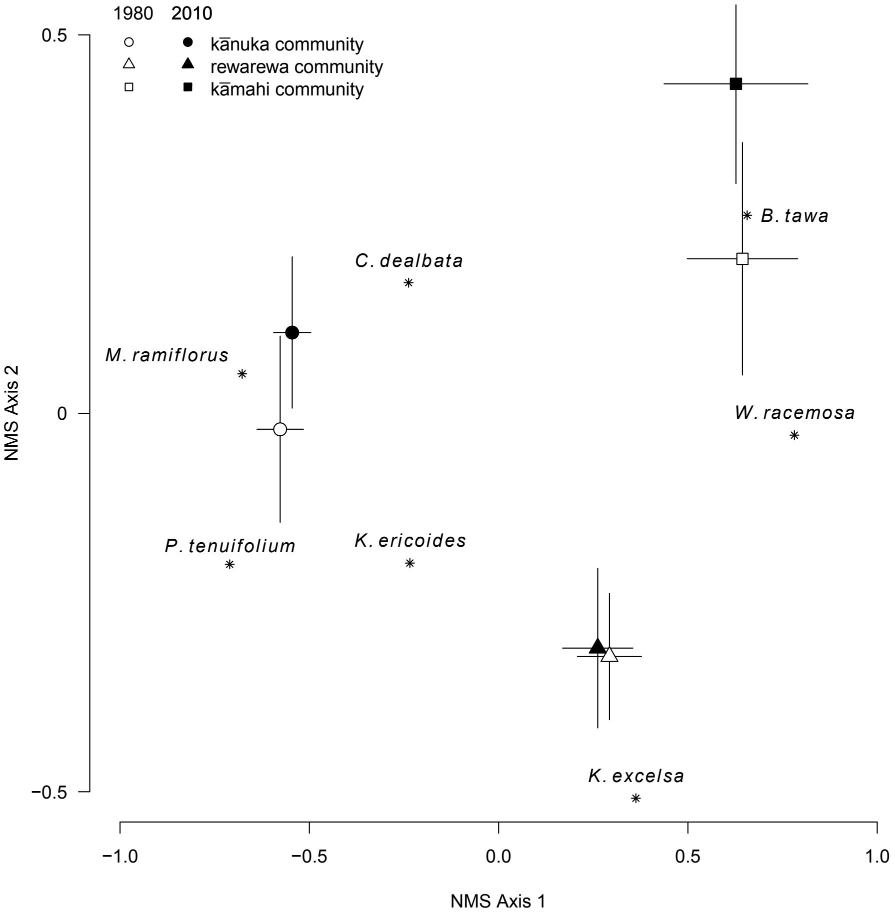

Figure 2. Non-metric multidimensional scaling ordination illustrating change in forest composition between 1980 and 2010 in three successional communities in the Waikare River catchment, Te Urewera, New Zealand, on the basis of basal area of stems ≥ 2.5 cm dbh in 16 plots. The mean positions of plots in each community are shown with 1 SE. Centroids for dominant species (*Beilschmiedia tawa, Cyathea dealbata, Knightia excelsa, Kunzea ericoides, Melicytus ramiflorus, Pittosporum tenuifolium* and *Weinmannia racemosa*) are shown with *. Permutational multivariate ANOVA (PERMANOVA) on the interaction term between community type and year: $F'_{2,26} = 0.56$, $P = 0.058$.

