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Assessing native woody composition, structure, and carbon stocks along elevation-climate gradients in mature *Pinus radiata* plantations as a baseline for transitional forestry: a regional pilot study

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Abstract

Background: The ecological science associated with transitioning exotic forest to native dominance (hereafter transitional forestry, transition forests) is currently limited, yet this form of forest has expanded rapidly. In part, this is related to forest-based carbon credit schemes which have driven large-scale afforestation in exotic trees. In other circumstances (e.g., for soil conservation or values-based reasons such as biodiversity conservation), forest owners wish to transition their exotic forest to native forest without harvest. Knowledge is required to inform management of realistic expectations for regeneration and succession both spatially and temporally.

Methods: Mature (>20-year-old) *Pinus radiata* plantations were surveyed along three elevation-climate gradients in the Waikato region of New Zealand to explore the composition and structure (including native carbon stocks) of plantation understories and whether these parameters vary spatially over several decades. Mammalian browsing was also recorded.

Results: Native woody stem densities were variable. Factors indicated as driving variability were stand age, elevation, topographic shelter, soil hydrology, solar radiation, and air temperature. On average, understories comprised five native woody species in the seedling tier, a single native species in the sapling tier, and a single native species in the tree tier. The most common species were the sub-canopy tree species *Melicytus ramiflorus*, *Geniostoma ligustrifolium*, and *Aristotelia* serrata. Tall old-growth species, such as *Beilschmiedia tawa*, *Podocarpus totara*, *Pectinopitys ferruginea*, and *Prumnopitys taxifolia*, occurred in only particular circumstances and on average at densities too low to form a meaningful part of a future forest canopy. Average species richness was low, although some diversity hotspots occurred. Carbon stocks in native trees and tree ferns in the understories were on average 1.55±0.38 tCha^{-1}. Heavy browsing by mammalian herbivores was recorded at 60% of plots.

Conclusions: These data indicate typical understorey conditions in mature *P. radiata* plantations for this area of New Zealand in the absence of management to promote a native transition. These data also highlight the importance of browser control, enrichment planting of tall old-growth species, and canopy manipulations to accelerate regeneration and succession in non-harvest *P. radiata* plantations. The data suggest transitional forestry should only be attempted at scales that can be reasonably managed, and there is a need for caution against large-scale establishment of *P. radiata* for transitional forestry as at large scales, achieving adequate levels of management are uncertain.

Keywords: Climate gradient, elevation gradient, forest regeneration, forest succession, *Pinus radiata*, transitional forestry

Introduction

The rise in carbon farming has resulted in the extensive establishment of non-harvest *Pinus radiata* plantations in New Zealand intended to be sites of permanent forest based on a transition occurring from exotic to native dominance (hereafter, transitional forestry or transition forest; Chaplow 2022; Casey et al. 2021). In addition to the tens-of-thousands of hectares of recently planted transition forests, thousands of hectares of *P. radiata* plantations exist with a current management intention to transition for reasons other than, or additional to, carbon storage. Such reasons include addressing land stability concerns or protecting freshwater ecosystems, economic or financial factors, or values-based preferences for native forest cover over retention of *P. radiata*. Although large areas of transition forests now exist, there has been relatively little research on the topic. The existing literature contains several surveys of understorey regeneration in *P. radiata* plantations (McQueen 1973; Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003; Forbes et al. 2019), however, few of these surveys were set in the modern context of transitional forests and all except Brockerhoff et al. (2003) are limited in their spatial applicability, relating to data collected from single forests.

One main area of uncertainty relates to the spatial variability of native forest regeneration in mature *P. radiata* plantations. It is unclear under which circumstances natural regeneration and succession in understories would be adequate to eventually achieve stable and permanent native forest. Further surveys of the *P. radiata* plantation understorey composition and structure along biotic and abiotic gradients are needed to establish clear expectations of what levels of regeneration and succession might realistically be achieved in a given location. Such expectations can then be used to inform management, and importantly, avoid unrealistic applications of transition forestry, such as might occur when economic incentives such as forest-based carbon credit schemes drive indiscriminate large-scale exotic tree planting.

The existing literature has established that native forest regeneration is driven by several key variables, including climatic and soil moisture parameters (Brockerhoff et al. 2003; Mason et al. 2013), and the availability of propagules via dispersal from seed sources (Moles & Drake 1999; Kelly et al. 2010). Therefore, a survey of plantation understorey composition and structure along elevation-climate gradients (hereafter elevation gradients) and a range of different land cover configurations was designed to capture the variability in climate and seed source proximity. The study was conducted as a pilot study to test the value in sampling along gradients with the potential to scale-up the survey to a national level (now completed; Forbes 2025), thus capturing a wider range of variability in key explanatory variables and yielding a larger dataset to support more advanced statistical analyses.

Plantation understories were sampled along three separate elevation gradients in the Waikato region of New Zealand, focusing on mature (>20-years-old) commercial rotational plantations as best available analogues for non-harvest stands. The composition and structure of understories was assessed in the context of forest regeneration. Also assessed were signs of succession to more mature phases of composition. Given the stands surveyed have received no specific management to promote a transition, these data represent a baseline of what can be expected to occur in this location of New Zealand over the first c. 20-30 years without applying such management interventions.

