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Opportunities and limitations of exotic *Pinus radiata* as a facilitative nurse for New Zealand indigenous forest restoration

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Abstract

Background: We investigated the long-term potential of non-harvest *Pinus radiata* plantations for the facilitation and restoration of a natural forest community dominated by indigenous woody species. We investigated the relationship between indigenous regeneration and light levels and the hypothesis that proximity to indigenous seed sources is critical. We studied nine *Pinus radiata* stands of different ages located within Kinleith Forest, which is a large (*ca.* 66 000 ha) commercial exotic plantation forest located in New Zealand's central North Island.

Methods: We constructed a chronosequence of *P. radiata* plantation stands aged 2–89 years to represent long-term natural forest regeneration following plantation establishment. We surveyed structural, compositional and contextual aspects of this secondary succession and compared these results with an old-growth indigenous forest reference site located within the study area.

Results: The exotic *P. radiata* canopy facilitated a regeneration trajectory characterised by shade-tolerant indigenous forest species. We found that the structure and composition of *P. radiata* understories were strongly influenced by stand age and proximity to indigenous forest. Stand age was important from the perspective of creating shaded conditions for the establishment of shade-tolerant woody forest species. Our results suggest that proximal indigenous forest was required for the consistent natural establishment of larger-fruited, bird-dispersed mature forest canopy species in *P. radiata* plantations.

Conclusions: Our results showed that, even at ecologically isolated sites, the microclimate conditions created by plantation *Pinus radiata* stands supported a suite of readily-dispersed indigenous forest plants. Based on these results we suggest that non-harvest *P. radiata* stands provide an important opportunity for the restoration of indigenous forest communities in New Zealand's production landscapes. Where restoration of forest composition similar to old-growth is the restoration objective, however, interventions might be necessary to direct and accelerate the secondary forest succession. Further replicated study is required into the relationship between native forest proximity and understorey regeneration patterns.

Introduction

Human habitation has caused vast reductions in the extent of natural forest cover across most of the world (Crowther et al. 2015). In New Zealand, for example, an estimated 71% (14 million ha) of natural forest cover has been cleared (Ewers et al. 2006). This loss of forest habitat has diminished many aspects of forest-related biodiversity (Gaston et al. 2003; Brockerhoff et al. 2008a; Gardner et al. 2009) and the principal responses have been the formulation of strategies to reduce further forest loss, to ensure that forests are managed sustainably, and to conserve forest biodiversity (e.g. the Bonn Challenge; IUCN, 2011). As of 2010, an estimated 6.6% (265 million ha) of the global forest area was planted forests, and New Zealand ranked ninth among the top-ten countries in absolute plantation area (Forest Stewardship Council [FSC] 2012). As increasing areas are afforested for timber production, methods to preserve or enhance indigenous biodiversity in these planted landscapes are also required (Brockerhoff et al. 2001; Carnus et al. 2006).

Existing research has examined the role of commercial plantations in facilitating the natural regeneration of indigenous forest flora (Lamb et al. 2005; Brockerhoff et al. 2008a). However, while commercial plantations might contribute ecologically by increasing landscape connectivity, buffering indigenous remnants, or providing sometimes scarce forest habitats (Brockerhoff et al., 2008a), the long-term potential for the recruitment of mature forest canopy species is usually truncated by the disturbance associated with the plantation harvest and subsequent site preparation operations (Allen et al. 1995; Chapman & Chapman 1996). An estimated 90% of plantation forest in New Zealand comprises *Pinus radiata* (Pinaceae; Ministry of Primary Industries [MPI] 2019) and these commercial plantations operate on a clear-fell rotation of 25–30 years (MPI 2019), meaning most of the indigenous regeneration is lost between harvest rotations. Alternatively, for various environmental (e.g. promoting water quality, soil conservation, or carbon sequestration), social (e.g. a shift in community aspirations), or economic (e.g. a high degree of technical difficulty or risk associated with harvesting) reasons, some *P. radiata* plantations are unlikely to be harvested. These "non-harvest" stands present opportunities for the restoration of indigenous forest species, with associated benefits to indigenous biodiversity (Norton & Forbes 2013).

Several European studies have assessed the role of *P. radiata* plantations as sites for the restoration of temperate forest species. Onaindia et al. (2013) assessed the potential for *P. radiata* plantations to be used as a passive restoration tool for the natural establishment of indigenous mixed-*Quercus* spp. forest in Spain. They found that with increasing plantation age, *P. radiata* plantations became compositionally more similar to natural *Quercus* forest. Diversity indices revealed, however, that *P. radiata* forest maintained a greater number of both rare and dominant species compared to natural *Quercus* stands, and several species indicative of old-growth forest were not found in the oldest *P. radiata*

stands (aged 40 years; Onaindia et al. 2013). An earlier study emphasised the role of adjacent indigenous forest remnants in providing a source of propagules to enrich regeneration patterns in *P. radiata* plantations (Onaindia & Mitxelena 2009).

Within *Pinus* spp. plantations, two key predictors of understorey regeneration patterns are recognised, being: (1) stand age (Keenan et al. 1997; Ogden et al. 1997; Onaindia & Mitxelena 2009); and (2) the proximity to indigenous forest seed sources (Zanne & Chapman 2001; Onaindia & Mitxelena 2009; Zamora et al. 2010). Age-related changes in the *P. radiata* plantation canopy structure alter understorey illumination (Porté et al. 2004). These temporal changes in understorey light levels make stand age an important predictor of understorey regeneration patterns (Ogden et al. 1997; Brockerhoff et al. 2003), and indicators of forest development such as woody species richness have been found to be positively correlated with *P. radiata* plantation age (Keenan et al. 1997; Ogden et al. 1997; Onaindia & Mitxelena 2009). The proximity of indigenous forest seed sources to *Pinus* spp. plantations is also of importance to patterns in understorey regeneration (Zanne & Chapman 2001; Onaindia & Mitxelena 2009; Zamora et al. 2010). This is particularly relevant to exotic *Pinus* spp. plantations in New Zealand, where the mainland forest flora is predominantly bird dispersed (*ca*. 70%; Clout & Hay 1989). Most of this dispersal, however, operates over short distances (e.g. typically within several hundred metres from the parent tree; Williams 2006; Wotton & Kelly 2012). It then follows that exotic conifer plantations, which do not produce nectar or fruit to attract key seed dispersing bird species, would have a limited ability to attract dispersers (Clout & Gaze 1984). This may impose limitations on the probabilities of the seed of indigenous species reaching and establishing within ecologically isolated *Pinus* spp. plantations.

Here we investigated the long-term potential of non-harvest *P. radiata* plantations in recruiting indigenous forest flora and developing a forest community dominated by indigenous woody species, characteristic of mature natural forest. We hypothesised that the establishment of indigenous species is dependent on suitable light levels in the plantation understorey, and also on the ability of species to reach the site via dispersal from nearby indigenous forest. Corresponding to modifications of the understorey light environment from the rapidly closing *P. radiata* canopy, we predicted an initial invasion of light-demanding early-successional woody species, followed by an accrual of shade-tolerant indigenous angiosperm forest canopy species. We also predicted that mature *P. radiata* stands will provide suitable establishment sites for angiosperm canopy species with high dispersal capability, but that many angiosperm species that are less dispersal capable will be limited in occurrence by the isolation of the *P. radiata* stand from an indigenous forest seed source, regardless of *P. radiata* stand age. We also expected that the relatively light-demanding conifer species of the Podocarpaceae family, which normally fill prominent canopy and emergent tiers in New Zealand's natural

forests, would not be present in older *P. radiata* stands due to either dispersal limitation or the heavy shade cast by a combination of both the *P. radiata* canopy and dense understorey vegetation. To represent natural forest regeneration over a period of nine decades following plantation establishment, we surveyed structural and compositional aspects over a chronosequence of *P. radiata* plantation stands aged 2–89 years and compared these results with an old-growth indigenous forest reference site located within the study area.