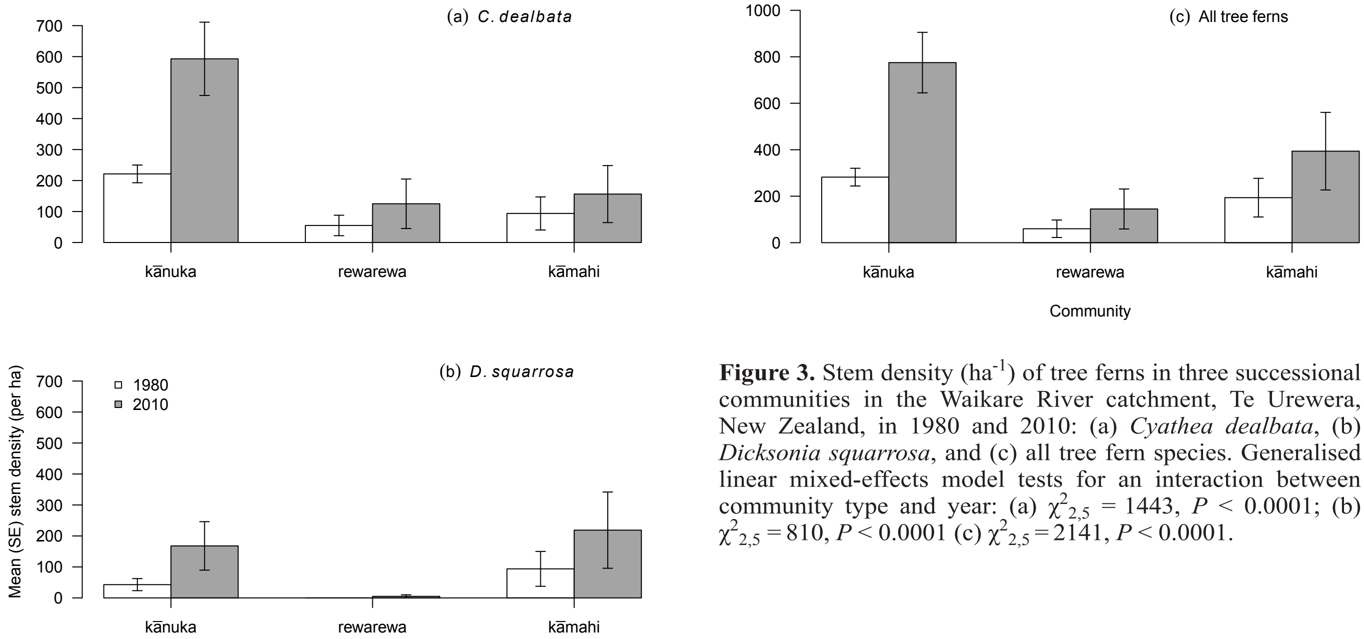

Figure 3. Stem density (ha^{-1}) of tree ferns in three successional communities in the Waikare River catchment, Te Urewera, New Zealand, in 1980 and 2010: (a) *Cyathea dealbata*, (b) *Dicksonia squarrosa*, and (c) all tree fern species. Generalised linear mixed-effects model tests for an interaction between community type and year: (a) $\chi^2_{2,5} = 1443$, $P < 0.0001$; (b) $\chi^2_{2,5} = 810$, $P < 0.0001$ (c) $\chi^2_{2,5} = 2141$, $P < 0.0001$.

Table 2. Canopy tree recruitment and mortality rates for stems ≥ 2.5 cm dbh between 1980 and 2010 in 16 permanent 400-m^2 plots in three successional forest communities in the Waikare River catchment, Te Urewera, New Zealand. Canopy tree species are those that reach ≥ 15 m (McGlone et al. 2010): *Beilschmiedia tawa, Dacrydium cupressinum, Knightia excelsa, Kunzea ericoides, Podocarpus cunninghamii* and *Weinmannia racemosa.*

Community	Initial no. trees	No. surviving	Recruits	Mortality rate (% per year)	Recruitment rate (% per year)
Kānuka	715	224	11	3.87	0.05
Rewarewa	458	275	9	1.70	0.06
Kāmahi	274	199	1	1.07	0.01

Table 3. Forest structure in 1980 and 2010 and change between those two times in three successional post-fire communities in the Waikare River catchment, Te Urewera, New Zealand. Data are means (± 1 SE) across the plots in that community type. All measures are based on stems with dbh ≥ 2.5 cm. Linear mixed-effects model *P*-values indicate the effects of year (Yr) and Community (C) on each measure (NS = $P > 0.05$) ($n = 32$ for all models). Data for basal area and live stem biomass were log$_{10}$-transformed for analysis.

	Year	Kānuka	Rewarewa	Kāmahi	Yr × C	Yr	C
Canopy tree sapling density (ha^{-1})	1980	704 (428)	40 (34)	450 (433)	<0.0001	-	-
	2010	21 (18)	5 (5)	206 (174)			
	Change	−682 (429)	−35 (35)	−244 (261)			
Species richness	1980	7.0 (0.5)	5.6 (1.1)	6.0 (1.1)	NS	NS	NS
	2010	8.6 (1.0)	5.4 (1.2)	6.0 (0.7)			
	Change	1.6 (0.8)	−0.2 (0.8)	0.0 (0.8)			
Mean diameter (cm)	1980	12.4 (2.1)	14.9 (1.5)	19.3 (2.4)	NS	NS	0.0326
	2010	15.2 (2.1)	19.8 (1.1)	19.9 (1.6)			
	Change	2.8 (3.5)	4.9 (0.7)	0.7 (1.2)			
Stem density (ha^{-1})	1980	3300 (853)	2505 (421)	2069 (976)	NS	NS	NS
	2010	3018 (481)	1650 (155)	1756 (592)			
	Change	−282 (1073)	–855 (339)	−313 (396)			
Basal area (m^2 ha^{-1})	1980	41.7 (2.1)	54.6 (8.8)	63.3 (10.0)	0.0043	-	-
	2010	67.3 (5.1)	63.7 (6.8)	66.8 (11.8)			
	Change	25.6 (5.3)	9.1 (2.7)	3.5 (3.9)			
Live stem biomass (Mg ha^{-1})	1980	141.9 (15.2)	225.3 (42.8)	247.4 (31.0)	NS	0.0003	0.0231
	2010	219.5 (10.8)	302.9 (29.8)	271.4 (47.0)			
	Change	77.5 (19.7)	77.5 (16.9)	23.9 (23.9)			

