Patterns of tree community composition along a coastal dune chronosequence in lowland temperate rain forest in New Zealand

Benjamin L. Turner · Andrew Wells ·
Kelly M. Andersen · Leo M. Condron

Abstract Soil chronosequences provide an opportunity to examine the influence of long-term pedogenesis on the biomass and composition of associated tree communities. We assessed variation in the species composition of trees, saplings, and seedlings, and the basal area of adult trees, in lowland temperate rain forest along the Haast chronosequence on the west coast of the South Island of New Zealand. The sequence consists of Holocene dune ridges formed following periodic earthquake disturbance and is characterized by rapid podzol development, including a marked decline in phosphorus concentrations, accumulation of a thick organic horizon, and formation of a cemented iron pan. Tree basal area increased for the first few hundred years and then declined in parallel with the decline in total soil phosphorus, consistent with the concept of forest retrogression. There were also marked changes in the composition of the tree community, from dominance by conifers on young soils to a mixed conifer–angiosperm forest on old soils. Although a variety of factors could account for these changes, partial Mantel tests revealed strong correlations between tree community composition and soil nutrients. The relationships differed among life history stages, however, because the adult tree community composition was correlated strongly with nutrients in the mineral soil, whereas the seedling community composition was correlated with nutrients in the organic horizon, presumably reflecting differences in rooting depth. The changes in the tree community at Haast are consistent with disturbance-related succession in conifer–angiosperm forests in the region, but the opposite of patterns along the nearby Franz Josef post-glacial chronosequence, where conifers are most abundant on old soils. The Haast chronosequence is therefore an important additional example of forest retrogression linked to long-term soil phosphorus depletion, and provides evidence for the role of soil nutrients in determining the distribution of tree species during long-term succession in lowland temperate rain forests in New Zealand.

B. L. Turner (✉) · K. M. Andersen
Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama
e-mail: TurnerBL@si.edu

A. Wells · L. M. Condron
Agriculture and Life Sciences, Lincoln University, PO Box 84, Lincoln 7647, Canterbury, New Zealand

Introduction

Long-term ecosystem development is characterized by a slow decline in soil phosphorus availability to plants (Walker and Syers 1976). This occurs through the

gradual loss of total phosphorus via leaching and erosion (Hedin et al. 2003) as well as chemical transformations of phosphorus compounds in the soil, including a depletion of primary mineral phosphate and an accumulation of phosphorus bound in secondary minerals and organic compounds (Crews et al. 1995; Parfitt et al. 2005; Turner et al. 2007). In the absence of rejuvenating disturbance, the decline in phosphorus availability leads to a corresponding decline in the biomass of the vegetation, termed 'retrogression' (Wardle et al. 2004), as well as changes in the diversity and composition of the plant community (Mark et al. 1988; Richardson et al. 2005; Walker et al. 1981; Wardle et al. 2008). Soil chronosequences therefore provide opportunities to obtain information on long-term drivers of plant community assembly (Peltzer et al. 2010; Walker et al. 2010).

One of the most well-studied soil chronosequences occurs at Franz Josef, on the west coast of the South Island of New Zealand. The sequence is formed in postglacial deposits up to 120,000 years old and exhibits a clear decline in phosphorus availability (Parfitt et al. 2005; Walker and Syers 1976), with a corresponding decline in forest biomass on the oldest surfaces (Wardle et al. 2004). A similar pattern occurs along the Waitutu chronosequence of marine uplift terraces, also on the South Island of New Zealand (Mark et al. 1988; Parfitt et al. 2005). There are marked changes in the forest community during ecosystem development along these two sequences, with dominance by evergreen angiosperms on young soils and an increasing abundance of conifers in the family Podocarpaceae as soils age (Coomes et al. 2005; Richardson et al. 2004).

The increasing abundance of conifers as ecosystem development proceeds is assumed to indicate the superior ability of the podocarps to survive on phosphorus-poor soils, having the advantage of slow growth, long-lived leaves, and other nutrient-conserving strategies (Coomes and Bellingham 2011; Richardson et al. 2005). The presence of tree ferns on young soils and waterlogging on old soils also appear to be important in structuring the podocarp community along the sequences (Coomes et al. 2005; Gaxiola et al. 2010). However, the trend toward increasing conifer dominance differs from disturbance-related successional patterns observed in the region, whereby large earthquakes along the Alpine Fault promote initial dominance by conifers, followed by slow progression to a mixed conifer–angiosperm forest (Ogden and Stewart 1995; Stewart et al. 1998; Wells

Fig. 1 The Haast chronosequence, showing **a** an aerial image ▶ of the entire sequence with the approximate transect line indicated by the *blue bar*, with youngest dunes on the *left* close to the road, and oldest dunes on the *right*; **b, c** a young dune (Dune 4, 517 years BP), with abundant tree ferns (*D. squarrosa* and *C. smithii*) under a canopy of large *D. cupressinum*, growing on a weakly developed soil (Typic Udipsamment); **d, e** an intermediate-aged dune (Dune 8, 1,826 years BP) with a mixed conifer–angiosperm tree community on a moderately-developed soil (Spodic Udipsamments) with a clear bleached eluvial horizon; **f, g** an old dune (Dune 12, 3,903 years BP) with a mixed conifer–angiosperm tree community on a well-developed Spodosol (Typic Placorthod) with a bleached eluvial horizon, a spodic B horizon, and a continuous cemented placic horizon (iron pan). Photo credits: **a** Land Information New Zealand; **b–f** B.L. Turner. (Color figure online)

et al. 2001). This suggests factors other than pedogenesis-driven changes in nutrient status might be more important in determining forest community composition in New Zealand temperate rain forests.

Here we report the results of a survey of tree communities along the Haast chronosequence, a progradational dune sequence formed by periodic disturbance events linked to earthquakes on the Alpine fault that runs through the spine of the South Island of New Zealand (Turner et al. 2012; Wells and Goff 2006). The Haast chronosequence provides a strong test of factors influencing plant community composition during ecosystem development, because the dunes are formed from the same parent material, have similar topography, occur in a small area of uniform climate, support undisturbed forest, and the dates of dune formation are reasonably well constrained. Our specific aims were (i) to quantify changes in the tree community along the sequence, including basal area and the species composition of the adult, sapling, and seedling communities, and (ii) assess the extent to which plant community composition was linked to dispersal limitation or changes in soil nutrients. We were particularly interested in whether patterns in the tree community would correspond to those observed at the nearby Franz Josef chronosequence, a very different sequence in terms of soil properties and sequence age, but under similar rainfall and vegetation.

Materials and methods

The Haast chronosequence

The Haast dune system is located northeast of the town of Haast, on the west coast of the South Island of New

Zealand (43°43′20″S, 169°4′30″E) (Fig. 1). The system extends ~10 km alongshore and 5 km inland, with dunes 20–100 m wide rising up to 20 m above the adjacent dune slacks. Dune building episodes are thought to result from earthquakes along the Alpine Fault, which cause widespread disturbance including landslides, rock falls, floodplain aggradation, and tree falls (Wells and Goff 2007). After each event, a pulse of sediment is transported rapidly to the ocean via the Haast River and then deposited as a linear dune either side of the river mouth. The youngest dune is thus located closest to the ocean, with dunes becoming progressively older inland.

Dune building is a regional phenomenon and has occurred following all known earthquakes since AD 1220, and presumably since sea level stabilized during the mid-Holocene, ca. 7,000 years ago (Wells and Goff 2007). This is supported by the consistent earthquake record spanning the last 8,000 years (Berryman et al. 2012). The earliest dunes have been dated precisely using tree rings and historical records (Wells and Goff 2007), while older dune dates are estimated based on a ^{14}C date for the oldest dune (see Turner et al. 2012). Parent material is assumed to be similar across the sequence based on the mineralogy of unweathered sand (Palmer et al. 1986).

Modern mean annual temperature is 11.3 °C and mean annual rainfall is 3,455 mm spread relatively evenly throughout the year, with no month having <200 mm (New Zealand Meteorological Service 1983). Climate at the site has varied considerably since the onset of dune formation, with evidence for a dry period between 3,000 and 4,000 years BP and a substantial cold period around 3,500 years BP (Li et al. 2008). However, forests in the region have been mixed conifer–broadleaf temperate rain forest since at least 7,700 years BP (Li et al. 2008).