Methods

Study area

The study was undertaken in Kinleith Forest, which is a large (*ca*. 66 000 ha) commercial exotic plantation forest located in New Zealand's central North Island (38°23'28"S 175°57'40"E). The climate is cool and moist. Annual average air temperature (1931–1990 average from Tokoroa in the middle of the study area; National Institute of Water and Atmospheric Research [NIWA] 2015) is 12°C. Annual average rainfall (1931–2003 average) is 1485 mm. Soils of the study area are pumice and were formed from tephra parent materials (Table 1; Landcare Research [LCR] 2015). These soils are characteristically coarse textured and free draining. Topography is variable and elevations range from 350 to 550 m above mean sea level (Table 1).

Mixed conifer-angiosperm forest is characteristic of the natural forests of the study area (Leathwick & Mitchell 1992). These forests typically comprise the angiosperm mature forest canopy species: *Beilschmiedia tawa* (Lauraceae), *Hedycarya arborea* (Monimiaceae), *Knightia excelsa* (Proteaceae), and *Weinmannia racemosa* (Cunoniaceae); and Podocarpaceae conifers: *Dacrydium cupressinum*, *Podocarpus totara*, *Prumnopitys ferruginea*, and *Prumnopitys taxifolia*. However, the extent of these forests within the study area has been reduced to a point where only small forest remnants exist. Larger tracts of indigenous forest occur > 15 km to the south (Pureora Forest Park) and the north (Kaimai-Mamaku Forest Park) of the study area.

Stand selection

For the purposes of a space-for-time substitution, we selected nine *Pinus radiata* plantation stands ranging in age from 2–89 years since establishment (Table 1). *Pinus radiata* stand selection aimed to vary only stand age and kept the following factors as uniform as possible: underlying soil type, topography, aspect, slope, consistency of silviculture interventions, stand size and shape sufficient to avoid edge effects, and proximity to other chronosequence stands (Table 1).

Field survey

In each of the nine stands, and in the indigenous forest reference site, four 10 × 10 m understorey vegetation plots were randomly positioned (random GPS coordinates were derived using numbered grids superimposed on satellite images), then located using a handheld GPS (Garmin GPSMAP 64s) and then surveyed. Plots were separated by a minimum of 50 m, and to avoid edge effects, plots were not located within 30 m of the plantation edge. Woody understorey plant cover, height in tiers, density and tree diameter (>2 cm diameter at 1.35 m above ground level; dbh) were assessed within understorey plots using the RECCE method (Hurst & Allen 2007). Cover-abundance for each understorey species was estimated using the scale: 1 = <1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; and 6 = 76–100%. Understorey species were recorded when they had live foliage present within the height tiers: <0.3; >0.3–2; >2–5; >5–12; >12–25; >25 m. Woody epiphytes were tallied separately.

All saplings (<2 cm diameter at breast height (dbh) & >1.35 m tall) and seedlings (<1.35 m tall) occurring within each 10 × 10 m understorey plot were identified to species level and tallied. Seedlings were tallied according to the height classes: <15, 16–45, 46–75, 76–105, 106–135 cm. All *P. radiata* trees occurring within a circular 0.03 ha plot centred on the 10 × 10 m understorey plot were identified and their dbh and height recorded. Tree heights were measured using a Vertex III hypsometer.

At each plot centre, we assessed topographic exposure using the Meso-scale Topographic Index (McNab 1993), which required measurement of eight equidistant slope to horizon measurements from each plot centre. Also measured at each plot were aspect, slope, physiography, canopy structure, and light transmission. Canopy structure and light transmission were estimated using hemispherical (fisheye) photographs, taken from plot centres at 1.35 m above ground level, using a Pentax K200 DSLR camera fitted with a Sigma 4.5 mm circular hemispherical lens. The proximity of *P. radiata* stands to indigenous forest was mapped using a combination of aerial photography and field inspections to verify vegetation extent and composition. Plant nomenclature and dispersal mode follows the New Zealand Plant Conservation website (www.nzpcn.org.nz, accessed September 1, 2015).

Indigenous forest proximity

The mean Proximity Index (*PX*; McGarigal & Marks 1995) was used to provide a measure of proximity to indigenous forest for each plot surveyed within the *P. radiata* chronosequence. The original *PX* is the sum of the ratio of indigenous forest patch size to distance from a focal patch to each indigenous forest patch (squared) within a search radius. However, we adapted the index to suit our plot-based study. Rather than calculating the edge-to-edge distance between each indigenous patch and the focal *P. radiata* stand, we calculated the distance from the indigenous forest edge to the *P. radiata* plot centre. Therefore, we expressed *PX* as the sum of indigenous forest patch area (m²) within the search radius, divided by the sum of all indigenous edges to *P. radiata* plot (squared (m²)) distances, for all indigenous forest patches whose edges were within 1 km (linear) of the focal plot centre. We chose 1-km lineal distance as the search radius as the distance further than which common New Zealand indigenous forest birds are unlikely to reliably disperse fleshy-fruited propagules (Wotton & McAlpine 2015). Sites with high *PX* value indicate higher levels of indigenous cover proximal to the survey plot.

TABLE 1. Forest stand details of the Kinleith Forest *Pinus radiata* plantation chronosequence, central North Island, New Zealand

Year Planted	Age	Silvicultural Treatment	Current Rotation	Soil Type^	Slope Aspect	Meso-scale Topography	Elevation	Coordinates
2013	2	P = 1; R = 1	3	TpH + NaH	3-18°, S	6.3	350	38°24'25"S 175°54'33"E
2009	5	P = 1; R = 1	3	TpH + NaH	0-22°, E	12.0	350	38°23'53"S 175°55'45"E
1999	15	T = 7	2	TpH + NaH	22-28°, E	11.4	450	38°22'38"S 175°56'15"E
1989	25	T = 6, 8	2	TpH + NaH	13-33°, N	9.8	350	38°24'06"S 175°55'14"E
1979	35	T = 7	2	OiH	17-30°, N	19.2	450	38°22'48"S 176°00'40"E
1970	44	–	1	W	25-35°, N	17.4	350	38°06'47"S 175°56'09"E
1954	60	T = 23	2	TpH	4-25°, S	12.8	350	38°23'57"S 175°58'22"E
1927	86	T = 16	1	TpH	0-25°, E	9.1	450	38°24'53"S 176°03'12"E
1925	89	–	1	Tpd	0-6°, E	4.1	350	38°16'40"S 175°50'18"E
N/A	NF	N/A	N/A	Na + Oi	5-24°, S	6.5	550	38°27'43"S 176°02'58"E

Note. Silvicultural treatments are: "P" = herbicide land preparation, "R" = herbicide release spray, "T" = thinning, "–" = no data available; the numeral(s) indicate the plantation age (yrs) at the time of silvicultural treatment(s). Elevations given are in 100 m vertical bands. Aspects given are the stand mean represented as the nearest cardinal direction. ^Soil abbreviations are: TpH = Taupo hill soils, Tpd = Taupo deep sand, NaH = Ngakuru hill soils, Na = Ngakuru loam, Oi = Oranui sand, OiH = Oranui hill soils, W = Waiohotu (silty loam). "NF" = natural forest reference site. Coordinates are shown in the WGS84 coordinate system.

Statistical analysis

All statistical analyses were undertaken using R (R Development Core Team Team [R] 2015). Vegetation plots were treated as individual units in the analyses. The effect of *Pinus* stand age on *P. radiata* basal area and indigenous tree fern basal area were assessed using generalised linear regression, applying the Gaussian family, and logarithm (for *P. radiata*) and identity (for tree ferns) links, with natural log conversion of the explanatory variable (*P. radiata* stand age). All regression models were tested for linearity, normality of the residuals, and homoscedasticity using diagnostic plots.

Canopy structure and light transmission data were extracted from hemispherical photographs using the imaging software Gap Light Analyzer (GLA, Version 2; Frazer et al. 1999). For GLA modelling, the growing season was defined as 1 September–31 March, the default solar constant used was 1367 Wm^{-2}, and the default cloudiness index, spectral fraction, and beam fraction were all set at 0.5.

The relationships between both percentage canopy openness and percentage photosynthetically active radiation (PAR), and *P. radiata* stand age, were estimated using nonparametric generalised additive models (GAM), through use of the mgcv package (Wood 2011). These GAMs were applied using beta family and logit link function.

Differences among *P. radiata* stands of varying age, and between *P. radiata* stands and the indigenous reference site, were assessed using nonparametric Kruskal-Wallis rank sum tests for the following variables.