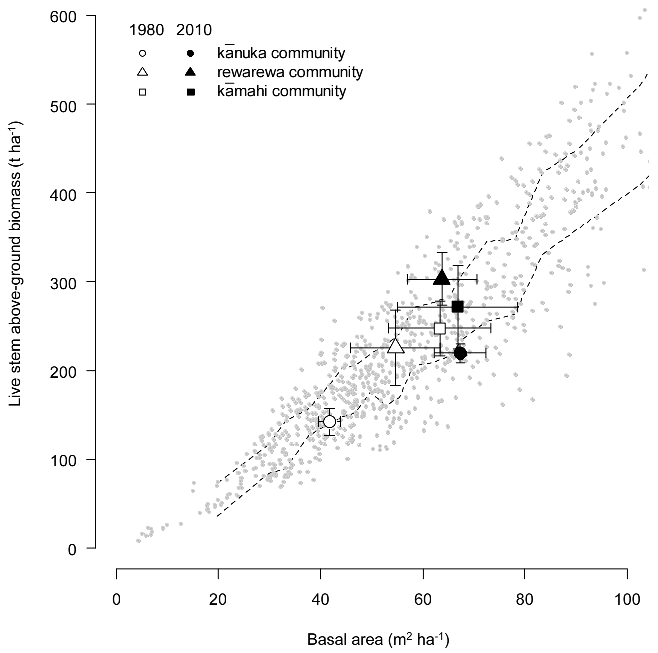

Figure 4. Changes in community mean basal area and above-ground live stem biomass in three successional communities between 1980 and 2010 in the Waikare River catchment, Te Urewera, New Zealand, viewed relative to basal area and above-ground live stem biomass data from 821 objectively located permanent plots in forests and shrublands throughout New Zealand (Beets et al. 2012) where basal area was <100 m^2 ha^{-1}. Each community is represented by two points – one showing the mean basal area and above-ground biomass in 1980, and another for 2010. Dashed lines show the upper and lower quartiles of the objective nationwide dataset.

Increasing basal area in the kānuka community was largely driven by tree ferns and hence was associated with only a modest increase in above-ground biomass (Fig. 4). Per-unit basal area, the kānuka community is supporting low live-tree above-ground biomass relative to the two, more developed successional communities (Fig. 4).

Discussion

Our analyses of remeasured permanent forest plots in post-fire successional forests in Te Urewera show strong support for the hypothesis of McKelvey (1955) that successional processes are arrested in these forests, most likely because of negligible recruitment of canopy tree species. Although the forests have accumulated above-ground biomass in accordance with general models of forest succession (Christensen 1977; Peet 1981; Saldarriaga et al. 1988) there was almost none of the compositional change essential for the development of mature rainforest communities. Importantly, regeneration was not even cyclical within a community, for example *Kunzea ericoides* was not replacing itself in the kānuka community, but was instead being replaced by tree ferns that occupy basal area and contribute little to above-ground biomass. Transitions to later successional states will not occur without recruitment of tall canopy dominants, and recovery to tall podocarp–tawa forest is likely to fail or be severely delayed without such recruitment.

Mechanisms limiting successional change

Successional change was limited by very low rates of canopy tree recruitment, notably the complete absence of *Weinmannia racemosa* recruitment into the kānuka community, and the very limited recruitment of podocarps into later-successional rewarewa or kāmahi communities. Detailed observations of forest succession in the Hawke's Bay (Tutira Station) indicate that sapling regeneration of mature rainforest species into *Leptospermum scoparium – Kunzea ericoides* communities can occur within a hundred years of burning (Wassilieff 1986). Many of the *Kunzea ericoides* individuals in our communities were ≥ 30 cm dbh, which we can assume to be at least 70 years old according to the size–age model of Payton et al. (1984). Even if these were first-generation individuals after fire, we would expect to see recruitment of late-successional canopy tree species in this community.

