Native understory characteristics of pine plantation stands in Tairāwhiti, New Zealand

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Tāne's Tree Trust
NATIVE FORESTS FOR OUR FUTURE
Hereherea te Wao-nui-a-Tāne

Contents

Abstract:

Permanent diverse native forest, particularly on steeplands, can provide many benefits such as reduced erosion, downstream flood protection, aquatic and terrestrial species habitat, and carbon sequestration. In response to past major climatic events, the government subsidised large-scale afforestation of erosion-prone steep hill country, primarily through the establishment of radiata pine plantations. These forests were intended to stabilise soil and reduce erosion while providing a future production crop. However, many of these pine plantations, particularly on steep terrain, are now proving uneconomic to manage. In addition, clearfelling on such sites often exacerbates downstream issues, including increased sedimentation and problems with slash. Therefore, there is increasing interest in the in-situ transition of exotic pine plantations particularly on erosion-prone hill country to native forest. However, there are many gaps in our knowledge about how to do this successfully. This study sampled pine forest plots across the Tairāwhiti region. This research aimed to determine whether pine canopy density and proximity to native seed source influenced regenerating understory of existing radiata pine stands.

Plot surveys followed the Reconnaissance (Recce) and Land Use and Carbon Analysis System (LUCAS) methods. Survey results were analysed for relationships between pine stand characteristics, distance to native seed sources, and browser pressure on understory vegetation characteristics.

We found species in the understory were overwhelmingly native (98.2 %). Understory carbon was only a small percentage of total carbon, averaging 22.5 tCO_2/ha or 1.3 % of total carbon including canopy pine trees. Understory carbon was disproportionately stored in understory tree fern, subcanopy tree and canopy tree species, although these growth habitats where not yet strongly represented in the understory species mix, which was dominated by shrub species. Density of understory stems, species richness, Shannon diversity index and carbon stored in the understory increased significantly with increasing age of the pine stand age and/or decreasing density of the pine canopy.

Proximity to seed sources positively influenced both seedling density and species richness Browsing was present across most sites and likely influenced understory characteristics.

The lack of canopy species in the upper understory tiers may indicate that the forests need more time for greater plant diversity (including recruitment of canopy species) to establish in significant numbers. Alternatively, it may indicate that appropriate seed source is missing, that canopy understory conditions are unfavourable, or that browse pressure is not allowing native species to grow beyond browsing height.

1 Introduction

> *“The use of public moneys to promote commercial activities (such as agriculture production) has in the past created distortions in the economy and led to unwanted environmental effects.”*
>
> *“Changing land use to enable a move towards sustainable land management is not easy.”*
>
> Helen Hughes, Parliamentary Commissioner for the Environment
> – Sustainable Land Management and the East Coast Forestry Project, 1994

Aotearoa New Zealand (NZ) is facing a double crisis of biodiversity loss and climate change. This is highlighted in the Tairāwhiti region where steep sedimentary geology, combined with clearfell forestry and farming, is resulting in unsustainable soil erosion (Stats NZ 2024, MPI 2017). The situation is made worse by the increasing frequency of large storm events that are degrading freshwater and coastal ecosystems and threatening downstream communities and infrastructure.

In Tairāwhiti, radiata pine *(Pinus radiata)* is the dominant plantation forestry species covering 145,126 hectares (MPI et al. 2024). Recent major storm events have highlighted the vulnerability of clearfell production exotic forestry practices on steep erosion-prone upper catchments to downstream communities and landuses with significant damage and loss of infrastructure, housing, livelihoods and biodiversity.

This research forms part of Tāne's Tree Trust’s ‘Transitioning Exotic Forest to Native’ project. It aims to investigate whether the native regenerating understory found within Tairāwhiti pine plantations is influenced by stand age, pine stem density, and distance to native seed source. It also seeks to understand if the understory species indicate the beginning of a transition to native forest and if not, what is holding such a transition back. This work is part of a wider transition study to help predict what is likely to occur if exotic plantation forestry is left unmanaged, as well as inform options for forest management required to enhance a transition of an exotic canopy to permanent native forest.