Kruskal tests were applied in this regard to percentage canopy openness, percentage PAR transmission, woody indigenous seedling densities, sapling densities, and indigenous tree basal area. Where Kruskal tests returned statistically significant results at α=0.05, pairwise post-hoc tests were carried out using Nemenyi tests. Any association between indigenous tree basal area within *P. radiata* stands and *P. radiata* stand age was assessed using the nonparametric Spearman's rank-order correlation.

Species turnover (beta diversity) was assessed from woody species presence-absence data using Jaccard similarity that was calculated using the Simba package (Jurasinski & Retzer 2012). The comparison of Jaccard similarity between paired stand ages provided an assessment of changes in the level of continuity in species composition over time. The possible spatial distribution of species across a pair of quadrats is expressed as follows: a' representing the total number of species common between both plots, b' representing the total number of species that occur in the neighbouring plot but are absent from the focal plot, and c' representing the total number of species that occur in the focal plot but not in the neighbouring one. Species turnover as expressed by a', b', and c' was visualised in similarity space using a ternary plot in accordance with the approach advocated by Koleff et al. (2003).

Nonmetric dimensional scaling (nMDS) was used to make inferences regarding compositional shifts, both across the *P. radiata* chronosequence and in relation to the indigenous forest reference site, using the metaMDS

function of the Vegan package (Oksanen et al. 2008). For nMDS ordination analysis, species importance values were calculated following Allen et al. (1995). The following weights were allocated to the RECCE cover classes (cover class = weight): 1 = 1.0; 2 = 2.0; 3 = 3.0; 4 = 4.0; 5 = 5.0; and 6 = 6.0. Epiphytes were given a nominal weighting of 0.5. Differences in ordination space among the different aged *P. radiata* stands and the indigenous forest reference site were tested using permutational multivariate analysis of variance with the adnois function in Vegan. The contribution of within-site variability was assessed using the function betadisper in Vegan. The nMDS ordination was further examined through similarity percentage analysis (SIMPER; Clarke 1993) to distinguish which species discriminate between stand ages and between the two forest types.

Results

Pinus radiata basal area and canopy height

Chronosequence stand summary statistics are given in Appendix S1. Stand age was a significant predictor of *P. radiata* basal area across the chronosequence ($F_{1,7}$ = 74.466, P<0.001; Appendix S2). Predicted *P. radiata* basal area increased from 9.7±4 m^2 ha^{-1} at year 2, to 49.6±5 m^2 ha^{-1} at year 30, and to 95.3±7 m^2 ha^{-1} at year 90. *Pinus radiata* canopy height increased rapidly during the initial 25 years, and more gradually thereafter, reaching an eventual mean canopy top height of 53.8±1.6 m (*n*= 32) in 86- and 89-year-old stands (Appendix S1).

Canopy openness and total PAR transmission

Percentage canopy openness differed significantly among *P. radiata* stand ages (χ^2(9) = 34.013, P<0.001). The 2- and 5-year-old stands had significantly greater canopy openness compared to the older stands of the chronosequence. Predicted mean percentage canopy openness decreased from initially completely open canopy, to 33±4% 15 years after establishment, and to 12±3% at 20 years, beyond which canopy openness plateaued at about 8% for the remainder of the chronosequence.

The amount of total PAR transmitted to the forest understorey also differed significantly across the chronosequence (χ^2(9) = 32.103, P<0.001). Over the first 15 years, total PAR transmission was reduced from about 100% to 30±6% (Fig. 1). The degree of light transmission to the forest understorey plateaued 25 years after plantation establishment; beyond 25 years, only about 25% of total available light reached the forest understorey. No significant differences in either canopy openness (all P>0.14) or total PAR transmission (all P >0.23) occurred among stands aged 15 years or older. Nor were there significant differences in either canopy openness (all P>0.22) or total PAR transmission (all P >0.14) between stands aged 15 years or older and the indigenous forest reference site.

Forest understorey vegetation structure

Woody seedling density

Indigenous woody seedling densities differed significantly among *P. radiata* stand ages, and also differed
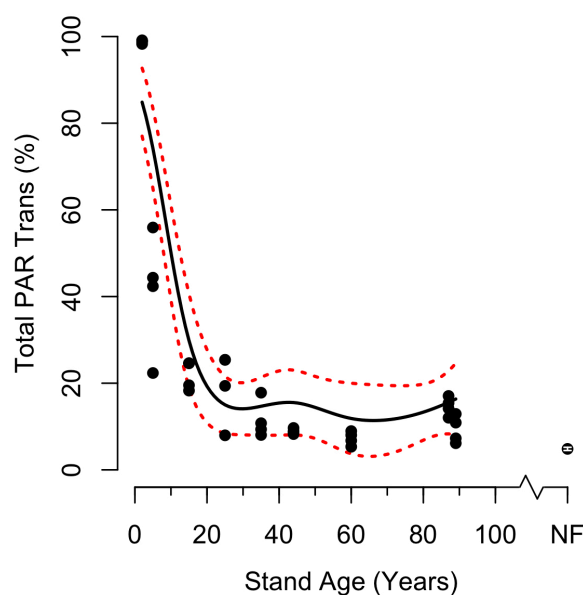

FIGURE 1: Fitted Generalised Additive Model of the percentage total photosynthetically active radiation (PAR) transmission assessed using hemispherical photographs taken at 1.35 m above ground level in a chronosequence of nine Pinus radiata plantation stands age. Dashed lines indicate the 95% CI. Mean value (±1SE) from the old-growth natural forest ("NF") reference site shown for comparative purposes.

from the seedling densities in the indigenous reference site (χ^2(9) = 27.348, P=0.002; Appendix S3). The highest indigenous woody seedling density within *Pinus* stands was found in the 44-year-old stand (3 050±581 stems ha^{-1}), where a significantly greater stem density was achieved compared to either 2-year-old (25±25 stems ha^{-1}; P=0.021) or 86-year-old *Pinus* stands (50±50 stems ha^{-1}; P=0.025). Indigenous woody seedling densities in all stands other than those aged 2 and 86 years were not significantly different to the seedling density in the indigenous forest reference site (3 750±1475 stems ha^{-1}; all P>0.35). Exotic seedlings were found in low densities in the 5-year-old (50±29 stems ha^{-1}), 15-year-old (75±49 stems ha^{-1}), and 25-year-old (125±95 stems ha^{-1}) stands and were absent from all other stands of the survey.

Sapling density

The density of indigenous saplings differed significantly across the chronosequence (χ^2(9) = 26.58, P=0.002). The contributing differences were between the 2-year-old stand (where saplings were absent) and both the 35-year-old stand (1525±394 stems ha^{-1}; P=0.05; *n*=61) and the indigenous forest reference site (2525±812 stems ha^{-1}; P=0.023; *n*=101; data not shown). Exotic saplings were present in only the 5-, 15-, and 25-year-old stands; and were most numerous in the 5-year-old stand (625±239 stems ha^{-1}; *n*=25) compared to either the 15-year (175 stems ha^{-1}; *n*=7) or 25-year stands (*n*=1).

Indigenous trees and tree ferns

There was no significant difference in indigenous tree basal area among the *P. radiata* stands (χ^2(7) =

13.17, P=0.068), nor was there a significant association between indigenous tree basal area and stand age ($r_s(6)$ = 0.619, P=0.115; Fig. 2A). Adult tree ferns entered the chronosequence between years 15 and 25. Stand age was not a significant predictor of tree fern basal area across the chronosequence ($F_{1,4}$ = 6.170, P=0.068, Fig. 2B). Over the chronosequence, the tree-fern community was dominated by *Dicksonia squarrosa* (Dicksoniaceae; range = 400±70–1125±433 stems ha⁻¹), with fewer numbers of *Cyathea*

medullaris (Cyatheaceae; range = 0–475±95 stems ha⁻¹) and of *C. dealbata* (Cyatheaceae; 0–125±75 stems ha⁻¹), and only a small number of *D. fibrosa* (Dicksoniaceae; *n* = 2). In the older (i.e. 44–89 years old) *P. radiata* stands, mean tree fern heights were *D. squarrosa* = 3.8±0.2 m (*n* =119), *C. medullaris* = 6.1±0.5 m (*n*=40), and *C. dealbata* = 3.4±0.8 m (*n*=8).