Methods

The surveys were carried out in the Waikato region of the central North Island, New Zealand. All field surveys were undertaken between October 2022 and May 2023. Commercial *P. radiata* plantations were sampled in three separate areas of the region: Mamaku; Pureora; and the Western Bay of Lake Taupo. One elevation gradient was sampled in each of these three areas. Physical details of each elevation gradient are given in Table 1.

Plant types studied

The survey's focus was to sample woody native species in the understories of mature (i.e., >20 years-old) commercially-operated, rotationally-harvested *P. radiata* plantations. Data describing these plantations are given by elevation gradient in Table 2. The understorey sampling covered native and exotic woody species as these directly relate to forest regeneration

TABLE 1: Physical characteristics of elevation gradients sampled at Mamaku, Pureora, and Western Bay Lake Taupo

Gradient	Elevation (m.a.s.l., mean(range))	Coordinates (WGS84)		Distance to native forest (m, mean(range))	Mean annual water deficit (mm, mean(range))
Mamaku	418 (217-568)	38°30’S - 38°50’S	175°50’E - 176°10’E	2100 (52-6704)	4.77 (0.34-20.21)
Pureora	555 (499-605)	38°29’S - 38°34’S	175°25’E - 175°29’E	88 (20-122)	2.22 (2.04-2.40)
Western Bay Lake Taupo	676 (516-805)	38°44’S - 38°48’S	175°37’E - 175°43’E	380 (123-540)	4.49 (2.04-7.43)

TABLE 2: Physical characteristics of plantations sampled at Mamaku, Pureora and Western Bay Lake Taupo

Gradient	**Mean age and age range (yrs)**	***Pinus* basal area, mean and range (m^2 ha^{-1})**	**Median annual precipitation at gradient start and end points (mm yr^{-1})**
Mamaku	23 (22-27)	49 (25-75)	1,350-1,700
Pureora	30 (26-33)	63 (45-90)	1,550-1,650
Western Bay Lake Taupo	22 (21-24)	63 (40-80)	1,350-1,450

and succession. Regarding native woody species, a response variable titled tall old-growth species was compiled. This variable included native tree species found in the canopy of tall old-growth forest. Few exotic woody individuals were recorded in the understories sampled (they occurred mainly in one plot) meaning that the stem density aspect of this paper relates to native woody species. Tree ferns were excluded from stem density tallies as they do not directly contribute to a long-term forest canopy and inclusion could be viewed as artificially boosting stem density estimates. However, tree ferns were included in estimates of cover, basal area, and carbon stocks.

Sampling design

Vegetation sampling was conducted along elevation gradients coinciding with areas of climate gradients (as mapped by Chappell 2014) to capture variability in climate, native seed source proximity, and a variety of other site factors. Gradients were located based on broad areas of suitable plantation age classes, gradients of mean annual rainfall (Chappell 2014), and elevation contours. Along a given gradient, a subjectively located position on a contour line served as a start point from which two or three vegetation plot (10 × 10 m) locations were randomly generated. Each plot was located at the randomly generated point using a hand-held GPS unit (Garmin GPSmap 62s). Plot clusters (either two or three) were located at consecutive 100 m vertical separations and between 50-150 m horizontal distance from one another to achieve independence among plots without varying too far from the nominated elevation for sampling. Plot locations were excluded within 30 m of a forest edge to avoid edge effects.

Sampling at Mamaku comprised five pairs of plots (ten plots in total), Pureora comprised two pairs (four plots in total), and Western Bay comprised three locations where three plots were located, and one location with two plots (eleven plots in total).

All exotic and indigenous woody species were identified to species level and all plants >15 cm were counted within each 10 × 10 m plot. Stem counts were assigned to height classes. Seedlings were either <15 cm (for these, only a presence/absence record was made), 16-45 cm, 46-75 cm, 76-105 cm, 106-135 cm. Saplings were >135 cm and less than 2.5 cm diameter at breast height (DBH, 1.35 m above ground level). Trees were >135 cm and >2.5 cm DBH.

Species cover was visually assessed on each plot reflecting both cover and abundance. The cover-abundance of all woody species (including tree ferns and the exotic vine, *Rubus fruticosus*) was estimated using the scale: 1 = <1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; and 6 = 76–100% within each plot (Hurst et al. 2022). Species cover-abundance estimates were recorded for live foliage present within each of the following height tiers: <0.3; >0.3–2; 2–5; 5–12; 12–25; and >25 m.

A set of site factors was measured at each plot. Slope (degrees) and slope aspect (predominant aspect in degrees, translated into the cardinal directions: N = 337.5–22.5; NE = 22.6–67.5; E = 67.6–112.5; SE = 112.6–157.5; S = 157.6–202.5; SW = 202.6–247.5; W = 247.6–292.5; and NW = 292.6–337.5, whereby sites of <5° slope were assigned to the class 'flat'), were measured and plot elevation (m a.s.l.) was determined using the hand-held GPS unit. Distance to mature indigenous forest was a desktop measure from each plot centre-point, calculated using satellite imagery (Google Earth Pro 2023), and stand age data (Table 2) were obtained from the forest owners.