Recruitment failure could be occurring at the seed (inadequate seed rain) or seedling (seedling mortality) stage. Inadequate seed rain is highly unlikely for *Weinmannia racemosa* given the abundance of this species in the Urewera region (McKelvey 1973) and its very small, wind-dispersed seeds (0.07 mg; Richardson et al. 2013). In contrast, all the podocarp conifers and many of the significant, later-successional angiosperm species in these forests (e.g. *Beilschmiedia tawa*, *Elaeocarpus dentatus*, *Nestegis cunninghamii* (Oleaceae)) have fleshy fruits and are bird dispersed. Both the richness and abundance of native avian dispersers have been unambiguously diminished by predation from introduced mammals (Lyver et al. 2008; Kelly et al. 2010). Loss of native avian dispersers has impacted on seed dispersal of large-fruited species but these effects are most often reported from highly fragmented landscapes (e.g. Wotton & Kelly 2011), which are not comparable with the extensively forested landscapes of Te Urewera. Seedling herbivory, by ungulates, possums and rodents, is more likely to be the mechanism limiting tree recruitment rates in the Waikare catchment. This assertion could only be tested by factorial seed addition in the presence and absence of ungulate or possum herbivory. Establishment of experimental exclosures would provide a complementary test of our conclusion, drawn here from longitudinal data. Explicit manipulation of ungulate densities during early succession, when selective herbivory has the greatest potential to alter community assembly processes (Mason et al. 2010), would be a powerful test of the hypothesis that ungulate herbivory limits recruitment of trees of canopy species, and thus drives arrested succession. However, a strong role for herbivory would be consistent with the observations of McKelvey (1955) in Te Urewera, and with observations elsewhere in New Zealand (e.g. Ogden & Buddenhagen 1994; Smale et al. 1995). More widely, herbivore-mediated arrested succession has been demonstrated in coastal *Acacia* forests in South Africa (Boyes et al. 2011), explicitly because herbivores – in this case, native herbivores – browsed seedlings of canopy tree species. A similar mechanism was inferred from stand reconstructions in *Juniperus* shrublands from northern Spain in which recruitment pulses by seedlings of canopy tree species were coincident with periods of low domestic animal densities (DeSoto et al. 2010). However, direct herbivory on tree seedlings need not occur for herbivores to impede succession; elephant trampling of nurse plants indirectly killed seedlings of canopy tree species in logged tropical rainforest in Uganda, thus preventing forest recovery (Paul et al. 2004).

Small-seeded canopy tree seedlings such as *Weinmannia racemosa* commonly regenerate epiphytically on tree ferns where it is claimed they 'escape' from browsing animals (Gaxiola et al. 2008). However, we saw no circumstantial evidence that tree ferns were facilitating *Weinmannia racemosa* regeneration in any community, despite the abundance of tree ferns. Tree ferns have a complex functional role in forest successions because they can both inhibit and promote canopy tree seedling establishment (Walker et al. 2010). We suggest that epiphytic establishment of canopy tree seedlings is a minor process in these forests. A comparative survey of *Weinmannia racemosa* seedling (≥ 15 cm) occurrence on tree ferns in compositionally-similar successional forests from the nearby Whakatāne River catchment, adjacent to our study area, revealed that <6% of *Cyathea dealbata* or *Dicksonia squarrosa* individuals hosted seedlings of any size, and <1.5% hosted seedlings ≥ 15 cm high (unpubl. data). This contrasts strongly with studies in perhumid forests from southern Fiordland where 24% of *Dicksonia squarrosa* and *Cyathea smithii* stems had seedlings ≥ 15 cm high (Gaxiola et al. 2008; Aurora Gaxiola, pers. comm.). We suggest that the combination of warm, dry summers and loose leaf bases retained on the stem of *Cyathea dealbata* drought-stresses small seedlings and few survive their first summer. Establishment beneath tree ferns is impeded by dense shade and deep accumulations of macrolitter (Gillman & Ogden 2005) that forms loose deposits that dry out in summer. Epiphytic establishment of *Weinmannia racemosa* seedlings has also been reported from rootplate mounds and coarse woody debris (Smale et al. 1997). Biomass of coarse woody debris across all plots (mean = 20.5 Mg ha^{-1} ± 4.7 SE) was significantly below the national average (54 Mg ha^{-1}) for New Zealand's forests (Richardson et al. 2009) and rootplate mounds were scarce in these early-successional forests because they generally lack large trees that are most likely to generate substantial rootplate mounds.