Species richness

Stand age was a significant predictor of indigenous woody species richness (*S*) in plantations across the chronosequence ($F_{1,6}$ = 9.745, P=0.021; Appendix S4). Meso-scale topography was not a significant predictor of *S*. Early in the chronosequence, predicted *S* increased rapidly until approximately 20-years old, and more gradually thereafter (Fig. 3). We found evidence based on patterns of seedling density, species turnover, and compositional data to suggest a positive relationship between *S* and the close proximity to indigenous forest seed source, but our lack of stand-level replication means we cannot determine a statistically significant cause-and-effect relationship. There is a need for further research on the role of proximity as a predictor of *S*. The 44-year-old stand had both relatively high *S* and the highest proximity to seed source, suggesting a positive effect on *S* from proximity. Exotic woody species richness was only a minor feature of the chronosequence, being limited to only 5-year-old (*S*=1.5±0.3), 15-year-old (*S*=1.25±0.3), 25-year-old (*S*=0.5±0.3), and 44-year-old (*S*=0.5±0.3) stands.

A

B
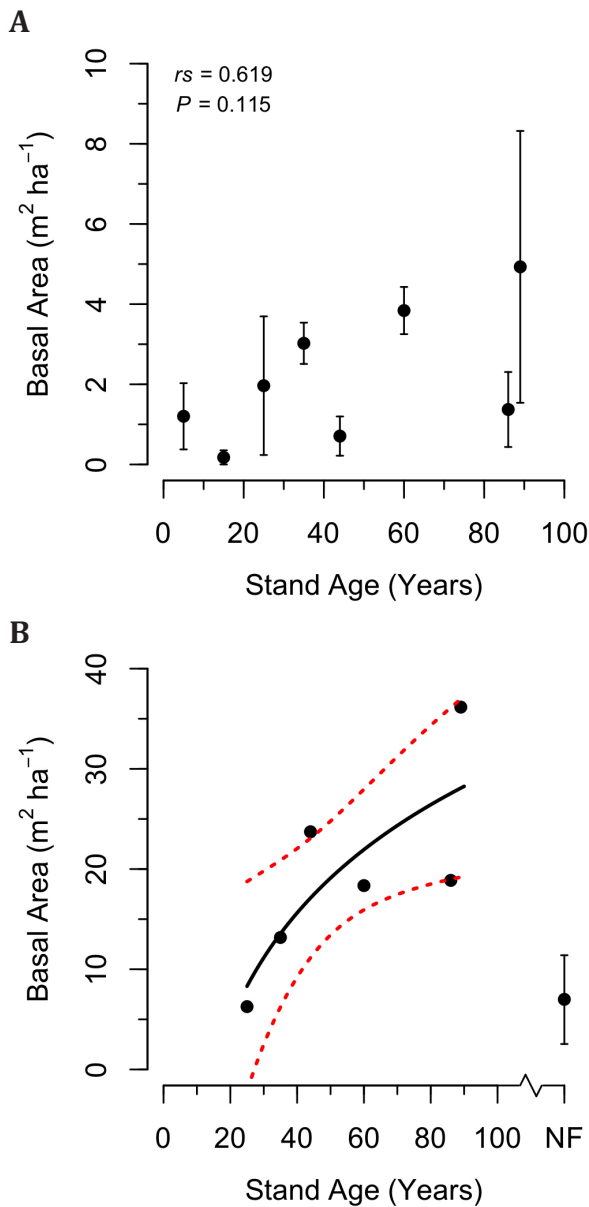
FIGURE 2: Basal area of indigenous (A) trees and (B) tree ferns across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. For comparative purposes, indigenous tree basal area at the old-growth natural forest was 164±33 m² ha⁻¹ (not shown in Fig. 2A) and the tree fern basal area from the old-growth natural forest ("NF") is shown in Fig. 2B. Error bars = ±1SE; dashed lines indicate the 95% CI.

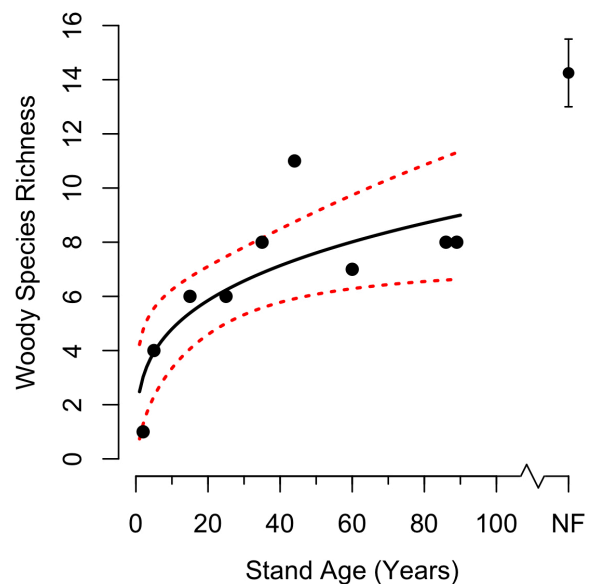FIGURE 3: Predicted indigenous woody species richness (S) as a function of stand age and meso-scale topographic exposure, across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. For comparative purposes, the S from an old-growth natural forest ("NF") reference site is shown. Error bars = ±1SE; dashed lines indicate the 95% CI.

Species turnover and composition

Patterns in woody species turnover were related to stand age and proximity to indigenous forest. The 2-year-old stands were species poor and shared few species with the older stands. These youngest stands featured light-demanding colonisers and were grouped in Jaccard similarity space near the highest extent of axis *b´* and the lowest extent of axis *a´* (Appendix S5), signalling a high degree of species gain and low continuity in this young phase of the chronosequence. Five- and 15-year-old stands still showed <50% similarity with stands of greater age. Stands >25-years of age showed the greatest between-stand continuity (i.e. sharing similarity values of 50% or greater). The 44-year-old stand was a notable exception. It showed only about 30% similarity with stands of greater age, and about 55% of species were discontinuous between the 44-year-old stand and either of the three older stands. This result was driven by the high rate of occurrence of indigenous forest species in the 44-year-old stand.

Species composition

The *Pinus* chronosequence comprised a total of 29 species of trees, tree ferns, and shrubs in the understorey (Appendix S6). The shade-tolerant mature forest canopy and emergent species, namely: *B. tawa*, *H. arborea*, *K. excelsa*, *Litsea calicaris* (Lauraceae), and *W. racemosa*, were present in some mature *P. radiata* stands, particularly in the 44-year-old stand where indigenous forest was in close proximity (Fig. 4; Appendix S7). Including the planted pines, four exotic tree and shrub species were present. The indigenous forest reference site featured eight additional woody species that were not found in the *P. radiata* chronosequence. However, fewer plots were measured in the indigenous forest (four plots), which is likely to underestimate species richness when compared to the stands where sampling was more extensive (32 plots). Species composition differed significantly among ($F_{9,29}$ = 8.921, P=0.001, R^2 = 0.73) but not within ($F_{9,29}$ = 0.687, P=0.715) the *Pinus* and indigenous forest stands (Fig. 4).

Changes in species composition over the first 15 years of the chronosequence were distinguished by the gain and subsequent loss of the light-demanding colonising species including *Coriaria arborea* (Coriariaceae), *Aristotelia serrata* (Elaeocarpaceae), and *Buddleja davidii* (Scrophulariaceae; exotic; Table 2; Fig. 4). Between 15 and 25 years, increased abundance of the tree fern *D. squarrosa* was the most distinguishing floristic change, along with increases in the abundance of the indigenous tree species *Schefflera digitata* (Araliaceae) and *Coprosma robusta* (Rubiaceae). Further accumulation of indigenous forest tree and tree fern species was apparent over the period 25–35 years. Most notable from the SIMPER analysis were the gains in abundance of *Melicytus ramiflorus*, *Cyathea medullaris*, and *Brachyglottis repanda*. *Hedycarya arborea* was the dominant tree in the indigenous forest reference site and was a distinguishing feature of the 44-year-old *Pinus* stand. The composition of the oldest *P. radiata* stand was most clearly distinguished from the indigenous forest reference site by the absence of *H. arborea* and the high abundance of both *D. squarrosa* and *Pseudopanax arboreus*. The 35- and 44-year-old *Pinus radiata* stands were closest in the ordination space to the indigenous forest reference site (Fig. 4).