The *P. radiata* overstorey was surveyed based on a 13.8 m radius circular-plot centred on each 10 × 10 m plot. The 13.8 m radius was a slope-corrected measurement determined using a range finder (Nikon Forestry Pro). Within each circular plot, *P. radiata* basal area was estimated using a factor 5 basal area prism.

Sampling yielded a number of response and explanatory variables for analysis (Table 3).

Data analyses

Native woody species stem density data were calculated by summing the number of each woody species >15 cm tall in each plot and converted to stems ha^{-1}. Average values for native woody stem density, native woody species richness, native tree height, native tree basal area, and carbon stocks were calculated taking results across all 25 plots and were calculated using the mean function in the R base package (R Core Team 2023). Where given, error terms are one standard error of the mean which were calculated in R using the Plotrix package (Lemon et al. 2006). Average values for mammalian browse were calculated as the mode value of the categorical data, in Microsoft Excel. Pearson correlations between response and explanatory variables were calculated using the pairs, cor, cor.panel and cor.test functions in the R base package.

The cover-abundance data for the classes: *P. radiata*, native woody species, tree ferns, tall old-growth species and exotic species were transformed to one Importance

TABLE 3: Response and explanatory variables yielded from the survey

Response variables	**Unit**	**Explanatory variables**	**Unit**
Carbon stocks[1]	tCha^{-1}	Annual solar radiation[2]	MJ/m^2/day
Cover by exotic species	Importance values (IV)	Annual water deficit	mm
Cover by native woody species	IV	Distance to native forest source	m
Cover by *Pinus radiata*	IV	Elevation	m.a.s.l
Cover by tall old-growth species[3]	IV	Litter cover	%
Cover by tree fern species	IV	Mammalian browse intensity	High, browse on most accessible shoots on most plants of a species; medium, >2 shoots but most plants of a species not browsed; low, browse on <2 shoots on only a few plants of a species; none, no browse
Native tree basal area	m^2 ha^{-1}	Mean minimum temperature of the coldest month[2]	°C
Native tree height	m	Meso-topographic exposure	Degrees
Native woody species richness	*S*	Monthly water balance ratio	Rainfall:evaporation
Native woody stem density	Stems ha^{-1}	October vapour pressure deficit	kPa
Pinus radiata basal area	m^2 ha^{-1}	*Pinus radiata* basal area	m^2 ha^{-1}
		Pinus radiata canopy cover	%
		Pinus radiata stand age	years
		Slope	Degrees
		Winter solar radiation[2]	MJ/m^2/day

[1] Carbon stocks were calculated following Beets et al. (2012); [2] Climate variables were taken from Land Environments of New Zealand (LENZ). Tall old-growth species are defined as those that occupy the canopy of tall old-growth forests.

Value (IV) as a response variable (Allen et al. 1995). The IVs were calculated from the sum of the above cover-abundance classes with the following weighting applied to the percent cover classes: 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%. Therefore, IVs, integrated both horizontal and vertical dimensions of vegetation structure, with the weighting applied to express the varying degrees of cover occurring for each IV class in height tiers.

Above and below-ground carbon stocks were calculated after Beets et al. (2012) as applied in Forbes et al. (2015, with the additional considerations here of tree fern allometry). The volume (m^3 tree^{-1}) of stem and large branches ≥10 cm diameter for native trees and shrubs was calculated based on diameter and total tree height data using the allometric formula:

$$V_{stem+br\geq 10} = 4.83\times10^{-5} \times (DBH^2\,H)^{0.978} \qquad \text{Equation 1}$$

where DBH is diameter (cm) and H is total tree height (m).

Tree fern above-ground carbon C_{agtrfn} (kg/tree) was estimated directly from DBH and height as follows:

$$C_{agtrfn} = 2.70\times10^{-3} \times (DBH^2\,H)^{1.19} \qquad \text{Equation 2}$$

where DBH is diameter (cm) and H is total tree height (m).

For trees and shrubs, the estimated volume was multiplied by the species-specific wood densities (given below, and assuming 50% of the mass is carbon) to which mass of branches <10 cm diameter (over bark) and foliage was added, which gave above-ground biomass carbon per tree (kg tree^{-1}):

$$C_{agtree} = 0.5 \times d_{stem} \times V_{stem+br\geq 10} + 1.75\times10^{-2} \times DBH^{2.20} + 1.71\times10^{-2} \times DBH^{1.75} \qquad \text{Equation 3}$$

where the constant d_{stem} is a species-specific basic wood density (kg m^{-3}).