Soil development and changes in nutrient availability

Detailed information on soil development and changes in soil properties are reported elsewhere (Eger et al. 2011; Palmer et al. 1986; Turner et al. 2012). In brief, the soils develop rapidly to podzols under the perhumid climate, from Typic Udipsamments (Entisols) on young dunes (<800 years BP) to Typic Placorthods (Spodosols) on older dunes (3,903–6,500 years BP) (Fig. 1)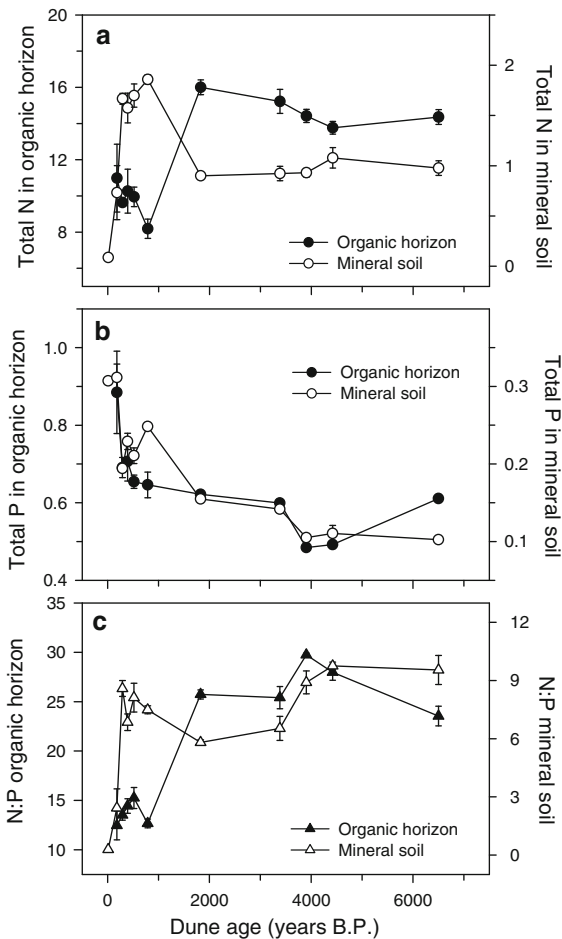. The latter soils are characterized by a thick organic horizon, a bleached eluvial horizon, a spodic B horizon (i.e., subsoil accumulation of iron and organic matter), and a cemented iron pan (placic horizon) that forms at around 10–20 cm depth in the mineral soil (Turner et al. 2012). The pan is likely to have ecological significance, because it impedes vertical water movement and root penetration, physically preventing access to nutrients in deeper horizons. The thickness of the organic horizon increases from <1 cm on the youngest dune to 17–28 cm on the older dunes and there is rapid acidification and depletion of exchangeable base cations in the early stages of pedogenesis. Soils are very acidic, with mineral soil pH (measured in water) ≤4.2 for the majority of the sequence and declining to ~3.5 on the oldest dunes (Turner et al. 2012; see supplementary material).

Patterns of total nitrogen and phosphorus along the sequence are summarized in Fig. 2. Total nitrogen concentrations increase from low values in the young soils to maximum and stable values in older soils, with a slight decline in the total nitrogen concentration with age (Fig. 2a). In contrast, total phosphorus concentrations in both organic and surface mineral soil horizons decline rapidly in the first few hundred years of pedogenesis, from high initial values in young soils to the lowest values in old soils (Fig. 2b). The corresponding N:P ratios increase with soil age (Fig. 2c). The decline in total phosphorus in mineral soil in the early stages of pedogenesis was accounted for by primary mineral phosphate (i.e., acid-extractable inorganic phosphate). Organic phosphorus accounted for 72–84 % of the total phosphorus for all but the youngest dune (~20 %) (Turner et al. 2012). Information on soil properties for the five dunes studied for vegetation is reported in supplementary material.

Vegetation measurements

We established three replicate 10 × 20 m vegetation plots on five of the eleven dunes studied previously (Turner et al. 2012): Dune 3 (312 years BP), Dune 4 (517 years BP), Dune 8 (1,826 years BP), Dune 13 (4,422 years BP), and Dune 17 (6,500 years BP). Plots were established around the intersection of the sampling transect across the dunes and were therefore effectively located randomly. The first plot was established at the intersection of the transect line with the dune crest, with the second and third plots located either side along the dune, beginning 30 m from the

Fig. 2 Changes in **a** total nitrogen (g N kg^{-1}), **b** total phosphorus (g P kg^{-1}), and **c** the N:P ratio in the organic horizon and mineral soil (0–20 cm) along the Haast dune sequence, Westland, New Zealand (data from Turner et al. 2012)

between 30 cm and 1.4 m in height) were identified and enumerated over the whole plot. Ground cover, including bryophytes, litter, ferns, and bare ground, was estimated over the entire plot using standard procedures in New Zealand forest ecology (Hurst and Allen 2007) (see supplementary material).

Statistical analysis

Multivariate analyses of tree communities, soil properties, and dune age were conducted using the statistical software package "vegan" version 1.17.3 (Oksanen 2010) in the R programming environment version 2.11.1 (R Development Core Team, www.r-project.org). We used Bray–Curtis dissimilarity indices to calculate between-dune differences in tree, sapling, and seedling communities based on mean species abundance data and absolute (m^2 ha^{-1}) and proportion (%) of the total basal area for the tree community. Floristic dissimilarity matrices were based on data from Turner et al. (2012), which were square root transformed and submitted to a Wisconsin double standardization procedure, with species data divided by their maxima and dunes standardized to equal totals (Oksanen 2010). We used double standardization because it ranks species regardless of their taxonomic status and adult stature. Analyses without double standardization yielded qualitatively similar results. The main difference was that the signal between the seedling community and the organic horizon was lost, while the sapling–mineral soil correlation was strengthened (data not shown). We used Euclidean distance to calculate between-dune differences in age, soil, and organic horizon. Dune age was used as a proxy for geographic distance.

Mineral soil and organic horizon data were simplified into three multivariate variables based on separate principal components analyses (PCA) prior to calculating distance matrices. For the mineral soil PCA, we included pH, total carbon, total nitrogen, inorganic nitrogen, readily-exchangeable phosphorus, C:N ratio, C:P ratio, sand, silt, and clay. Mineral soil PCA axis 1 captured 70.5 % of the variation, with C:N and silt loading positively and readily-exchangeable phosphate, pH, and sand loading negatively. Mineral soil PCA axis 2 captured 15.5 % of the variation in soil variables, with total carbon and nitrogen loading positively. Mineral soil PCA axis 3 captured 11.0 % of the variation in soil variables, with inorganic nitrogen

edge of the first plot. The plot size (200 m^2 rather than the standard 400 m^2) and shape were necessitated by the narrow shape of the dune ridges. Plots were positioned 20 m along the dune crest and 10 m down the inland side of the dune ridge; the coastal side was not sampled because colonization of this portion of dune ridge by trees is delayed until after the next youngest dune has formed (Wells and Goff 2007). The triplicate plots on each dune gave a total area of 600 m^2 per dune.

All stems ≥10 cm diameter at breast height (dbh) (1.4 m) were identified and measured for calculation of basal area. Saplings (stems <10 cm dbh and taller than 1.4 m) were identified and enumerated, but diameters were not recorded. Seedlings (stems

and C:P ratio loading positively and clay loading negatively. For the organic horizon PCA, we included horizon depth, pH, total carbon, total nitrogen, total phosphorus, and C:N ratio. Organic horizon PCA axis 1 captured 70.7 % of variation, with total nitrogen, total carbon, and depth loading negatively, and pH loading positively. Organic horizon PCA axis 2 captured 18.2 % of the variation, with C:N ratio loading positively. Axis 3 captured 10.8 % of the variation, with total phosphorus loading negatively. Thus, for both mineral and organic soils, the three axes accounted for 99.7 % of the variation and each axis accounted for at least 10 % of the variation.

Mantel tests were performed to assess the correlation between plant floristic distance matrices and the mineral soil, organic horizon, and dune age distance matrices. Partial Mantel tests were used to examine the correlation between pair-wise differences in the plant matrices and mineral soil and organic horizon matrices controlling for dune age ("pure mineral" and "pure organic") and between pair-wise differences in the

plant matrices and dune age controlling for soil variables ("pure age"). The standardized Mantel test statistic (r) was calculated based on the Pearson's product-moment correlation coefficient and significance was assessed using randomization tests with 1,000 permutations. In addition, we examined correlations between soil properties and stem density, relative abundance, and basal area of adult conifers, woody angiosperms, and tree ferns.