Discussion
Forest regeneration processes

As predicted, we found that the structure and composition of *Pinus radiata* understories were strongly influenced by stand age, and we found some, albeit limited, evidence of the importance of proximity to indigenous forest. Over the first 15-year period of the forestry cycle, conditions were most suitable for the light-demanding colonising species such as *Coriaria arborea*, *A. serrata*, and the exotic *Buddleja davidii*. Then as *P. radiata* canopy cover and shade increased, these species were replaced by generalist forest tree species with greater shade tolerance such as *S. digitata*, *Melicytus ramiflorus*, and *Brachyglottis repanda*. Although these are relatively early-successional species, they do have the ability to form a forest canopy. Although not the focus of this study, the successional direction observed is consistent with the acquisition of traits associated with later-successional species. Through the chronosequence there was a shift towards species with larger seeds, greater stature, and greater longevity (Weiher et al. 1999).

Stand age was a significant predictor of *S*. Where indigenous forest was in close proximity, we found both a greater density of indigenous woody seedlings and a greater abundance of mature forest canopy species of closer compositional similarity to indigenous forest.
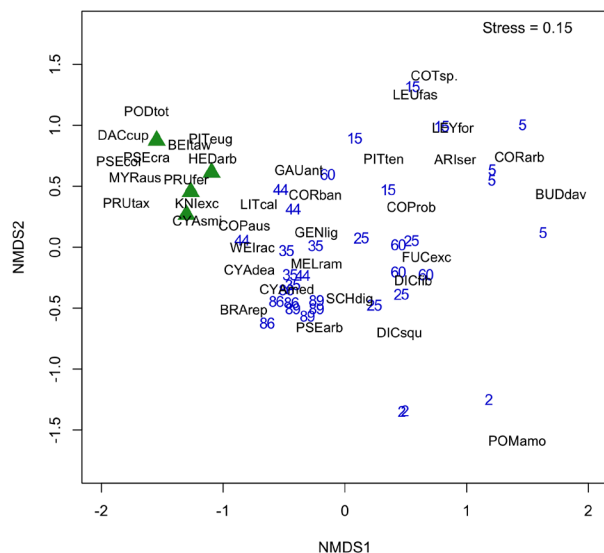

FIGURE 4: Nonmetric dimensional scaling (nMDS) ordination of species composition across chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. The composition of an old-growth natural forest reference site is also included, shown by triangles. Six-letter species codes are described in Appendix S6.

TABLE 2. Similarity percentage (SIMPER) analysis of species composition from a chronosequence of nine plantation stands ranging in age 2–89 years located in Kinleith Forest, central North Island, New Zealand. The three species discriminating most between consecutive stand ages (% Contribution = "Contr."), and the cumulative percentage discrimination ("Cum.") are given. Old-growth natural forest ("NF") reference site included.

Species	Stand age																	
	2–5		6–15		16–25		26–35		36–44		45–60		61–86		87–89		90–NF	
	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.
CORarb	**26±7**	**29**	16±4	22														
ARlser	**22±14**	**52**	14±8	40														
BUDdav	**15±13**	**69**	9±6	52														
DICsqu					**16±7**	**23**					7±4	**25**	6±4	36	**5±3**	**29**	11±3	30
SCHdig					**9±1**	**36**												
COProb					**8±3**	**49**												
MELram							**10±4**	**17**	6±2	13								
CYAmed							7±4	**30**			10±3	15	**8±6**	**27**	5±3	40		
BRArep							6±5	**41**	5±4	25			**11±5**	**16**	7±4	16		
HEDarb									**5±2**	35	6±2	35					**13±5**	**16**
PSEarb																	8±3	40

Note. Numerals in bold signify a gain in abundance, non-bold signifies a loss in abundance, underlined signifies no change in abundance. Species codes are given in Appendix S6.

This result was most apparent in the 44-year-old stand where areas of indigenous forest were as close as 260 m from the sample plots and both species richness and woody seedling density were the highest of any of the plantation ages. The 44-year-old stand had a northern aspect and silty loam soils, and these attributes might also have assisted the establishment and growth of woody indigenous forest species due to warm and sunny microclimate and higher soil quality. In the absence of replicated stand ages, we are unable to generalise our findings from the 44-year-old stand. Further research is required to investigate the effects of differing proximity and composition of indigenous forest seed sources on understorey regeneration patterns in *P. radiata* plantations.

In addition to the generalist shade-tolerant forest tree species, larger-fruited, bird-dispersed species such as *Beilschmiedia tawa*, *H. arborea*, and *Litsea calicaris* were found in high abundances in the 44-year-old stand. Yet, these species were either in low numbers or were absent from stands of greater age. This finding supports our expectations that stand age is important from the perspective of creating shaded conditions for the establishment of shade-tolerant species. However, we suggest that proximal indigenous forest is required for the consistent natural establishment of larger-fruited, bird-dispersed mature forest canopy species in *P. radiata* plantations.

Our results regarding the importance of stand age and the proximity to indigenous forest are consistent with existing national (Allen et al. 1995; Brockerhoff et al. 2003) and international literature. In the wet tropics of northern Queensland, Australia, *Pinus caribaea* plantations aged 5–31 years showed a significant increase in tree species richness with age ($R^2 = 0.788$), and 10–50-year-old *P. caribaea* plantations supported a total of 45 species of indigenous trees and shrubs, with the proportion of later-successional species increasing with age (Keenan et al. 1997). In the temperate Ethiopian Highlands, seed dispersal from adjacent areas of natural forest was identified as being important to enable incorporation of later-successional species into the understories of *Pinus patula* plantations (Senbeta et al. 2002).

The importance of nearby seed sources for understorey regeneration

Of New Zealand's *ca*. 240 woody plant species occurring in mainland forests, about 70% are bird dispersed (Clout & Hay 1989), and of the 21 tree and shrub species surveyed from the *P. radiata* chronosequence, 16 (76%) were dispersed by birds. Aside from less frequent long-distance dispersal, effective bird and wind dispersal operates over typically short distances in New Zealand. Wotton and Kelly (2012) found that mean dispersal distance of *B. tawa* by New Zealand pigeon (*Hemiphaga novaeseelandiae*) was 95±171 m. Only 21% of seeds were dispersed >100 m, and <1% of seeds were dispersed >1 000 m. We found numerous seedlings of *B. tawa* in the 44-year-old *P. radiata* understorey located close to indigenous seed sources, whereas *B. tawa* was

scarce or absent from understories of more isolated stands. New Zealand pigeon is the only extant native bird species capable of dispersing the large fruit produced by *B. tawa* (Clout & Hay 1989). Given the presence of *B. tawa*, and considering the species dependence on New Zealand pigeon for seed dispersal, we can conclude that the dispersal of *B. tawa* was by frugivory from adjacent natural forest, and therefore that bird dispersal was operational at the 44-year-old stand, where species richness and seedling densities were greatest.

Studies of the ubiquitous European blackbird (*Turdus merula*) have also shown that most seeds are dispersed by this species within only 50 m, rarely up to 1 km or more (Williams 2006). Nectar-feeders and frugivores are major components of New Zealand's avifauna, and given the *Pinus* genus does not provide nectar or fruit resources, important insectivorous and frugivorous dispersers are only sometimes present in *P. radiata* plantations (Clout & Gaze 1984). Therefore, the presence of mature indigenous vegetation in the surrounding landscape matrix is important for both the presence of indigenous dispersal vectors and the availability of indigenous forest propagules. This importance is reflected in our results.

Factors potentially affecting podocarp regeneration

We predicted that the relatively light-demanding (in seedling and sapling stages) podocarp species would not be present in mature *P. radiata* plantations due to either heavy shading or ecological isolation from indigenous forest seed sources. Even where mature indigenous forest was proximal, we found no conifer species, and while this makes it difficult to confirm the reasons for their absence, possible explanations are found in the existing literature. Regeneration of New Zealand's long-lived podocarps is disturbance related, insofar as a competitive release is required for the successful establishment and growth of seedlings (McKelvey 1963; Carswell et al. 2012).