2 Methods

2.1 Study sites

The survey was intended to focus on older stands of radiata pine forest covering a wide range of stand densities. Tairāwhiti (Gisborne Region) was chosen as the study area due to its predominance of highly erodible steep land and suitability for permanent forest cover (Figure 1).

Tairāwhiti has a mean annual temperature of around 14°C for low-lying coastal areas, whereas the higher-elevation Raukumara Range experiences a mean annual temperature of around 9°C. mean annual precipitation varies with coastal rainfall around 1300–1800 mm north of Gisborne to East Cape, to less than 1000 mm near Gisborne and further inland (Chappell 2016).

The region has supported historic forest cover characterised by mixed broadleaved-conifer forests. Native forest remnants within the region are mapped as secondary broadleaf communities with pockets of primary forest that escaped clearance and fire (GDC 2023). The geology of Tairāwhiti is characterised by hill country developed on crushed argillite, sandstone, or greywacke, with severe gully-dominated erosion and mid-aged (late Pleistocene/early Holocene) tephra or tephric loess. The predominantly orthic recent soils[1] are generally mapped

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[1] https://soils-maps.landcareresearch.co.nz/

as LUC7e land[2]. In comparison with regions exposed to the west, the Gisborne/Tairāwhiti region experiences a greater number of weather and climatic extremes (Chappell 2016). Long term it is predicted to become warmer and drier with climate change (MFE 2025).

Survey sites were chosen after discussions with forestry managers taking account of stand age (>20 years old) and ease of access. Sites were targeted to provide a wide geographical coverage within the Tairāwhiti region including inland and coastal sites and secondary and tertiary sedimentary geology. Stand proximity to native seed sources was also considered. Weather events before and during the field surveys, constrained site selection as access to many otherwise suitable sites was often deemed unsafe. Where access was safe, field reconnaissance then determined whether selected sites contained the prerequisite conditions such as stand size and integrity to allow plot/s to be established with at least a 30m buffer from the forest edge. A total of 24 radiata stands were chosen as suitable sites (see Figure 1) and 45 survey plots were surveyed between February 2023 and August 2024.

2.2 Sampling design

At each site one or more 0.06-hectare circular Permanent Sample Plots (PSPs) were established following Herries et al. (2019) and MPI (2023). A treated wooden 50 mm x 50 mm peg was established in the plot centre and its location recorded by GPS. Each plot was marked using a vertex to identify a 13.82 m radius circular boundary (adjusted for slope). A sub-plot for assessing saplings and seedlings was also marked out, centred on the plot peg with a 5.64m radius (100m^2) adjusted for slope. All plots were photographed.

Within the main plot, vegetation was surveyed using a combination of the methods used in the LUCAS plantation forest and natural forest inventories (Beets et al 2011 and DOC 2019). Plot location and site data using the RECCE plot (Reconnaissance Plot) guidelines described by Hurst et al (2022). This included recording slope, aspect, topography, disturbance etc along with any anecdotal information from land managers regarding stand history. Canopy cover was visually estimated for total canopy cover above 1.35m and also canopy cover of the pine plantation. Browse scoring was determined by estimating the level (light/medium/heavy) on understory vegetation. Observations of browse species presence were also noted.

Tree heights and distances were measure using a Haglöf vertex III hypsometer.

Stems were classified into trees, saplings or seedlings using the following criteria:

Trees:	Diameter at breast height,1.35m (DBH) ≥ 2.5cm
Saplings:	DBH < 2.5cm and height ≥ 1.35m
Seedlings:	Height < 1.35m

The following vegetation assessment/measurements (understory and plantation species) were recorded in the main plots:

- Reece assessment including cover-abundance of all species present assessed in seven standard height tiers (>25m, 12-25, 5-12, 2-5, 0.3-2, <0.3m, epiphytes at any height). Six standard, simplified Braun-Blanquet cover-abundance classes were used (< 1% cover, 1–5%, 6–25%, 26–50%, 51–75%, 76–100%).
- Trees - All stems ≥ 2.5 cm DBH at 1.35m height were measured in each plot, recording species, DBH and height.