Results

Plant diversity in forest census plots

There were three key stages of forest structure along the chronosequence (Fig. 1). Fourteen species were present along the sequence as individuals ≥10 cm dbh, including five species in the Podocarpaceae, two tree ferns, and seven woody angiosperms (Table 1). Note that we include *Phyllocladus* within the Podocarpaceae,

Table 1 Basal area (m^2 ha^{-1}) of trees ≥10 cm dbh at five sites along the Haast dune sequence, New Zealand

Species	Family	Dune 3 (392 BP)	Dune 4 (517 BP)	Dune 8 (1,826 BP)	Dune 13 (4,422 BP)	Dune 17 (6,500 BP)
				Basal area (m^2 ha^{-1})		
Conifers						
Dacrydium cupressinum	Podocarpaceae	108.2 ± 12.1	181.3 ± 12.0	36.8 ± 8.6	54.1 ± 38.1	0.0
Phyllocladus alpinus	Podocarpaceae	0.0	0.0	0.0	1.1 ± 1.1	0.8 ± 0.6
Podocarpus hallii	Podocarpaceae	0.0	0.0	1.2 ± 0.6	0.9 ± 0.9	1.7 ± 1.5
Podocarpus totara	Podocarpaceae	7.5 ± 7.3	0.0	0.0	0.0	0.0
Prumnopitys ferruginea	Podocarpaceae	8.0 ± 3.3	6.2 ± 3.3	11.2 ± 7.4	15.4 ± 7.5	10.0 ± 3.7
Total conifers		123.7 ± 2.8	187.5 ± 14.3	49.1 ± 2.4	71.4 ± 42.8	12.4 ± 4.5
Woody angiosperms						
Elaeocarpus dentatus	Elaeocarpaceae	0.0	0.0	0.0	0.2 ± 0.2	0.0
Elaeocarpus hookerianus	Elaeocarpaceae	0.0	0.0	0.0	0.4 ± 0.4	0.4 ± 0.4
Hedycarya arborea	Monimiaceae	0.0	0.8 ± 0.8	0.0	0.0	0.0
Metrosideros umbellata	Myrtaceae	0.0	0.0	0.0	0.3 ± 0.3	0.0
Nothofagus menziesii	Fagaceae	0.0	0.0	0.0	0.3 ± 0.3	15.9 ± 8.3
Pseudopanax crassifolius	Araliaceae	0.0	0.0	0.0	0.0	0.1 ± 0.1
Weinmannia racemosa	Cunoniaceae	0.6 ± 0.2	0.3 ± 0.3	25.0 ± 11.7	29.1 ± 4.6	31.7 ± 17.9
Total woody angiosperms		0.6 ± 0.2	1.1 ± 0.7	25.0 ± 11.7	30.3 ± 4.4	48.2 ± 20.6
Tree ferns						
Cyathea smithii	Cyatheaceae	19.1 ± 2.0	10.6 ± 1.6	0.0	0.0	0.0
Dicksonia squarrosa	Dicksoniaceae	11.9 ± 6.4	6.6 ± 0.2	0.2 ± 0.2	0.0	0.0
Total tree ferns		31.0 ± 6.3	17.1 ± 1.6	0.2 ± 0.2	0.0	0.0

Values are mean ± standard error of three replicate 200 m^2 plots located along the dune ridge at each site

because the recent elevation of the genus to family level (Phyllocladaceae) is not supported by phylogenetic analyses (Biffin et al. 2011). One conifer, *Dacrycarpus dacrydioides* (Podocarpaceae), occurred as saplings throughout the sequence, but not as tree-sized individuals (see below). The youngest dune studied supported a further species of woody angiosperm (*Pseudowintera colorata*, Winteraceae) as a sapling-sized plant, as well as seedlings of two other angiosperms in the Araliaceae (*Pseudopanax arboreus* and *Schefflera digitata*).

Basal area of trees ≥10 cm diameter at breast height

Basal area for stems ≥10 cm dbh was initially high for the two youngest dunes studied and then declined (Table 1; Fig. 3). Maximum basal area (206 ± 13 m² ha⁻¹) was recorded on Dune 4 (517 years BP) and the minimum basal area (60.6 ± 24.5 m² ha⁻¹) was recorded on the oldest dune (6,500 years BP). An increase in basal area on Dune 13 (4,422 years BP) was due to a single large *D. cupressinum* individual of 161 cm dbh, reflected in the large standard error for conifer basal area at this site (Table 1; Fig. 3).
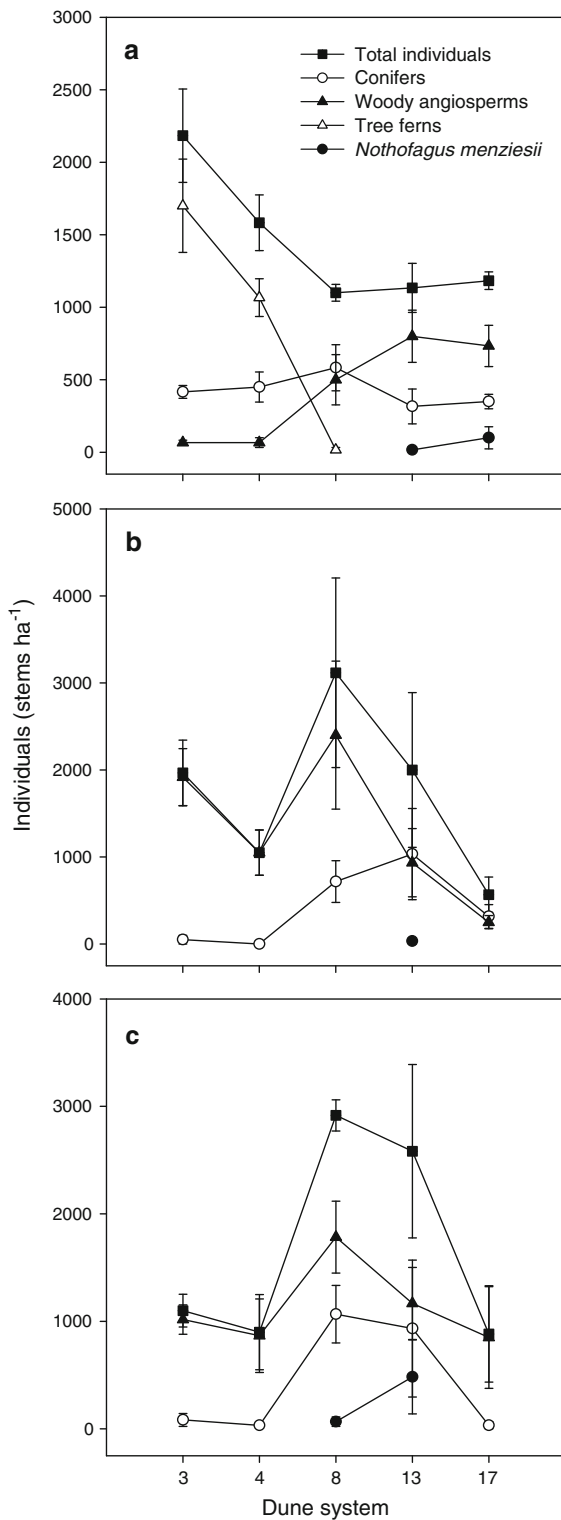
Most of the basal area (≥80 %) on the two youngest dunes studied was accounted for by podocarps (124–188 m² ha⁻¹, Table 1), although they declined markedly as dunes aged, accounting for only 12.4 m² ha⁻¹ (23 % of total basal area) on the oldest dune (Fig. 3). Tree ferns accounted for 31 and 17 % of the total basal area on the two youngest dunes studied, respectively. Both *Cyathea smithii* and *Dicksonia squarrosa* were present along the sequence, with *C. smithii* always in greatest abundance (Table 1, supplementary material). Tree ferns were absent from plots on the two oldest dunes studied (Table 1; Fig. 3), although a few individuals were noted outside the plots on these dunes.