Therefore, it is plausible that if seeds were dispersed to *Pinus radiata* plantations, these conifer species would benefit from the disturbance of both the homogenous plantation canopy and any dense understorey growth to increase understorey light levels and stimulate podocarp seedling growth. We note however, both *Prumnopitys ferruginea* and *Prumnopitys taxifolia* have been found to inhabit multiple mature *Pinus radiata* plantations across New Zealand (Brockerhoff et al. 2003). Podocarp dispersal is dependent on frugivory (Beveridge 1964), so in our study the absence of podocarps in the *P. radiata* chronosequence might also be attributed to the fragmented nature of the surrounding indigenous forest landscape, and to a general scarcity of podocarp seed sources in proximity to mature *P. radiata* stands.

Existing studies have identified two reasons for compositional differences between mature *P. radiata* stands and natural forest: insufficient stand age required to provide conditions suitable for regeneration requirements (Onaindia et al. 2013), and ecological isolation (Onaindia et al. 2009). Interventions to create more heterogeneous light conditions in *P. radiata*

plantations might assist with the recruitment of missing mature forest tree species (Onaindia et al. 2013). There are grounds to expect canopy interventions (creation of canopy gaps or thinning) or understorey manipulations would benefit podocarp establishment and seedling growth in mature *P. radiata* plantations (Tulod et al. 2018).

Our results strongly suggest that birds were dispersing indigenous forest seeds into the 44-year-old stand. However, sufficient stand age, proximal indigenous forest sources, and suitable light levels such that might be created by canopy gaps are all probable prerequisites for the reliable establishment of New Zealand's long-lived podocarps in *P. radiata* plantation forests.

The scarcity of mature forest canopy species colonising mature *P. radiata* plantations, and in particular isolated *P. radiata* sites, has implications for the composition of future forests at these sites. We consistently found generalist and small tree species colonising mature *P. radiata* understories, such as *B. repanda*, *Pseudopanax arboreus*, *Pittosporum tenuifolium*, *S. digitata*, *Myrsine australis*, and *Melicytus ramiflorus*. The *Pinus radiata* understories also featured a high density of tree ferns. Where mature forest seed sources were proximal, we found the mature forest canopy species *B. tawa*, *H. arborea*, *K. excelsa*, and *Litsea calicaris*. However, even in those instances, we found no podocarps. This absence of podocarps in vegetation communities of similar ages to our *Pinus* stands is consistent with the findings from studies of podocarp regeneration in indigenous broadleaved forest. Where a podocarp seed source is available, a nurse crop of broadleaved angiosperms, or *Leptospermum scoparium* or *Kunzea* spp. (Myrtaceae), is normally required for podocarps to establish themselves. In these natural successions the development of nursery conditions suitable for podocarp establishment is known to take 30–60 years or longer (McKelvey, 1955; Cameron, 1960).

These results suggest that, at ecologically isolated *P. radiata* stands, the future forest composition would be dominated by shorter-statured species with relatively short life expectancy, and that these forests would be distinguished from nearby natural tall forests by the absence of characteristic, very-long lived, old-growth forest canopy species, such as *B. tawa* and *D. cupressinum*. Where mature forest canopy species were present in higher densities due to the close proximity of natural forest, the presence of species such as *B. tawa*, *H. arborea*, and *K. excelsa* provide an indication of convergence towards natural forest composition. However, the absence of podocarps means that a major compositional component of intact natural forests appears to be missing. Where attainment of natural forest composition is the restoration objective, these results suggest that management interventions to address competition for light and seed dispersal limitation might be required to direct the regeneration processes operating in ecologically isolated mature *P. radiata* stands, in order for the stands to develop towards states more representative of natural forest.

Considerations when managing non-harvest stands as restoration sites

Even-aged monoculture plantations are usually initially low in structural diversity and this may limit understorey plant species richness (Gamfeldt et al. 2013), recruitment of future canopy tree species on the site (Royo & Carson 2006), and the potential of wider forest biodiversity values (Lindenmayer et al. 2006). Heterogeneity in canopy cover through formation of canopy gaps, or variation in the vertical structure of the forest may take a long time to develop naturally (Lust et al. 1998; Kuuluvainen et al. 2002). In particular, we note that interventions mimicking the effects of disturbance, such as the creation of artificial canopy gaps, are likely to benefit the establishment and growth of podocarps. For these reasons, we suggest that early interventions such as the creation of small-scale artificial canopy gaps (by felling or stem poisoning) to increase canopy heterogeneity may provide important opportunities to maximise the biological diversity of exotic *P. radiata* plantations.

In addition to the competitive shading effects of the plantation canopy, after several decades, additional competitive effects may result if dense understorey growth develops (Royo & Carson 2006), such as heavily shading herbaceous or fern dominated understories (De la Cretaz & Kelty 2002). This result might mean that even if *P. radiata* canopy openness increases with age, secondary competitive effects from a dense understorey will still limit forest floor regeneration processes. In the understories of mature Spanish *P. radiata* plantations, species from the genera *Rubus* and of the family Poaceae grew rapidly, demonstrating fast lateral spread, achieving dominance and, as a result, were highly competitive on forest floor regeneration processes. Management interventions were recommended to address these competitive effects on forest regeneration (Onaindia et al. 2013). We found that adult tree ferns entered the chronosequence between 15 and 25 years and continued to increase in dominance over the next 50 years or more, reaching densities of 1125±433 stems ha^{-1}. Ogden et al. (1997) also found the understorey composition in older *P. radiata* stands was dominated by tree ferns (tree fern stem densities of 2000–3000 stems ha^{-1}). In such conditions, the same competitive shading effects that have been reported from New Zealand's indigenous forests (Coomes et al. 2005; Gaxiola et al. 2008; Brock et al. 2018) may apply, limiting regeneration processes in these exotic plantation forests.

Where the natural dispersal of old-growth forest canopy species is limited, their active introduction might be required. Within Kaingaroa Forest, Forbes et al. (2015) found that underplanting of podocarps under a degraded *Pinus ponderosa* canopy accelerated forest succession by establishing the structural dominance of long-lived mature forest canopy species within only 50 years. Similar interventions involving the underplanting of non-harvest plantation understories to incorporate late-successional species have also been successful in Sri Lankan (Ashton et al. 1997), Spanish (Rodriguez-

Calcerrada et al. 2008), and German (Noack 2011) *P. radiata* plantations.

Implications for biodiversity conservation in New Zealand

Our results show that, even at ecologically isolated sites, the microclimate conditions created by plantation *Pinus radiata* stands can support a suite of readily-dispersed indigenous forest plants. The structural and compositional aspects of indigenous forest regeneration in older *P. radiata* stands are broadly comparable to New Zealand's mid-successional natural forest communities (Allen et al. 1995; Ogden et al. 1997); and are superior in comparison to exotic pastoral landscapes. In such systems, indigenous forest species are typically restricted in distribution to degraded remnant habitat patches, or to scattered or solitary remnants, or have become locally extinct (Norton & Miller 2000; Brockerhoff et al. 2008b). Our results emphasise the importance of maintaining indigenous cover in production landscapes (Craig et al. 2000) and show how the benefits of doing so can extend beyond the boundaries of those indigenous communities, by boosting biodiversity values in adjacent exotic planted forests (Carnus et al. 2006). Non-harvest *P. radiata* stands provide an important opportunity for the restoration of indigenous forest communities in New Zealand's production landscapes. However, where restoration of mature forest composition is the restoration objective, interventions might be necessary to direct and accelerate the secondary forest succession.

Consent for publication
All authors consent for the publication of this manuscript and its content.

Additional files
Additional file 1: Appendices 1–7.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
AF helped conceive the study, and designed the chronosequence, collected and analysed the data. Led the manuscript preparation and responses to reviewers. DN and FC helped conceive the study and contributed to manuscript preparation.

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Additional File 1.

Opportunities and limitations of exotic *Pinus radiata* as a facilitative nurse for New Zealand indigenous forest restoration.