Wood density values used were after Beets et al. (2012) as follows: subcanopy tree 493 kg m^{-3} for *Aristotelia serrata*, *Schefflera digitata*, *Geniostoma ligustrifolium*, *Pittosporum tenuifolium*, and *Carpodetus serratus*; *Coprosma* genus 333 kg m^{-3} for *Coprosma autumnalis*; shrub 333 kg m^{-3} for *Pseudowintera colorata*; and canopy tree 476 kg m^{-3} for *Melicytus ramiflorus*, *Fuchsia excorticata*, and *Pseudopanax arboreus.*

Following Beets et al. (2012), the default (Intergovernmental Panel on Climate Change [IPCC] 2003) root/shoot ratio of 25% of the total above ground biomass for trees and shrubs, and 20% for tree ferns, to accommodate the dry mass of roots, provided total tree biomass. Carbon storage was then calculated using stand density (density ha^{-1}) data and expressed as C-stock (tCha^{-1}).

Results

Native woody stem densities

Native woody stem densities were variable, with most individuals occurring as seedlings and the remainder as saplings or trees. On average, total native woody stem densities were 4112 stems ha^{-1} and ranged 0-18600 stems ha^{-1} (Table 4). Native woody seedlings and total native woody stem densities showed positive relationships with stand age (seedlings: r = 0.52, p = <0.01; total: r = 0.46, p = 0.02), Figure S1.

Understorey composition

On average, the most abundant native woody species was *Melicytus ramiflorus* (with 1116 stems ha^{-1}), followed by *Geniostoma ligustrifolium* (724 stems ha^{-1}), *Aristotelia serrata* (544 stems ha^{-1}), and *Brachyglottis repanda* (200 stems ha^{-1}), with a further 32 native woody species occurring at <200 stems ha^{-1} (Table 5).

While five tall old-growth species were observed, these species occurred only in the seedling or sapling tiers, and usually at low densities: *Beilschmiedia tawa*, 48 stems ha^{-1}; *Podocarpus totara*, 8 stems ha^{-1}; *Pectinopitys ferruginea*, 8 stems ha^{-1}; *Prumnopitys taxifolia*, 4 stems ha^{-1}; and *Pterophylla racemosa,* 4 stems ha^{-1} (Table 5).

Native woody species richness

A total of 36 native woody species was recorded across 25 plots (Table 5). On average, there were five native woody species (per plot) in the seedling tier, a single species in sapling tier, and a single species in the tree tier. Average species richness was six native woody species in a plot, with richness ranging from as few as one to as many as 16 native woody species (Table 4). Elevated native woody species richness was most closely associated with higher stand age (r = 0.62, p = <0.01), Figure S2.

Native tree height, basal area, and carbon stocks

Native trees occurred in 76% of plots. On average, native tree heights were 4.9±0.3 m. The tallest native tree measured was 11.4 m (a *Carpodetus serratus*). On average across all plots, native tree basal area was 2.7±0.8 m^2 ha^{-1} (range, 0.1–13.5 m^2 ha^{-1}).

Carbon stocks associated with woody vegetation across all plots on average were 0.86±0.21 tCha^{-1} in native trees, 0.67±0.28 tCha^{-1} in tree ferns, and 1.55±0.38 tCha^{-1} in native trees combined with tree ferns.

Vegetation cover

On average, the combined cover of native species in the understorey contributed the most cover IV (IV 15), and the least cover IV was found in tall old-growth species (IV 1; Table 6). The cover IV of native woody species showed associations with stand age (r = 0.59, p = <0.01) and elevation (r = -0.39, p = 0.051). The cover IV of tall old-growth species was associated with stand age (r = 0.67, p = <0.01). The cover IV of exotic species was most closely associated with water balance ratio (r = -0.50, p = 0.01), water deficit (r = 0.46, p = 0.02), and *P. radiata* basal area (r = -0.41, p = 0.04), Figure S3.

Mammalian browse

On average, browse by mammalian herbivores was heavy, with browse on most accessible shoots on most plants of a species. Heavy browse was observed in 60% of plots, with the balance being 20% of both light browse intensity (browse on <2 shoots on only a few plants of a species) and medium browse intensity (>2 shoots but most plants of a species not browsed). In addition to browsing of vegetation, bark stripping from antler rubbing and also toppling of understorey vegetation by mammals was observed.

Discussion

Native regeneration in the understorey and possible successional trajectories

Regeneration of native woody species was found to be spatially variable in terms of stem density and composition, and this is consistent with other studies

TABLE 4: Native woody stem densities and richness in seedling, sapling, tree (and combined) tiers across 25 plots within *Pinus radiata* plantations aged >20 years in three areas of the Waikato region.

	Summary statistics							
	Seedlings		Saplings		Trees		Total	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Native woody stem densities (stems ha^{-1})	2940	0–14300	876	0–4500	296	0–2000	4112	0–18600
Native woody species richness (S)	5	0–16	1	0–6	1	1–4	6	1–16

TABLE 5: Species-level native woody stem densities in seedling, sapling, tree (and combined) tiers across 25 plots within *Pinus radiata* plantations aged >20 years in three areas of the Waikato region.