Woody angiosperms accounted for only a small proportion of the basal area on the youngest dunes (<1 m² ha⁻¹, <1 % total basal area), but increased on the older dunes to a maximum of 48.2 m² ha⁻¹ (77 % of the total basal area) (Table 1; Fig. 3; supplementary Table 1). The majority of the basal area of woody angiosperms ≥10 cm dbh was *W. racemosa*, which accounted for 31–49 % of the total basal area on the oldest three dunes (Table 1; supplementary Table 1). In addition, *Nothofagus menziesii* accounted for 27 %
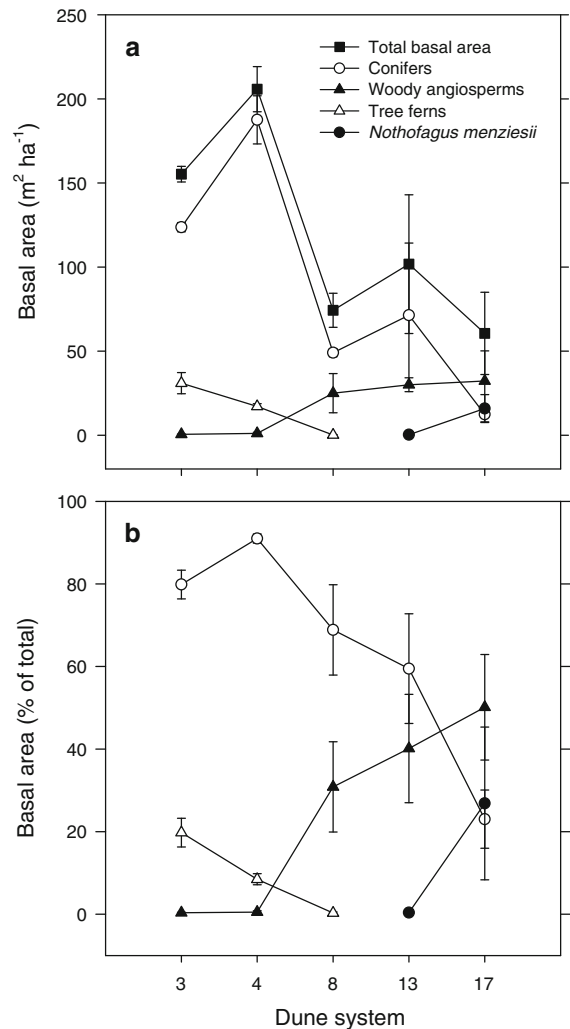
Fig. 3 Basal area of individuals ≥10 cm dbh at five sites of contrasting age along the Haast dune sequence, Westland, New Zealand. Values are the mean ± standard error of three replicate 10 m × 20 m plots located along the dune crest at each site. *N. menziesii* is shown separately from the woody angiosperms to illustrate the pattern for the only ectomycorrhizal species that occurs along the sequence and is not included in the woody angiosperms data

of the total basal area on the oldest dune (15.9 ± 8.3 m² ha⁻¹) (Table 1; Fig. 3; supplementary Table 1). This species is shown separately from other woody angiosperms in Figs. 3 and 4, because it represents the only ectomycorrhizal species along the sequence. Other woody angiosperms present as trees ≥10 cm dbh in the plots included *Hedycarya arborea*, *Metrosideros umbellata*, *Pseudopanax crassifolius*, and two species of *Elaeocarpus* (Table 1).

Abundance of adult trees, saplings, and seedlings along the chronosequence

The number of individuals ≥10 cm dbh ranged from 1,100 to 2,183 stems ha^{-1}, being highest on the youngest dunes and lowest on the three oldest dunes (Table 2; Fig. 4). The majority of the stems ≥10 cm dbh on the youngest two dunes were tree ferns (>1,500 stems ha^{-1} on Dune 3), with woody angiosperms constituting the majority of stems on the oldest two dunes (Fig. 4). These were dominated by *W. racemosa* (59 % of total stems ≥10 cm dbh), with a smaller contribution of *N. menziesii* (9 % of total stems ≥10 cm dbh) (supplementary material). Podocarps accounted for a relatively consistent number of stems ≥10 cm dbh across the five dunes (317–583 stems ha^{-1}) (Fig. 4).

The number of saplings was greatest on Dune 8 (3,117 ± 1,090 stems ha^{-1}) and smallest on the oldest dune (567 ± 203 stems ha^{-1}) (Table 2; Fig. 4). In contrast to individuals ≥10 cm dbh, the number of woody angiosperm saplings declined, and podocarp saplings increased, along the sequence, at least as a proportion of the total saplings (Fig. 4). Saplings were rarely >5 m tall and therefore did not reach the canopy. Most of the saplings on the youngest three dunes were woody angiosperms, mainly species in the genus *Coprosma*, as well as a considerable number of *W. racemosa* individuals. Five species of *Coprosma* have been recorded along the sequence (Dickinson and Mark 1994). In our plots, they accounted for >1,000 stems ha^{-1} of sapling-sized individuals on the three youngest dunes, including virtually all the saplings (98 ± 2 %) on Dune 4 (392 years BP); however, *Coprosma* spp. accounted for only around 10 % of the total saplings on the oldest two dunes

Table 2 Summary of vegetation at five sites of contrasting age along the Haast dune sequence, Westland, New Zealand

Dune stage	Dune age (years BP)	Basal area	Individuals		
		Trees[a] m^2 ha^{-1}	Trees[a] Stems ha^{-1}	Saplings[b]	Seedlings[c]
Dune 3	392	155.2 ± 4.6	2,183 ± 322	1,967 ± 377	1,100 ± 153
Dune 4	517	205.8 ± 13.4	1,583 ± 192	1,050 ± 260	900 ± 350
Dune 8	1,826	74.3 ± 10.1	1,100 ± 58	3,117 ± 1,090	2,917 ± 145
Dune 13	4,422	101.7 ± 41.2	1,133 ± 169	2,000 ± 889	2,583 ± 806
Dune 17	6,500	60.6 ± 24.5	1,183 ± 60	567 ± 203	883 ± 448

Values are the mean ± standard error of three replicate 10 m × 20 m plots located along the dune crest at each site

[a] Stems ≥10 cm dbh

[b] Stems <10 cm dbh (1.4 m) and ≥1.4 m high

[c] Stems >30 cm and <1.4 m in height

(see supplementary material). *Coprosma* saplings undoubtedly increase the total basal area of woody angiosperms on the young dunes, although we estimate this to be <3 m^2 ha^{-1} out of a total basal area of >150 m^2 ha^{-1}. *Nothofagus menziesii* occurred as saplings only on Dune 13 (33 stems ha^{-1}), contributing 1 % of the total saplings (Fig. 4). Podocarps represented a considerable proportion of the total saplings on the oldest three dunes studied (23–53 %), being particularly abundant on Dunes 8 and 13 (717–1,033 stems ha^{-1}, respectively), but were rare on the two youngest dunes (≤2 % of total saplings) (Fig. 4). Thus, saplings on the youngest two dunes were almost all woody angiosperms, while on the oldest two dunes saplings were evenly distributed between angiosperms and conifers.

Seedling abundance varied between 883 and 2,917 individuals per hectare along the sequence, with the highest values recorded for Dune 8 and Dune 13 (Table 2; Fig. 4). Seedlings followed a similar pattern to saplings, with young dunes dominated by woody angiosperms and relatively similar numbers of angiosperms and podocarps on older dunes. In fact, the majority of the seedlings on all dunes were woody angiosperms (63–96 % of total seedlings). Most of these were *Coprosma* spp., which accounted for 617–1,100 stems ha^{-1} and up to 93 % of the total seedlings (see supplementary material). In addition, *W. racemosa* (17–433 stems ha^{-1}, 3–15 % of total seedlings) and *P. crassifolius* (up to 9 % of total seedlings) were abundant along the entire sequence (see supplementary material). Podocarp seedlings were abundant only on Dune 8 and 13 (~1,000 stems ha^{-1}), mainly

as two species (see below), but were rare on both the youngest and oldest dunes (<100 stems ha^{-1}) (Fig. 4). Seedlings of *N. menziesii* occurred only on Dune 8 and 13; on the latter dune, there were 483 stems ha^{-1}, accounting for 31 % of the total seedlings at that site (Fig. 4). It was notable, however, that no seedlings or saplings of *N. menziesii* were present in plots on the oldest dune, despite the presence of several adults ≥10 cm dbh.