Adam S. Forbes, David A. Norton, Fiona E. Carswell[2]

Appendix S1. Chronosequence stand summary statistics. Kinleith Forest *Pinus radiata* plantation chronosequence, central North Island, New Zealand. Forest stand statistics refer to *P. radiata* only

Year Planted	Age (Years)	*n*	Density (Stems ha^{-1})	Basal Area (m^2 ha^{-1})	Mean Diameter (cm)	Canopy Height (m)	*PX*
2013	2	62	542±86	0.13±0.03	2.2 ±0.05	1.7 ±0.02	0.117
2009	5	67	558±34	8.7±0.6	14±0.4	9.2±0.2	0.001
1999	15	48	400±45	46±3	37±1	26±1	0.000
1989	25	24	200±36	43±5	52±2	38±1	0.041
1979	35	37	308±28	65±8	50±2	36±2	0.867
1970	44	39	325±34	55±3	45±2	31±1	54.774
1954	60	29	167±24	71±11	70±5	46±3	0.006
1927	86	15	125±25	82±23	89±6	55±3	0.066
1925	89	17	142± 44	107±30	95±6	52±2	0.000

Note. *n* = number of trees sampled. *PX* = Proximity Index: A landscape scale index representing the degree of ecological isolation of survey plots within *Pinus* stands from adjacent indigenous forest cover.

Appendix S2. Generalised Linear Regression of *Pinus radiata* basal area from nine *P. radiata* plantation stands aged 2–89 years, located in Kinleith Forest, central North Island, New Zealand. Dashed lines indicate the 95% CI.
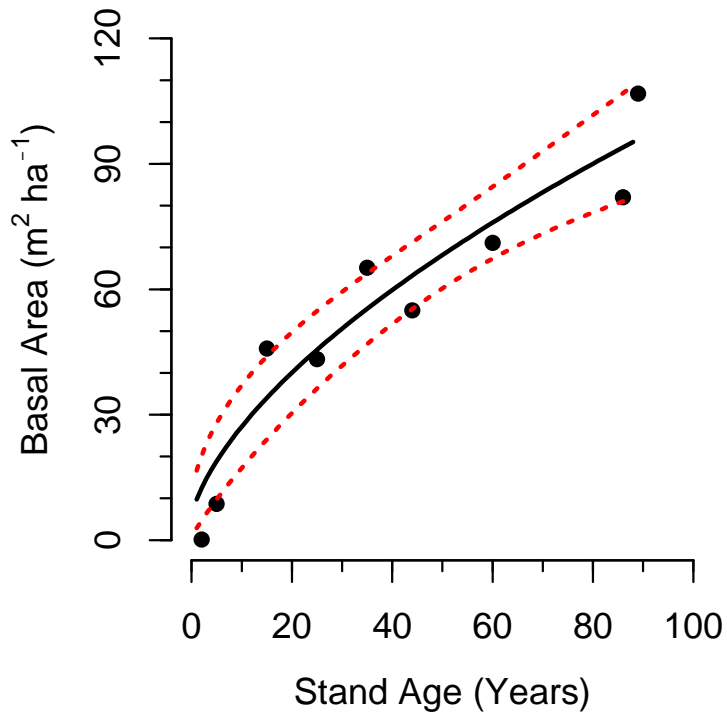
Appendix S3. Indigenous woody seedling densities across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. The notation * indicates significant differences in mean values at the significance level *P* < 0.05. Error bars = ±1SE. Mean seedling density from an old-growth natural forest ("NF") reference site shown for comparative purposes.
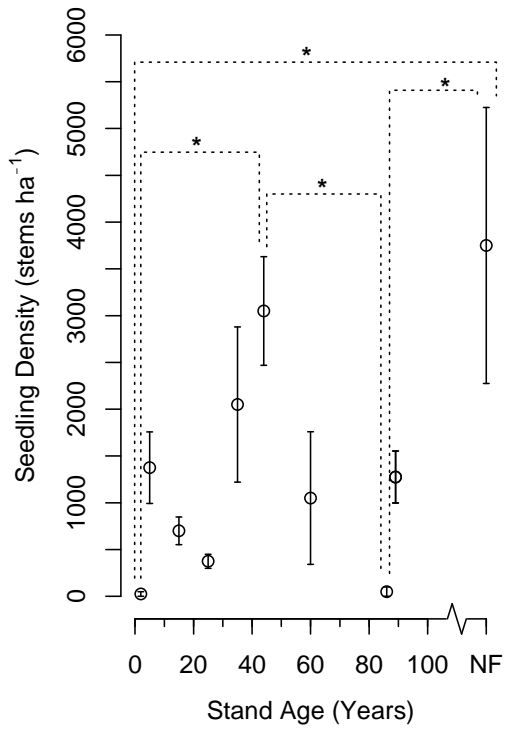
Appendix S4. Analysis of Deviance table from a Generalised Linear Model fitted to estimate the effect of *Pinus radiata* plantation age and meso-scale topographic exposure on the number of indigenous trees and shrubs found in the *P. radiata* understories. Data collected from a chronosequence of nine plantation stands ranging in age 2–89 years. Plantation stands located in Kinleith Forest, central North Island, New Zealand.

Analysis of Deviance Table: Woody Indigenous Species Richness				
	SS	Df	F	P
Log Age	20.610	1	9.745	0.021 *
Meso-scale Topography	8.124	1	3.841	0.097 †

Appendix S5. Ternary plot of pairwise age comparisons of Jaccard similarity from woody species presence/absence data collected across a chronosequence of *Pinus* plantations aged 2–89 years old, located in Kinleith Forest, central North Island, New Zealand. *Pinus* stand ages shown as numerals.
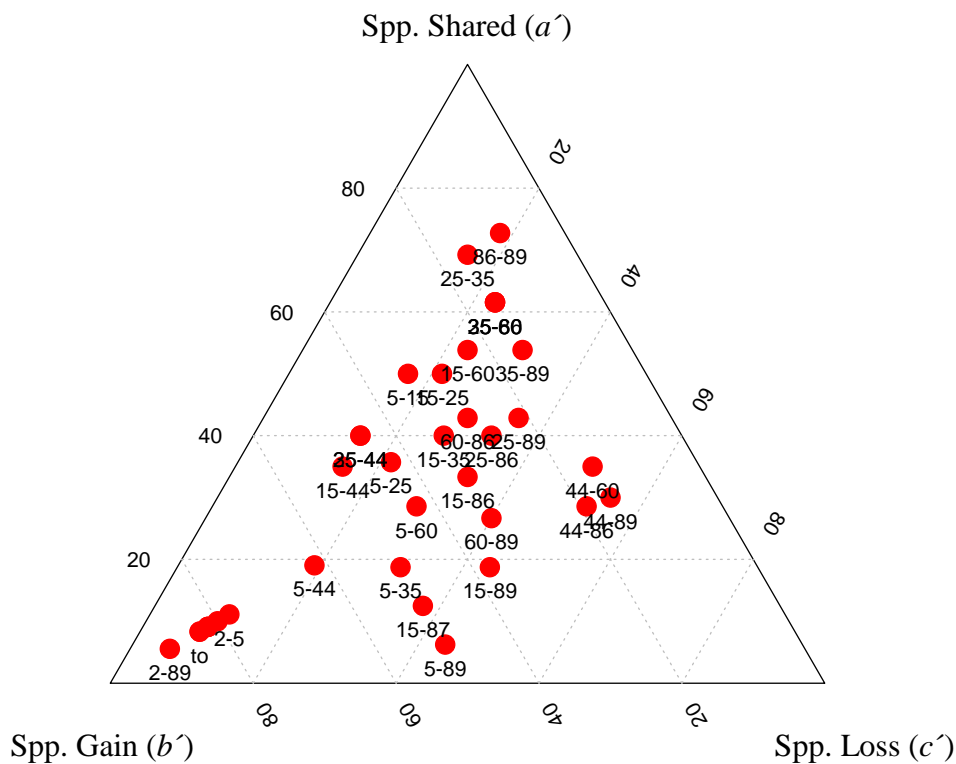
Appendix S6. Woody species found in Kinleith Forest *Pinus radiata* plantation chronosequence (including indigenous reference site), central North Island, New Zealand