Scientific name	**Stem density (stems ha^{-1})**				
	Seedlings	**Saplings**	**Trees**	**Total**	**Range**
Melicytus ramiflorus	952	136	28	1116	0–7900
Geniostoma ligustrifolium	492	216	16	724	0–3900
Aristotelia serrata	176	312	56	544	0–4700
Brachyglottis repanda	144	52	4	200	0–2400
Fuchsia excorticata	184	4	8	196	0–1800
Hedycarya arborea	176	0	0	176	0–2500
Pseudopanax crassifolius	100	48	24	172	0–1400
Schefflera digitata	100	4	20	124	0–1200
Pseudopanax arboreus	112	0	8	120	0–1700
Coprosma crassifolia	4	48	60	112	0–2700
Carpodetus serratus	72	4	12	88	0–500
Coprosma autumnalis	44	8	12	64	0–600
Beilschmiedia tawa	48	0	0	48	0–600
Coprosma lucida	48	0	0	48	0–400
Pennantia corymbosa	48	0	0	48	0–900
Knightia excelsa	40	0	0	40	0–500
Coprosma sp.	8	8	20	36	0–600
Coprosma robusta	32	0	0	32	0–800
Coprosma propinqua	24	4	0	28	0–500
Pittosporum eugenioides	24	0	0	24	0–600
Coprosma tenuifolia	20	0	0	20	0–500
Elaeocarpus hookerianus	8	12	0	20	0–500
Myrsine australis	20	0	0	20	0–200
Pittosporum tenuifolium	12	0	8	20	0–200
Griselinia littoralis	4	8	4	16	0–300
Cordyline australis	0	0	12	12	0–200
Veronica stricta	12	0	0	12	0–200
Melicope simplex	12	0	0	12	0–300
Pseudowintera colorata	8	0	4	12	0–200
Coriaria arborea	4	4	0	8	0–200
Podocarpus totara	8	0	0	8	0–200
Pectinopitys ferruginea	8	0	0	8	0–100
Leucopogon fasciculatus	0	4	0	4	0–100
Melicytus lanceolatus	0	0	4	4	0–100
Prumnopitys taxifolia	0	4	0	4	0–100
Pterophylla racemosa	4	0	0	4	0–100

TABLE 6: Importance values calculated from summed cover scores across all tiers for *P. radiata*, tree ferns, native woody species, tall old-growth and exotic species from tiers across 25 plots within *P. radiata* plantations aged >20 years in three areas of the Waikato region.

Forest component	**Importance values**	
	Mean	**Range**
Pinus radiata	9	5–16
Tree ferns	6	0–17
Native understorey	15	3–30
Tall old-growth species	1	0–4
Exotic species IV	2	0–11

that have found measures of forest regeneration to vary at national, regional (Mason et al. 2013) and site scales (Forbes et al. 2021). Brockerhoff et al. (2003) surveyed 60 plots across four age (ca. 5-27 years)/ density classes in four regions, finding stand age as well as density to be key drivers. Correlations between structural measures of native forest regeneration and succession and explanatory variables suggest that stand age and elevation are factors driving spatial variability. Distance to native seed source consistently showed a weak negative association with native understorey response variables; however, none of those associations were significant. This might be because the dominant native woody species found in plantations are generalist species (e.g., *M. ramiflorus*, *G. ligustrifolium*, *A. serrata*) and not strongly dependent on immigration from a consolidated native forest source (such as is discernible from satellite imagery).

Typically, (at the plot scale) the woody composition of the understorey is simple, normally with one native species in the tree tier and six native species in total. Similar levels of native woody diversity have been recorded in *P. radiata* plantations in other areas of the Waikato region (Ogden et al. 1997). The three most abundant tree species (*M. ramiflorus*, *G. ligustrifolium*, and *A. serrata*) are widely distributed (both in the Waikato and nationally), short-statured, relatively short-lived sub-tree species which produce seeds in small fruits which are spread by a wide range of native and exotic bird species (Thorson et al. 2009). These same dominant tree species have also been recorded as dominant in *P. radiata* plantations in other parts of the Waikato region (Allen et al. 1995). These three dominant tree species occur in the landscape distant from mature forest seed sources so their relatively high representation in plantation understories is logical.

In contrast, tall old-growth species (i.e., *B. tawa, P. totara, P. ferruginea, P. taxifolia,* and *P. racemosa*) are present only in certain circumstances in the forests surveyed and on average were too few to form a meaningful part of the future forest composition (Table 5). This result indicates that on average across the forests surveyed there is little evidence of a reliable forest succession toward tall old-growth forest compositions.

In the present study, average (4112 stems ha^{-1}) and range (100-18600 stems ha^{-1}) values for native woody stem density are similar to native woody seedling densities measured in central North Island exotic conifer clear-fells (mean = 3855, range = 0–16300 stems ha^{-1}; Forbes et al. 2021) where extensive (i.e., >50% of the land area) supplementary planting with native trees was recommended to achieve adequate levels of native forest cover. In the present study, many understorey plots contained low stem densities and simple compositions which would be inadequate to form an independent forest canopy (such as occurs in a healthy native forest or classical restoration planting) in the foreseeable future (e.g., 50 years from planting or longer). In the native forest context, native woody species richness was low, with some diversity hotspots.