Distribution of the Podocarpaceae along the chronosequence

Six species of podocarps were identified in plots on the five dunes studied and their distribution varied markedly along the sequence. On the three youngest dunes, most of the basal area and total individuals ≥10 cm dbh were accounted for by *D. cupressinum*, but this species declined along the sequence and was present in plots on the oldest dune only as saplings (Fig. 5, supplementary material). Seedlings of this species occurred only on the youngest dune in very low numbers. Occasional large individuals of *D. cupressinum* are, however, present as scattered emergents outside our plots on the oldest dune.

In contrast, *Prumnopitys ferruginea* increased markedly along the sequence, eventually forming the dominant podocarp in terms of both basal area and number of individuals (as both trees and saplings) on the oldest dune. Of the other podocarp species, *Podocarpus totara* was present on Dune 3 but not elsewhere, while *P. hallii* was absent on young dunes but present on older dunes (Fig. 5). Both *Podocarpus*
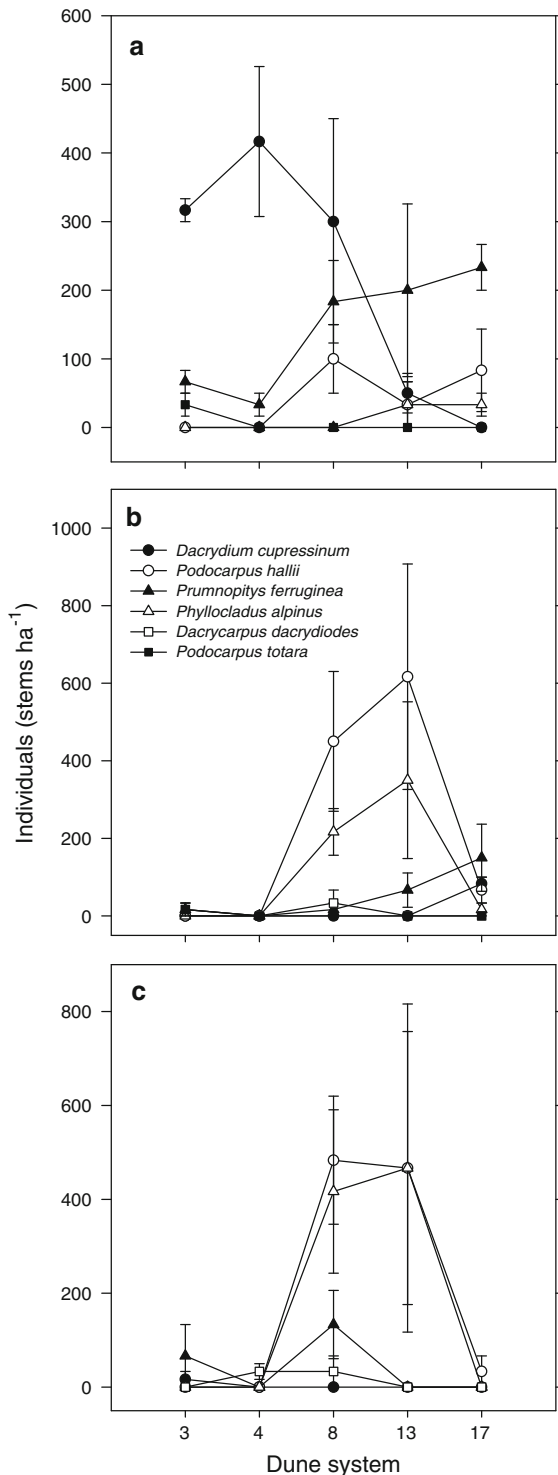
Fig. 5 Number of individual **a** trees, **b** saplings, and **c** seedlings of the five podocarp species at five sites of contrasting age along the Haast dune sequence, New Zealand. Values are the mean ± standard error of three replicate 10 m × 20 m plots located along the dune crest at each site

species made a relatively small contribution to the basal area of trees ≥10 cm dbh along the sequence, although there were a large number of saplings and seedlings of *P. hallii* on Dunes 8 and 13 (but low numbers on other dunes) and *P. totara* does occur on the older dunes of other sequences in the region (A. Wells, personal observation). Similarly, there were large numbers of saplings and seedlings of *Phyllocladus alpinus* on Dunes 8 and 13, but few elsewhere, and this species made only a small contribution to the total basal area, with adults present only on the two oldest dunes studied (Fig. 5). *Dacrycarpus dacrydioides* was the only podocarp not present as individuals ≥10 cm dbh anywhere along the sequence, and saplings and seedlings of this species were infrequent on all dunes studied. Thus, *Dacrydium cupressinum* dominates on young soils, *Prumnopitys ferruginea* dominates the conifer community on old soils, but only *Podocarpus hallii* and *Phyllocladus alpinus* (and to a lesser extent *Prumnopitys ferruginea*) appear to be regenerating successfully under the existing canopy.

Plant communities in relation to dune age, mineral soil, and organic horizon

A number of significant correlations ($p < 0.05$) occurred between forest composition, soil properties, and dune age. Notably, conifer basal area was positively correlated with mineral soil nitrogen and readily-exchangeable phosphate (both $r = 0.94$), angiosperm basal area was correlated negatively with soil pH ($r = -0.98$) and total phosphorus in mineral soil ($r = -0.96$), while tree fern basal area was correlated positively with soil pH ($r = 0.89$) and total phosphorus in mineral soil ($r = 0.91$), and negatively with the N:P ratio in the organic horizon ($r = -0.92$). Dune age was correlated positively with the basal area of angiosperms ($r = 0.95$), but not conifers or tree ferns. Dune age was, however, correlated negatively with soil pH ($r = -0.96$) and total phosphorus in mineral soil ($r = -0.94$). A full correlation table is presented in supplementary material, including correlations for abundance and relative basal area.

Mantel tests showed significant associations between the plant communities, soil variables (as PCA axes), dune age, and/or the organic horizon variables for at least one plant community variable (Table 3; Fig. 6). Differences in mineral soil variables were related to dune age ($r = 0.72$, $p = 0.04$),

Table 3 Mantel and partial Mantel tests examining the relationship between floristic dissimilarity as a function of differences in soil and organic horizon variables and age between dunes

Community	Mantel tests			Partial Mantel tests		
	Mineral soil	Organic horizon	Age	'Pure mineral' (mineral soil | age)	'Pure organic' (organic horizon | age)	'Pure age' (age | soil)
Abundance						
Trees (stems ha^{-1})	0.95*	0.45	0.78*	0.90*	0.52	0.28
Saplings (stems ha^{-1})	0.42*	0.18	0.21	0.41	0.17	−0.17
Seedlings (stems ha^{-1})	0.04	0.55**	−0.11	0.12	0.58*	−0.17
Basal area						
Tree basal area (m^2 ha^{-1})	0.94*	0.47	0.87*	0.87*	0.66	0.72**
Relative dominance (%)	0.94*	0.43	0.88*	0.87*	0.62	0.77**
Soil properties						
Mineral soil (0–20 cm)	–	–	0.74*	–	–	–
Organic horizon	–	–	0.17	–	–	–

Values represent the Mantel test statistic (r) based on the Pearson's product-moment correlation coefficient

* $p < 0.05$, ** $p < 0.01$

whereas differences in organic horizon variables were independent of dune age ($r = 0.18$, $p > 0.05$).

For trees ≥10 cm dbh, community composition based on abundance of individuals was correlated with mineral soil properties ($r = 0.95$, $p < 0.05$) and dune age ($r = 0.76$–0.87, $p < 0.05$), but not organic horizon properties ($r = 0.45$, $p > 0.05$) (Table 3; Fig. 6). However, partial Mantel tests also revealed that while the "pure mineral soil" effect was correlated significantly with the tree community composition ($r = 0.90$, $p < 0.05$), the "pure organic horizon" and "pure age" effects were not correlated significantly (Table 3; Fig. 6).

For sapling community composition, there was a significant relationship with mineral soil properties ($r = 0.42$, $p < 0.05$), but not with dune age or organic horizon (Table 3; Fig. 6). When correcting for variation associated with dune age, neither "pure mineral soil" nor "pure organic horizon" was correlated significantly with the sapling community.

The seedling community composition was not correlated significantly with either mineral soil properties or dune age, but was correlated significantly with organic horizon properties ($r = 0.55$, $p < 0.01$), including after correction for variation related to age ($r = 0.58$, $p < 0.05$) (Table 3; Fig. 6). A separate

analysis of seedling community against either organic horizon nutrients or organic horizon depth showed that the seedling community was only correlated with the nutrient matrix (results not shown).