Ecosystem consequences of arrested successions

Species, through their functional traits, exert a strong effect on the development of forest biomass during succession. Alternative compositional successional pathways can yield contrasting outcomes for forest biomass and other emergent ecosystem properties, particularly early during succession when mature forest canopies are still developing and initial compositional differences are maintained (Wardle 1980; Peet 1981; Christensen & Peet 1984). Early-successional woody species commonly have plant traits suitable for taking advantage of short-lived canopy gaps, such as low wood density, short maximum height, a short lifespan and rapid height growth (Brown & Lugo 1990). Consequently, early-successional communities usually have low biomass. Early-successional communities in New Zealand are somewhat unusual in this regard as they are commonly dominated by *Kunzea ericoides*, which has dense wood (Table 2) and a maximum height of 25 m, which is comparable with many later-successional canopy tree species (McGlone et al. 2010). Transition of kānuka communities to those with later-successional species that have lower stem tissue density may therefore be associated with a short-term decline in biomass stocks.

Failure of late-successional tree species to establish in these communities has limited the accumulation rate of above-ground biomass. Traditional models of succession based on species composition are now being augmented by knowledge of how rapidly biomass (and by extension, carbon) accumulates following disturbances of varying intensities and scales, how species turnover drives carbon accumulation, and whether trends can be generalised across forest ecosystems (Carswell et al. 2012). Maintenance of existing forest biomass and restoration of formerly forested lands are current management priorities to mitigate the effects of carbon emissions, and the trends reported here indicate that the accumulation of forest biomass during succession can be slowed by forces that limit recruitment of canopy tree species (e.g. ungulate browse; Holdaway et al. 2012), and the arrival and expansion of tree fern species, which contribute little biomass relative to their basal area. The large increase in tree fern biomass we report here relies to some extent on the estimated diameters and heights applied to count data from 1980. This approach will introduce uncertainty into our analyses but we are confident that our results are qualitatively robust because of the substantial increases in tree fern stem density recorded between 1980 and 2010 (Fig. 3). Biomass typically increases during the initial stages of succession, at which point, death of long-lived early-successional species offsets biomass gained by later-successional species (Saldarriaga et al. 1988). Biomass accumulation is slow after that point as it relies on slow growth of late-successional species to large individuals to accrue further biomass. Without recruitment of those species though, there is little prospect of these forests recovering biomass to pre-fire levels.

Future successions in Te Urewera

Forecasting the long-term outcomes of past disturbance events is challenging for forest ecosystems dominated by long-lived, slow-growing tree species, but can be assisted by historical and palaeoecological records. Our approach has been to rely on historical records of successional change against which we can test our observations from 30 years of permanent-plot data. Our permanent-plot data have captured significant mortality of the *Kunzea ericoides* canopy in the kānuka community. This tree canopy has been replaced by tree ferns (see also Ogden & Buddenhagen 1994) and in some areas by the shrub species *Brachyglottis repanda* (Asteraceae), and without intervention these communities will become short-statured tree fern – shrub communities. Similar predictions have been made for forest remnants in North Island hill country, exposed to domestic grazing (Smale et al. 2008).

Our 30 years of data did not capture widespread death of mature *Knightia excelsa* and *Weinmannia racemosa* stems in their respective communities, but, given the modest and increasing basal area of tree fern species in the latter community, and the negligible recruitment rates and sapling densities in both communities, we anticipate greater tree fern abundance and reduced above-ground biomass. Multi-stemmed individuals of *Weinmannia racemosa* may persist through resprouting, but this process will only be plausible above the deep shade cast by tree ferns, and beyond browse damage. Browsing intensity has almost certainly varied over the period 1980–2010 covered by our permanent-plot observations, and since McKelvey (1955) first described the impacts of ungulate herbivory in these forests. Historical and current ungulate densities in Te Urewera can only be inferred from descriptions in McKelvey (1955, 1973) and regional compilations of data from ungulate faecal pellet counts (Forsyth et al. 2011). These information sources suggest that browsing pressure would have been greatest in the 1950s, least in 1980 when our plots were established, and moderate now (2010 to the present). Successions initiated under the current environment – of low disperser densities, moderate ungulate browsing, and propagule pressure from exotic tree species (Smale 1990) – will follow even less desirable trajectories than those outlined here. Future forest successions will be characterised by high tree fern abundance, low biomass at local scales, and limited transitions to tall tree cover, and be vulnerable to exotic tree invasion.

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