This finding is similar to forest successions within mature stands of the exotic shrub *Ulex europaeus* (gorse), where the species richness and composition of native understorey regeneration were less than that found in similar statured native *Kunzea ericoides* (kanuka) forest understories (Sullivan et al. 2007). These differences between mature stands of *U. europaeus* and *K. ericoides* indicated a lack of successional convergence between the native and exotic stand identities (Sullivan et al. 2007), which may also be occurring in *P. radiata* plantation understories. Other studies have found podocarps entering native woody successions 20-30 + years after stand establishment (e.g., McKelvey 1955). Over the age classes surveyed here, it is not possible to differentiate the effect of time from the variables measured in this study on the occurrence of tall old growth species. What can be said is that in a few spatially-constrained circumstances, tall old growth species had established, meaning their establishment in *P. radiata* plantations is not completely dependent on time. Factors such as propagule availability (Moles & Drake 1988), forest microclimate conditions (Ebbett & Ogden 1988), and soil characteristics (Carswell et al. 2007) would exert strong controls over their establishment.

Browsing by introduced mammalian herbivores is heavy in most plots and the mammal species of main concern across the study area are *Cervus elaphus* (red deer) and *Dama dama* (fallow deer; although it is unclear whether this species is present), *Trichosurus vulpecula* (brushtail possum), *Notamacropus eugenii* (dama wallaby), *Notamacropus parma* (parma wallaby), and the omnivore *Sus scrofa* (feral pig) which has the additional effect of disrupting the soil profile, and with it, destroying regenerating vegetation. Browsing mammals present a serious limiting factor for diverse native forest regeneration and successional development (King et al. 2015) and these effects are expressed within the plantation understories surveyed.

These results represent the levels of native woody understorey regeneration and forest successional development that are occurring in this location of New Zealand over two to three decades without specific restoration interventions. Stand age is indicated to be the strongest driver of native woody stem density, species richness, and native cover IV which is a finding consistent with previous studies (Ogden et al. 1997; Brockerhoff et al. 2003). However, variables other than stand age also showed associations and there are grounds for more extensive sampling at a national scale to further examine the effects of biotic and abiotic factors on understorey regeneration and successional development.

Carbon stocks in the understorey

In native trees and tree ferns combined, carbon stocks contained in plantation understories were 1.55±0.38 tCha^{-1}. While it could be considered positive that some atmospheric carbon is being sequestered and stored in native understorey vegetation without specific management interventions, this carbon storage volume is small compared to other forest types over similar timeframes. For instance, natural *Leptospermum scoparium*/*Kunzea* spp. (manuka/kanuka spp.) scrubland contained 51 tCha^{-1} (Ausseil et al. 2013), and 25-year-old *P. radiata* plantations in the Waikato region are cited as containing 676 tCha^{-1} (Ministry of Primary Industries 2017). Also of note is the dominance by short-statured, short-lived, low-volume tree species and, conversely, the limited occurrence of tall old-growth species in the plantations surveyed which is an unfavourable situation where plantations are intended to serve as long-term carbon sinks.

These results indicate that in this location of New Zealand, unmanaged *P. radiata* plantation understories over the first few decades are storing low volumes of carbon. Taking these data and considering the future, the few signs of tall old-growth species joining the compositions suggest these plantation understories will on average continue to store relatively low volumes of carbon in the foreseeable future, and successional development towards higher-volume, diverse native forest would be limited and strongly spatially variable.

Management requirements

Where a transition from non-harvest *P. radiata* to native forest dominance is the objective, these results provide further evidence that adequate levels of active management interventions would be essential. These results highlight the degrading effect that mammalian herbivore populations are having on regenerating vegetation, and professionally conducted landscape-scale culling is one method of comprehensively addressing this threat in a cost-effective manner especially to achieve low population numbers in remote and inaccessible areas (Nugent & Choquenot 2004). This would be consistent with established ecological restoration principles which recommend addressing ecological threats (in this case excessive mammalian herbivory) as a matter of priority (Norton et al. 2018). In some locations environmental plant pests (such as those listed in McAlpine & Clayson 2024) would present a significant threat to achieving long-term outcomes and those threats would need to be assessed and addressed. Given the low representation of tall old-growth species, the need for enrichment planting these species and other ecologically important species (i.e., those that support ecosystem functions and provide habitat) is also highlighted by these data as essential in most of the plots surveyed. Enrichment planting *Dacrydium cupressinum* (rimu) beneath a degraded (and therefore open-canopied) *P. ponderosa* stand in a near-by location of the central North Island yielded 32.3±3.9 tCha^{-1} in the planted *D. cupressinum* over 50-years (Forbes et al. 2015). Other assessments of planted native trees (not under pines) have also shown good potential for both biodiversity restoration and carbon sequestration and storage (Kimberley et al. 2022; Marden et al. 2025).