Tree basal area, expressed both as absolute values (m^2 ha^{-1}) and relative dominance (% of the total basal area), was correlated significantly with mineral soil properties ($r = 0.94$, $p < 0.05$) and dune age ($r = 0.85$–0.87, $p < 0.05$), but not organic horizon properties ($r = 0.43$–0.47, $p > 0.05$) (Table 3; Fig. 6). Similarly, partial Mantel tests showed that tree basal area matrices were correlated with "pure mineral soil" and "pure age," but not "pure organic horizon" (Table 3; Fig. 6).

Discussion

Changes in forest structure and composition during ecosystem development

Clear changes in the forest community occurred along the Haast chronosequence, including a marked decline in basal area of trees ≥10 cm dbh and a shift in the relative dominance of tree species. The decline in basal area is consistent with the concept of forest
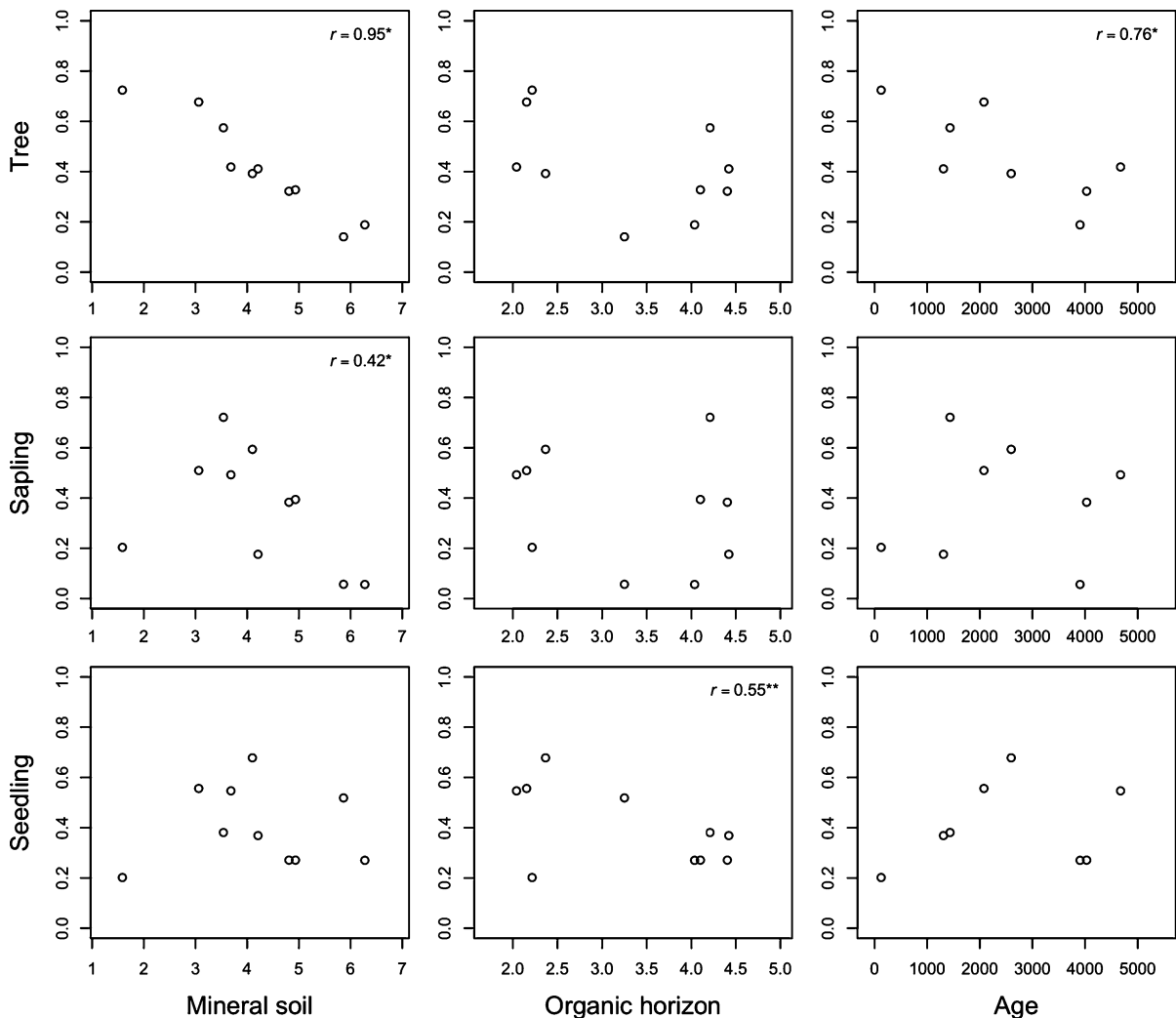
Fig. 6 Floristic similarity of tree, sapling, and seedling communities (Y axes) for all pairs of dunes as a function of differences in soil nutrients and age between the pairs. Floristic similarity was based on species abundance per dune. The mineral soil and organic horizon distance matrices were calculated using the first three axes of PCA. * $p < 0.05$, ** $p < 0.01$

"retrogression" during long-term ecosystem development (Wardle et al. 2004), although it also reflects in part the transition from monodominant *D. cupressinum* stands to a mixed conifer–angiosperm community. Retrogression linked to a long-term reduction in phosphorus availability is a characteristic of chronosequences with a variety of climates and parent materials and is distinct from shorter-term changes in basal area linked to successional trends, such as age-related declines in forest productivity, because it occurs over multiple generations and is driven by long-term pedological processes (Peltzer et al. 2010). Although retrogression has been most commonly observed over

long time scales (>100,000 years), it can also occur over relatively short time scales of a few thousand years (Wardle et al. 1997) and is likely to have been driven at Haast by the rapid rate of soil development and associated phosphorus loss (Turner et al. 2012).

Basal areas reported here for the young dunes at Haast are at the upper end of the range for *D. cupressinum* stands in New Zealand, but are representative of young dunes on similar sequences in the region (A. Wells, personal observations). There was no bias in the positioning of our plots, which were effectively located randomly based on the intersection of the transect line with the dune crests. However, it is possible that our

transect passed through particularly dense stands of *D. cupressinum* on the young dunes that are not representative of the area as a whole. A previous study of vegetation in a single 10×20 m plot on each of six alternating dune–slack features along the Haast sequence reported basal areas of stems >10 cm dbh up to 78.5 m^2 ha^{-1} and tree densities of 229–1,415 stems ha^{-1} at breast height (Dickinson and Mark 1994). We measured larger basal areas and stem densities in our plots on young dunes dominated by emergent *D. cupressinum*, although these were similar to values reported previously for mixed conifer–angiosperm forest in the Westland region, which typically contain 200–500 stems ha^{-1} of *D. cupressinum* >10 cm dbh (Ogden and Stewart 1995). Basal area estimates of *D. cupressinum* stands include up to 133 m^2 ha^{-1} for stems >5 cm dbh on moraines (Stewart et al. 1998).

Unlike the chronosequence on the Hawaiian Islands, where a single tree species, *Metrosideros polymorpha*, forms the dominant canopy tree across the entire 4.1 million year sequence and retrogression appears to be clearly linked to nutrient status (Herbert and Fownes 1999), the changes in basal area along the Haast sequence occurred in parallel with marked changes in the tree community composition. Although this means that the changes at Haast more closely represent how most ecosystems respond to long-term soil development, it complicates the assignment of the decline in basal area to changes in nutrients alone, because other factors such as population dynamics and dispersal limitation might also be involved. For example, it has been suggested that dispersal effects (distance from the seed source) play a greater role than site age or soil development in shaping species distribution along the early stages of the Glacier Bay chronosequence (Fastie 1995). Given the relatively limited age of the Haast sequence, the pronounced changes in the forest community might be regulated by the strong nutrient gradient, dispersal limitation, or successional patterns unrelated to pedogenesis. Wider patterns of forest succession and disturbance dynamics over multiple generations, which may occur regardless of changes in nutrient status, must also be considered (discussed below).