Species	Code	Family	Growth Form
Aristotelia serrata	ARIser	Elaeocarpaceae	Tree
Beilschmiedia tawa	BEItaw	Lauraceae	Tree
Brachyglottis repanda	BRArep	Compositae	Tree
*Buddleja davidii**	BUDdav	Scrophulariaceae	Shrub
Coprosma grandifolia	COPgra	Rubiaceae	Tree
Coprosma robusta	COProb	Rubiaceae	Tree
Coriaria arborea	CORarb	Coriariaceae	Tree
Cordyline banksii	CORban	Asparagaceae	Tree
Cotoneaster sp.*	COTsp.	Rosaceae	Shrub
Cyathea dealbata	CYAdea	Cyatheaceae	Tree fern
Cyathea medullaris	CYAmed	Cyatheaceae	Tree fern
*Dacrydium cupressinum^*	DACcup	Podocarpaceae	Tree
Dicksonia squarrosa	DICsqu	Dicksoniaceae	Tree fern
Dicksonia fibrosa	DICfib	Dicksoniaceae	Tree fern
Cyathea smithii	DICsmi	Cyatheaceae	Tree fern
Fuchsia excorticata	FUCexc	Onagraceae	Tree
Gaultheria antipoda	GAUant	Ericaceae	Shrub
Geniostoma ligustrifolium	GENlig	Loganiaceae	Shrub
Hedycarya arborea	HEDarb	Monimiaceae	Tree
Knightia excelsa	KNIexc	Proteaceae	Tree
Leucopogon fasciculatus	LEUfas	Ericaceae	Shrub
*Leycesteria formosa**	LEYfor	Caprifoliaceae	Shrub
Litsea calicaris	LITcal	Lauraceae	Tree
Melicytus ramiflorus	MELram	Violaceae	Tree
*Myrsine australis^*	MYRaus	Primulaceae	Tree
*Pinus radiata**	PINrad	Pinaceae	Tree
*Pittosporum eugenioides^*	PITeug	Pittosporaceae	Tree
Pittosporum tenuifolium	PITten	Pittosporaceae	Tree
*Podocarpus totara^*	PODtot	Podocarpaceae	Tree
Pomaderris amoena	POMamo	Rhamnaceae	Shrub
*Prumnopitys ferruginea^*	PRUfer	Podocarpaceae	Tree
*Prumnopitys taxifolia^*	PRUtax	Podocarpaceae	Tree
Pseudopanax arboreus	PSEarb	Araliaceae	Tree
*Pseudopanax crassifolius^*	PSEcra	Araliaceae	Tree
*Pseudowintera colorata^*	PSEcol	Winteraceae	Tree
Schefflera digitata	SCHdig	Araliaceae	Tree
Weinmannia racemosa	WEIrac	Cunoniaceae	Tree

Note. * = exotic flora. ^ = species found only in the mature natural forest reference site.

Appendix S7. Chronosequence vegetation plot matrix, species importance values (IV). Kinleith Forest *Pinus radiata* plantation chronosequence, central North Island, New Zealand.

Site	ARIser	BEltaw	BRArep	BUDdav	COPaus	COProb	CORarb	CORban	COTsp.	CYAdea	CYAmed	DACcup	DICfib	DICsmi	DICsqu	FUCexc	GAUant	GENlig	HEDarb	KNIexc	LEUfas	LEYfor	LITcal	MELram	MYRaus	PITeug	PITten	PODtot	POMamo	PRUfer	PRUtax	PSEarb	PSEcol	PSEcra	SCHdig	WEIrac
89a	0	0	5.5	0	0	0	0	0	0	8	3	0	0	0	11	0	0	2.5	0	0	0	0	0	6	0	0	0	0	0	0	0	7.5	0	0	0	1
89b	0	0	1	0	0	0	0	0	0	3	4	0	0	0	14	0	0	5	0	0	0	0	0	2	0	0	0	0	0	0	0	6	0	0	3	0
89c	0	0	1	0	0	0	0	0	0	0	2	0	0	0	12	0	0	4	0	0	0	0	0	8	0	0	0	0	0	0	0	7	0	0	3	0
89d	0	0	2	0	0	0	0	0	0	2	3	0	0	0	12	0	0	2	0	0	0	0	0	10	0	0	0	0	0	0	0	12	0	0	4	0
86a	0	0	11	0	8	0	0	0	0	1	0	0	0	0	8	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	2.5	0	0	0	0
86b	0	0	2.5	0	0	0	0	0	0	4	7	0	0	0	9	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	6	0	0	0	6
86c	0	0	10	0	4	0	0	0	0	8	4	0	0	0	10	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	5	0	0	0	0
86d	1	0	5.5	0	0	0	0	0	0	0	10	0	0	0	5	0	0	4.5	0	0	0	0	0	2.5	0	0	0	0	0	0	0	3.5	0	0	0	0
60a	4	0	0	0	6	2	0	0	0	0	3	0	0	0	0	0	0	4	0	0	0	0	0	6	0	0	8	0	0	0	0	0	0	0	0	0
60b	6	0	0	0	8	4	0	0	0	0	0	0	0	0	11	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60c	2	0	0	0	1	4	0	0	0	0	0	0	4	0	13	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60d	0	0	0	0	1	6	0	0	0	0	0	0	0	0	8	3	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
44a	0	1	0	0	2	0	0	0	0	9	9	0	0	2	5	0	0	3	3	0	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0
44b	0	0	0	0	1	0	0	0	0	0	7	0	0	0	8	0	0	3	2	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	2	0
44c	0	1	0	0	2	2	0	0	0	0	7	0	0	0	6	0	1	8	6	4	2	0	2	2	0	0	0	0	0	0	0	0	0	0	1	0
44d	0	2	0	0	2	2	0	2	0	4	7	0	0	0	9	0	0	9	7	0	1	0	1	2	0	2	0	0	0	0	0	0	0	0	2	0
35a	0	0	0	0	11	0	0	0	0	3	0	0	2	0	8	0	0	7	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	9	0
35b	0	0	4	0	3	0	0	0	0	0	7	0	0	0	7	0	0	4	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	5	0
35c	0	0	9	0	0	0	0	0	0	4	7	0	0	0	10	0	0	7	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	1	0
35d	2	0	5	0	0	6	0	0	0	4	7	0	0	0	4	0	0	6	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	3	0
25a	5	0	0	0	0	5	0	0	0	3	0	0	0	0	8	0	0	4	0	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	0
25b	1	0	0	0	0	3.5	0	0	0	0	0	0	0	0	9	0	0	4	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0
25c	0	0	0	0	0	2	0	0	0	3	0	0	4	0	9	0	0	1	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	6	0
25d	0	0	0	0	0	3	0	0	0	0	3	0	0	0	9	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0
15a	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1	0	0	0	6	0	2	0	0	2	0	0	0	0	0	0	0	0	0
15b	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	4	0	1	0	0	1	0	0	0	0	0	0	0	0	0
15c	3	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	1	0	0	0	6	0	0	0	0	2	0	0	0	0	0	0	0	0	0
15d	0	0	0	0	1	9	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0
5a	7	0	0	2	0	2	6	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
5b	13	0	0	3	0	2	7	0	0	0	0	0	0	0	6	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5c	8	0	0	3	0	3	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5d	0	0	0	6	0	1	6	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

2c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2d	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nfa	0	1	0	0	7	0	0	0	0	0	0	0	0	2	2	0	0	4	10	7	0	0	0	8	1	0	0	0	0	2	0	0	2	1	2	7
Nfb	0	3	0	0	5	0	0	0	0	1	0	6	0	0	0	0	0	1	16	1	0	0	0	2	0	0	0	1	0	0	0	0	1	0	1	0
Nfc	0	0	4	0	9.5	2	0	0	0	7	0	11	0	0	0	0	0	11	12	9	0	0	0	5	3	2	0	1.5	0	0	0	0	0	2	0	11
Nfd	0	0	0	0	12	0	0	0	0	5	2	7	0	0	1	0	0	2	13	15	0	0	0	9	6	0	0	0	0	0	0	0	2	0	2	0

Note. Site = number-letter represents stand age and plot replicate reference (a-d). Nf = native forest reference site. Species six-letter codes are consistent with Appendix S6.