An aspect of enrichment planting is to choose or create favourable forest microclimate conditions for the planted trees and traditionally planted and managed *P. radiata* plantations are known to cast shade and reduce growth rates of some species of native tree seedlings (Forbes et al. 2016a). Mimicking small-scale disturbance to reduce competition for light to more favourable levels for understorey regeneration and succession have been demonstrated elsewhere in *P. radiata* plantations (in both canopy and understorey tiers; Brockerhoff et al. 2003; Forbes et al. 2016a; Forbes et al. 2016b) and in natural seral forests (Tulod & Norton 2020) and therefore canopy manipulations are another important management intervention.

Future research needs

This study has served as a regional-scale pilot and to explore the composition and structure of unmanaged mature *P. radiata* plantations. Further work is needed at a national scale to better understand the spatial variability in composition and structure especially according to climate gradients, seed source amount versus proximity, and seed source composition. The potential and application of other factors such as stand structure and stand manipulations also need research attention to provide empirical examples and these aspects can be addressed through manipulation experiments to isolate intervention effects.

Conclusions

This regional assessment of mature, unmanaged *P. radiata* plantations shows that native woody species are spatially variable in terms of stem density, cover and species richness. Correlations between structural measures of forest regeneration and succession and a range of explanatory variables suggest that stand age and elevation are key factors driving spatial variability. Native seed sources are known to be critical; however, these data highlight the complexities and variability of how seed sources contribute propagules to exotic plantations and the difficulty in quantifying those processes. These findings provide a starting point for more extensive examination of the landscape-scale variability in understorey regeneration at a national scale. The unmanaged *P. radiata* plantation understories surveyed are storing low volumes of carbon. Tall old-growth species are present only in certain circumstances and this presents a major limitation on a successful transition to permanent and high-biomass native forest.

Management would be essential for a transition to occur in the stands surveyed, and the key measures necessary in the plantations studied are reducing mammalian herbivore populations, enrichment planting, and stand manipulations. (e.g., canopy gap creation). Given the typically high levels of intervention that would be required to transition stands such as those surveyed it is recommended that transitions be only attempted at scales that are reasonably manageable (both financially and feasibly). Caution should be exercised against large-scale establishment of new *P. radiata* transition forests as at large-scales achieving adequate levels of management is uncertain and assurances around successful transitions and forest permanence cannot be given.