Regional patterns of disturbance-related forest succession

Disturbance is a key factor shaping forest communities in lowland conifer–angiosperm forests of New Zealand (Duncan 1993; Ogden 1985; Veblen and Stewart 1982; Wells et al. 2001). Large scale disturbances such as landslides, flooding, and volcanic eruptions cause major soil disturbance and favor extensive even-aged cohorts of either angiosperms or conifers with high basal area and low seedling density (Rose et al. 1992; Stewart and Rose 1990; Stewart et al. 1998; Wells et al. 2001). Without further major disturbance, the initial cohort collapses through smaller scale (gap phase) canopy disturbances and is replaced by a forest with a lower basal area but greater compositional and structural diversity (Kershaw and McGlone 1995; Ogden and Stewart 1995; Stewart and Rose 1990; Veblen and Stewart 1982). This favors the regeneration of fast growing angiosperms such as *W. racemosa* and promotes shade tolerant conifer species such as *P. ferruginea*, the most shade-tolerant of the New Zealand podocarps (Ogden and Stewart 1995), which regenerates in tree-fall gaps (Stewart et al. 1998) or even in the absence of gaps (Lusk and Smith 1998). Many of these successional changes are directly related to the diversity and structural complexity of micro-sites for seedling establishment, reflected in part in the marked changes in ground cover along the Haast sequence (see supplementary material Fig. S1). Overall, the effect is that smaller scale disturbances tend to lead to greater diversity in site conditions and therefore a more diverse forest community (e.g., Duncan 1993). This is reflected in the composition of the tree community on old dunes at Haast, which indicates that gap-phase disturbance has been dominant for at least several centuries.

Dacrydium cupressinum appears to quickly colonize freshly exposed sand dunes and then dominate the basal area of the forest for hundreds of years (Dunes 1–6). This species is light demanding and presumably well dispersed by birds (Norton et al. 1988). This is followed by increasing dominance by angiosperms, greater abundance of shade-tolerant podocarps, and a much lower basal area (Dunes 8–17). There were very few seedlings or saplings of *D. cupressinum* on any dune, indicating the importance of open sites (perhaps also associated with high nutrient availability) for this species to become established. However, seedlings and saplings of *Phyllocladus alpinus*, *Podocarpus hallii*, and to a lesser extent *Prumnopitys ferruginea*, were abundant on 1,800–3,900 year-old dunes. This pattern may be linked to the presence of tree ferns, which were abundant on young dunes, but virtually

absent on older dunes. Tree ferns are relatively nutrient demanding and are therefore common on young fertile soils (Richardson et al. 2005), where they appear to play a key role in suppressing podocarp regeneration through intense shading (Coomes et al. 2005). Thus, changes in tree community composition along the Haast chronosequence are broadly consistent with the regional pattern of disturbance-related succession in lowland conifer–angiosperm forests.

Soil nutrients versus dispersal in the regulation of tree community composition

Although the Haast chronosequence is characterized by marked changes in soil nutrients with soil age (Turner et al. 2012), the distribution of tree species might also be influenced by dispersal limitation and successional patterns unrelated to pedogenesis (Fastie 1995; Johnson and Miyanishi 2008). Given the relatively short distances between dunes at Haast, it might be expected that chance and dispersal limitation are of minor significance in structuring the forest community. However, dispersal is important in the colonization of young sites, because well-dispersed species (e.g. *W. racemosa*) are most likely to establish quickly after the stabilization of a new dune. Even species like *N. menziesii*, sometimes assumed to disperse slowly (Wardle 1991), can colonize young surfaces within a few years of stabilization (Wardle 1980). As *N. menziesii* has been present in forests around the Haast chronosequence for the last several thousand years (Li et al. 2008), it seems likely that it had opportunity to colonize young dunes, suggesting that factors other than dispersal have determined its distribution along the chronosequence.

Fortunately, the close proximity of the Haast dunes, despite marked differences in their ages, allows examination of the relative importance of nutrients and dispersal in determining the plant community composition along the sequence, because the age sequence can be used as a measure of geographic distance. Dispersal limitation theory states that there should be a log-linear relationship between distance and floristic similarity (Condit et al. 2002), so at Haast we would expect a similar relationship between dune age and floristic similarity. The adult tree community shows decreasing floristic similarity between dunes as the age (i.e. distance) difference between them increases. However, there was no relationship between floristic similarity and difference in age of the dunes for the sapling or seedling community, indicating that processes other than dispersal limitation, such as soil nutrients, may be important in filtering the plant community.

The role of soil nutrients in structuring the plant community at Haast is demonstrated clearly by the results of the Mantel and partial Mantel tests, which showed that tree species distribution is explained by soil nutrients to a much greater extent than dispersal (i.e. dune age). The significance of nutrients was further emphasized by the finding that the abundance and basal area of adult tree species (and to a lesser extent sapling species abundance) along the sequence were related strongly to nutrients in the mineral soil, whereas the distribution of seedling species was related strongly to nutrients in the organic horizon. This presumably reflects differences in rooting depth: adults are rooted in mineral soil throughout the sequence, whereas seedlings are rooted predominantly in the organic horizon, particularly on the older dunes with thick organic horizons. Thus, seedlings obtain nutrients from organic soil rather than the mineral soil, especially during the early stages of their growth. These results indicate strong environmental filtering of plant communities at all life history stages based on soil nutrient status.

Leaf litter is certainly known to exert species-specific effects on seedlings regeneration in temperate and tropical forests (Molofsky and Augspurger 1992; Sydes and Grime 1981), but this is primarily related to litter depth rather than nutrient content. Importantly, there are few examples where adults and seedlings of the same species show different habitat associations based on nutrient availability. Webb and Peart (2000) suggested that seedlings would be more strongly related to a habitat than adults if seedling establishment occurred in suboptimal habitats, which would indicate the importance of negative density dependence (Comita et al. 2010). However, seedlings and adults at Haast are associated most strongly with nutrients in the organic horizon and mineral soil, respectively, corresponding to their likely patterns of rooting depth. It therefore seems likely that seedlings are widely dispersed, consistent with the relatively small distance across the dune sequence, and that nutrient availability, rather than density dependence, is the most likely explanation for the observed patterns in plant community composition along the chronosequence.

Comparison of the Haast chronosequence with the nearby Franz Josef chronosequence

Although the pattern of tree community composition along the Haast chronosequence is consistent with that following large-scale disturbance in Westland, it differs markedly from the pattern of vegetation change at the nearby Franz Josef chronosequence, despite a similar overall species pool (although *N. menziesii* is not present at Franz Josef). At Haast, podocarps dominate the basal area on young dunes, with an increasing proportion of the basal area formed by woody angiosperms as soils age. At Franz Josef, in contrast, young soils support only angiosperms, *D. cupressinum* adults first appear on intermediate-aged soils (12,000 years BP), and podocarps become a major proportion of the tree community on only the oldest soils (Richardson et al. 2004). Stevens (1968) termed this pattern "backward succession" with reference to the absence of podocarps on the high glacial terraces in Westland, as opposed to "forward succession" associated with decreasing fertility and podzolisation. A similar pattern to Franz Josef occurs along the Waitutu chronosequence (Coomes et al. 2005; Mark et al. 1988), although this is perhaps linked to waterlogging on the older terraces, because the podocarp species that occur there, including *Halocarpus biformis* and *Lepidothamnus intermedius*, appear to be flood-tolerant (Gaxiola et al. 2010). In contrast, the dune soils at Haast are sandy and well drained, even on older soils with an iron pan, so waterlogging does not appear to be an important factor in structuring the plant community along the sequence.

Soil nutrient status appears to play an important role in structuring the vegetation communities along New Zealand chronosequences. The modern distribution of podocarps in New Zealand is biased toward harsh edaphic conditions (Leathwick 1995) and the increasing abundance of podocarps as soils age along the Franz Josef and Waitutu chronosequences has been attributed to their superior ability to tolerate nutrient-poor soils, being slow growing and having long-lived leaves that retain nutrients for long periods (Coomes et al. 2005; Richardson et al. 2005). Could differences in nutrient status reconcile the differences in vegetation patterns between the Haast and Franz Josef chronosequences? (Although Waitutu represents another example of soil and forest change over a long time scale, we exclude it here because the youngest surfaces are $\sim$79,000 years old.) Phosphorus certainly seems to offer a potential explanation for the presence of *D. cupressinum* along the two sequences. The early stages of the Franz Josef chronosequence, for example, contain much greater concentrations of total phosphorus ($\sim$800 mg P kg^{-1}) than early stages of the Haast ($\sim$300 mg P kg^{-1}) sequence (Parfitt et al. 2005; Turner et al. 2012). This is a product of the marked differences in parent material between the two sequences: slightly weathered sand grains at Haast, compared with unweathered coarse moraine at Franz Josef. Along both sequences, however, *D. cupressinum* appears on soils with total phosphorus concentrations of $\sim$300 mg P kg^{-1}; these are only a few hundred years old at Haast, but $\sim$12,000 years old at Franz Josef. In addition, soils with $\sim$100 mg P kg^{-1} of total phosphorus along both sequences support canopies containing podocarps and woody angiosperms in approximately equal proportions.