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Supplemental Data

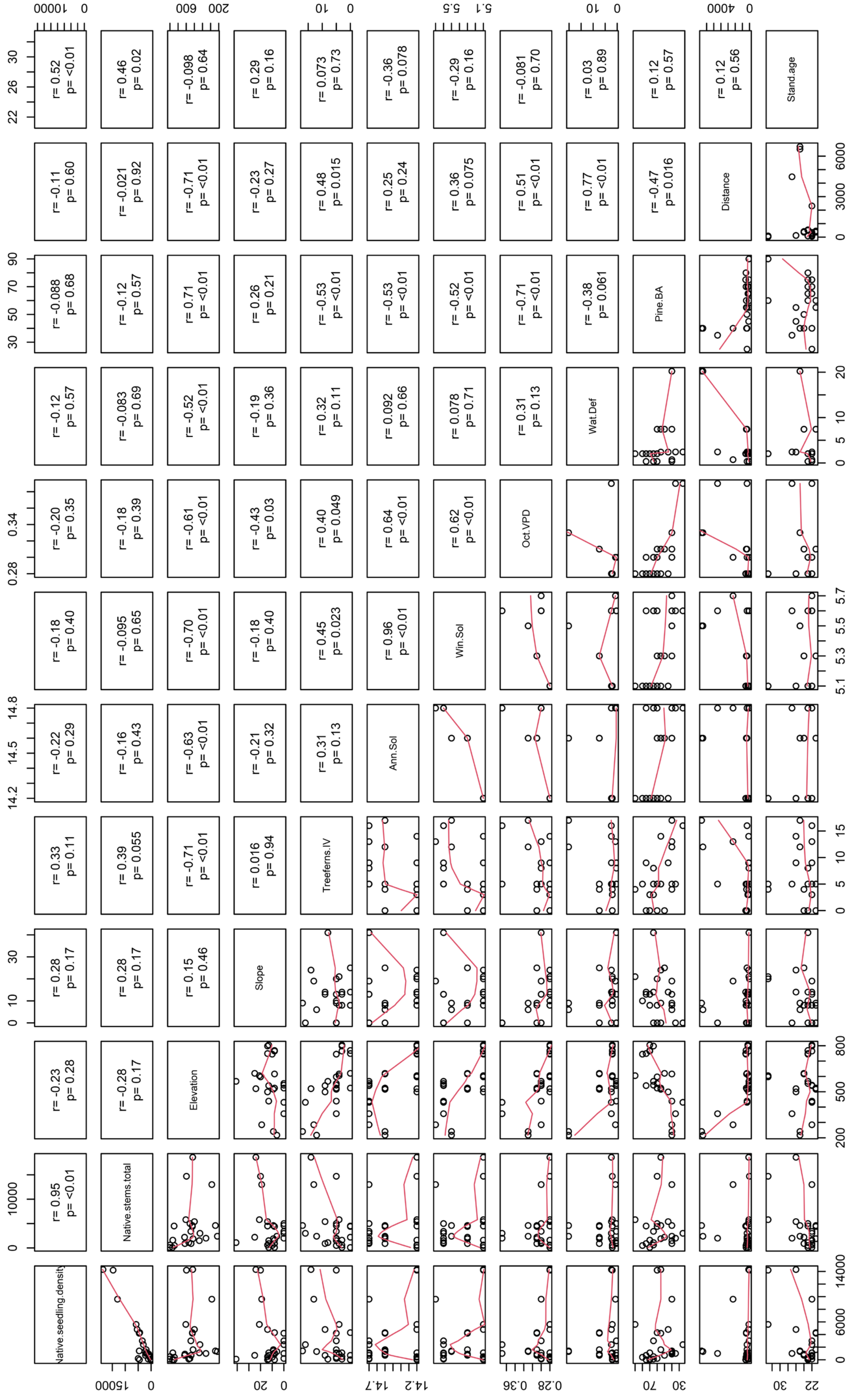

FIGURE S1: Associations among native stem density response variables and explanatory variables

FIGURE S2: Associations among the response variable native species richness and explanatory variables

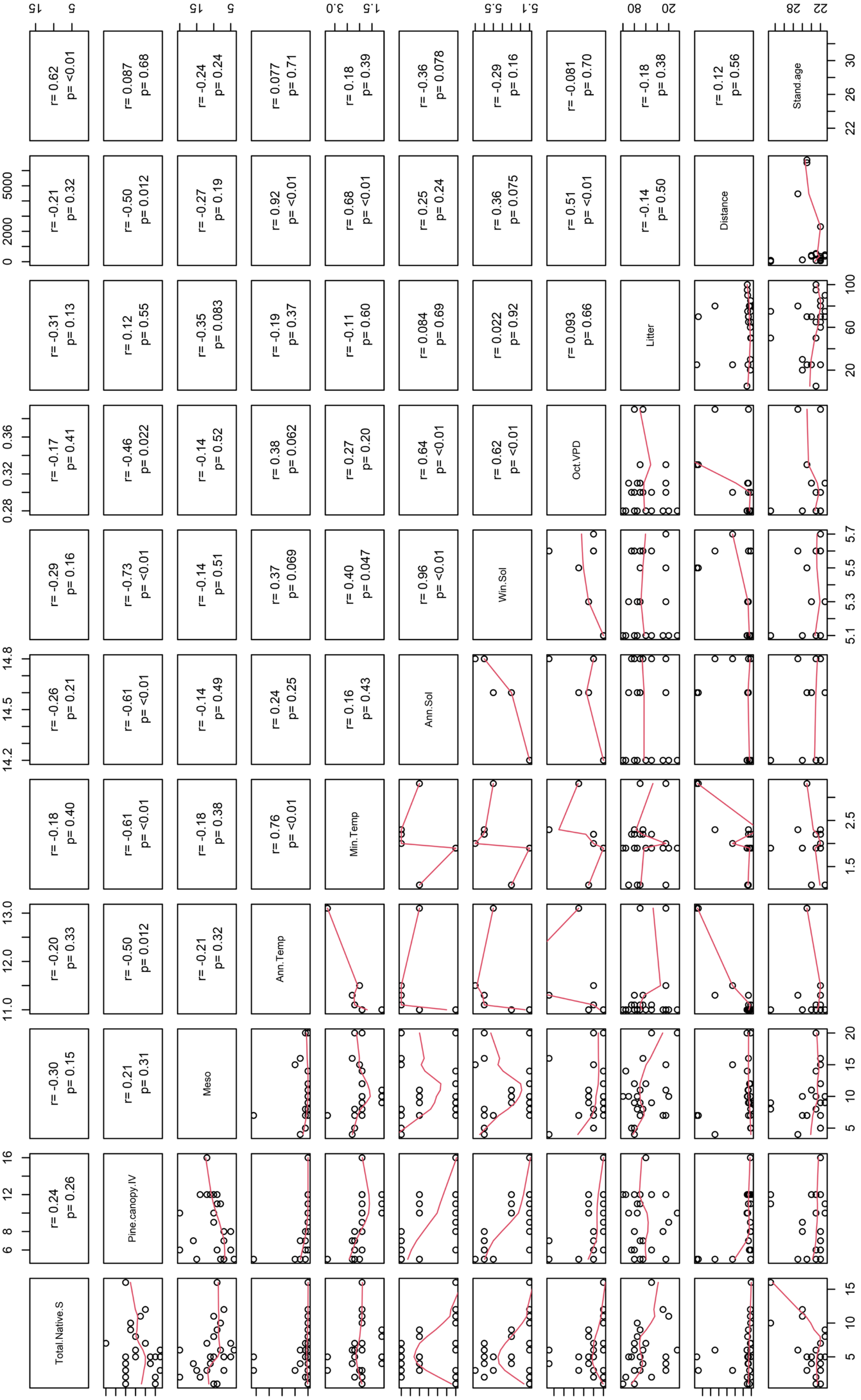

FIGURE S3: Associations among response variable Importance Values and explanatory variables