We therefore conclude that pedogenic changes in soil nutrients not only influence variation in tree community composition along the Haast chronosequence, but might also help to reconcile differences in community development among sequences. The link between soil phosphorus and the distribution of tree species warrants further investigation, perhaps through studies on additional sequences in the region developed on contrasting parent materials.

References

Berryman KR, Cochran UA, Clark KJ, Biasi GP, Langridge RM, Villamor P (2012) Major earthquakes occur regularly on an isolated plate boundary fault. Science 336:1690–1693

Biffin E, Conran J, Lowe A (2011) Podocarp evolution: a molecular phylogenetic perspective. In: Turner BL, Cernusak LA (eds) Ecology of the Podocarpaeae in tropical forests. Smithsonian Institution Scholarly Press, Washington, DC, pp 1–20

Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. Science 329:330–332

Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G, Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. Science 295:666–669

Coomes DA, Bellingham PJ (2011) Temperate and tropical podocarps: how ecologically alike are they? In: Turner BL, Cernusak LA (eds) Ecology of the Podocarpaceae in tropical forests. Smithsonian Institution Scholarly Press, Washington, DC, pp 119–140

Coomes DA, Allen RB, Bentley WA, Burrows LE, Canham CD, Fagan L, Forsyth DM, Gaxiola-Alcantar A, Parfitt RL, Ruscoe WA, Wardle DA, Wilson DJ, Wright EF (2005) The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. J Ecol 93:918–935

Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76:1407–1424

Dickinson KJM, Mark AF (1994) Forest–wetland vegetation patterns associated with a Holocene dune–slack sequence, Haast Ecological District, south western New Zealand. J Biogeogr 21:259–281

Duncan RP (1993) Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. J Ecol 81:403–416

Eger A, Almond PC, Condron LM (2011) Pedogenesis, soil mass balance, phosphorus dynamics and vegetation communities across a Holocene soil chronosequence in a super-humid climate, South Westland, New Zealand. Geoderma 163:185–196

Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76:1899–1916

Gaxiola A, McNeill SM, Coomes DA (2010) What drives retrogressive succession? Plant strategies to tolerate infertile and poorly drained soils. Funct Ecol 24:714–722

Hedin LO, Vitousek PM, Matson PA (2003) Nutrient losses over four million years of tropical forest development. Ecology 84:2231–2255

Herbert DA, Fownes JH (1999) Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. Ecosystems 2:242–254

Hurst JM, Allen RB (2007) The RECCE method for describing New Zealand vegetation—expanded manual. Version 4. Landcare Research, Lincoln

Johnson EA, Miyanishi K (2008) Testing the assumptions of chronosequences in succession. Ecol Lett 11:1–13

Kershaw AP, McGlone MS (1995) The quaternary history of the southern conifers. In: Enright NJ, Hill RS (eds) Ecology of the southern conifers. Smithsonian Institution Press, Washington, DC, pp 30–63

Leathwick JR (1995) Climatic relationships of some New Zealand forest tree species. J Veg Sci 6:237–248

Li X, Rapson GL, Flenley JR (2008) Holocene vegetational and climatic history, Sponge Swamp, Haast, south-western New Zealand. Quat Int 184:129–138

Lusk CH, Smith B (1998) Life history differences and tree species coexistence in an old-growth New Zealand rain forest. Ecology 79:795–806

Mark AF, Grealish G, Ward CM, Wilson JB (1988) Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 1: The vegetation and soil patterns. J R Soc N Z 18:29–58

Molofsky J, Augspurger CK (1992) The effect of leaf litter on early seed establishment in a tropical forest. Ecology 73:68–77

New Zealand Meteorological Service (1983) Summaries of climatological observations to 1980. New Zealand Meteorological Service Miscellaneous Publication 177

Norton DA, Herbert JW, Beveridge AE (1988) The ecology of Dacrydium cupressinum: a review. N Z J Bot 26:37–62

Ogden J (1985) An introduction to plant demography with special reference to New Zealand trees. N Z J Bot 23:751–772

Ogden J, Stewart GH (1995) Community dynamics of the New Zealand conifers. In: Enright NJ, Hill RS (eds) Ecology of the southern conifers. Smithsonian Institution Press, Washington, DC, pp 81–119

Oksanen J (2010) Multivariate analysis of ecological communities in R: vegan tutorial

Palmer RWP, Doyle RB, Grealish GJ, Almond PC (1986) Soil studies in south Westland, 1984/1985. Soil Bureau District Office Report NP 2. Department of Scientific and Industrial Research, New Zealand

Parfitt RL, Ross DJ, Coomes DA, Richardson SJ, Smale MC, Dahlgren RA (2005) N and P in New Zealand soil chronosequences and relationships with foliar N and P. Biogeochemistry 75:305–328

Peltzer DA, Wardle DA, Allison VJ, Baisden WT, Bardgett RD, Chadwick OA, Condron LM, Parfitt RL, Porder S, Richardson SJ, Turner BL, Vitousek PM, Walker J, Walker LR (2010) Understanding ecosystem retrogression. Ecol Monogr 80:509–529

Richardson SJ, Peltzer DA, Allen RB, McGlone MS, Parfitt RL (2004) Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. Oecologia 139:267–276

Richardson SJ, Peltzer DA, Allen RB, McGlone MS (2005) Resorption proficiency along a chronosequence: responses among communities and within species. Ecology 86:20–25

Rose AB, Pekelharing CJ, Platt KH (1992) Magnitude of canopy dieback and implications for conservation of southern rata-kamahi (Metrosideros umbellata–Weinmannia racemosa) forests, central Westland, New Zealand. N Z J Ecol 16:23–32

Stevens PR (1968) A chronosequence of soils near the Franz Josef Glacier. Lincoln College, University of Canterbury, Canterbury

Stewart GH, Rose AB (1990) The significance of life history strategies in the developmental history of mixed beech (Nothofagus) forests, New Zealand. Vegetatio 87:101–114

Stewart GH, White JC, Duncan RP (1998) The structure and dynamics of rimu-dominated forests on glacial moraines, South Westland. N Z For 42:22–27

Sydes C, Grime JP (1981) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. J Ecol 69:249–262

Turner BL, Condron LM, Richardson SJ, Peltzer DA, Allison VJ (2007) Soil organic phosphorus transformations during pedogenesis. Ecosystems 10:1166–1181

Turner BL, Condron LM, Wells A, Andersen KM (2012) Soil nutrient dynamics during podzol development under lowland temperate rain forest. Catena 97:50–62

Veblen TT, Stewart GH (1982) On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwilli* stands on South Island. J Ecol 70:413–436

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. Geoderma 15:1–19

Walker J, Thompson CH, Fergus IF, Tunstall BR (1981) Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. In: West DC, Shugart HH, Botkin DB (eds) Forest succession: concepts and application. Springer, New York, pp 107–131

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. J Ecol 98:725–736

Wardle P (1980) Primary succession in Westland National Park and its vicinity, New Zealand. N Z J Bot 18:221–232

Wardle P (1991) Vegetation of New Zealand. Cambridge University Press, Cambridge

Wardle DA, Zackrisson O, Hörnberg G, Gallet C (1997) The influence of island area on ecosystem properties. Science 277:1296–1299

Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513

Wardle DA, Bardgett RD, Walker LR, Peltzer DA, Lagerström A (2008) The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. Oikos 117:93–103

Webb OW, Peart DR (2000) Habitat associations of trees and seedlings in a Bornean rain forest. J Ecol 88:464–478

Wells A, Goff J (2006) Coastal dune ridge systems as chronological markers of palaeoseismic activity: a 650-yr record from southwest New Zealand. Holocene 16:543–550

Wells A, Goff J (2007) Coastal dunes in Westland, New Zealand, provide a record of paleoseismic activity on the Alpine fault. Geology 35:731–734

Wells A, Duncan RP, Stewart GH (2001) Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake-induced disturbance. J Ecol 89:1006–1018