In each 100m^2 sub-plot saplings and seedlings were recorded as follows:

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[2] https://ourenvironment.scinfo.org.nz/maps-and-tools/app

- Saplings – all stems <2.5cm DBH and ≥ 1.35m height were recorded by species and height.
- Seedlings – all plants not deemed trees or saplings were counted by species within 5 height classes based on the DOC (2019) vegetation data collection field protocol height classes: 0-15 cm, 16-45, 46-75, 76-105, 106-135 cm.

The proximity to native seed supply was assessed as either primary or secondary forest and where possible the common tree species were identified. Distance to seed source was measured from the plot centre to the nearest native forest edge. This was based on mapped vegetation layers (e.g. DOC estate, GDC Protection Management Areas, LCDB[3]), local observations and satellite aerial assessment, to determine presence and proximity of native vegetation and maturity of the forest. It is assumed that later successional forest will have greater plant diversity and inclusion of tall canopy species.

2.3 Statistical analysis

Trees (stems ≥ 2.5 cm DBH) measured in the 0.06ha main plots were classified as either pine stand or understory trees. Radiata pine trees with DBH > 20 cm were defined as pine stand trees, and all other trees including radiata pine < 20 cm DBH were classified as understory stems.

Because stem heights were only recorded for a sample of stems, heights were predicted for stems not measured for height using type 1 Petterson height/DBH functions fitted to stems with measured heights. Separate curves were fitted for pine stand trees and understory trees in each plot. Because tree ferns show no relationship between height and DBH, they were not included in the understory height/DBH functions. Instead, the mean height of tree ferns measured for height in each plot were used to predict heights for all tree ferns not measured for height.

Carbon in pine stand trees was calculated using the C-Change model (Beets et al. 2011). Carbon in understory trees was calculated using the methods described in Beets et al. (2012). To apply this method, stem volume was calculated for each stem using an allometric function and multiplied by wood density tabulated by species to estimate stem biomass. Other allometric functions were used to estimate carbon in the branches and foliage. Above ground carbon of tree ferns was estimated using an allometric equation given by Beets et al. (2012). Below ground biomass was estimated using root/shoot ratios of 0.234 for broadleaves and palms, 0.245 for conifers, and 0.194 for tree ferns. To convert biomass to carbon, carbon fractions of 0.48 were used for broadleaves and 0.51 for conifers. Carbon in saplings and seedlings was estimated from stem height (m) using the following nonlinear regression model fitted to the tree data using the R nls function: Carbon (kg) = $0.00835 \times \text{Height}^{3.611}$. All carbon estimates were converted to CO_2 equivalents by multiplying by 3.67.

Various metrics for both pine stand and understory trees were estimated for each plot. For pine stand trees, the standard forestry metrics: stand density (stems/ha), mean top height (MTH, m), basal area (BA, m^2/ha) and carbon (t CO_2/ha) were calculated. For understory vegetation, stand density of both trees, MTH, BA, and carbon were calculated along with the number of species present, and the Shannon diversity index:

$$H = \sum_i p_i ln(p_i)$$

where, p_i is the proportion of stems in species i. These metrics were calculated both for trees only, and for all stems (trees + saplings + seedlings). Stand density, carbon and BA were calculated by summing the stem values and dividing by plot or sub-plot area. Understory species were classified according to their growth form (canopy tree, subcanopy tree, shrub, tree

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[3] Broadleaved Indigenous Hardwoods, Indigenous Forest

fern) as defined by Paul et al. (2021) and biostatus (native, adventive) based on the New Zealand National Vegetation Survey (NVS) Databank available on the Landcare website. The estimated carbon in each growth form and biostatus group was then calculated for each plot.

Relationships between understory metrics and stand characteristics were initially examined by calculating correlations (R cor function) and then tested using Generalised Additive Mixed Models (GAMMs) fitted using the R gamm function. Generalised additive mixed models test for relationships between a dependent variable and one or more independent variables allowing for nonlinear relationships which are fitted using smoothing splines. The independent variables included in these models were pine stand age, pine stand stand density, distance to native seed source, and elevation. The models also and included a plot-within-stand error structure. The dependent variables were understory carbon, understory stem density, species richness (number of species per plot) and Shannon diversity index. Separate models were fitted for the tree data only (stems ≥ 2.5cm DBH), and for all stems (trees + saplings + seedlings). A regression model predicting carbon stock as a function of stand age and stand density was also fitted.

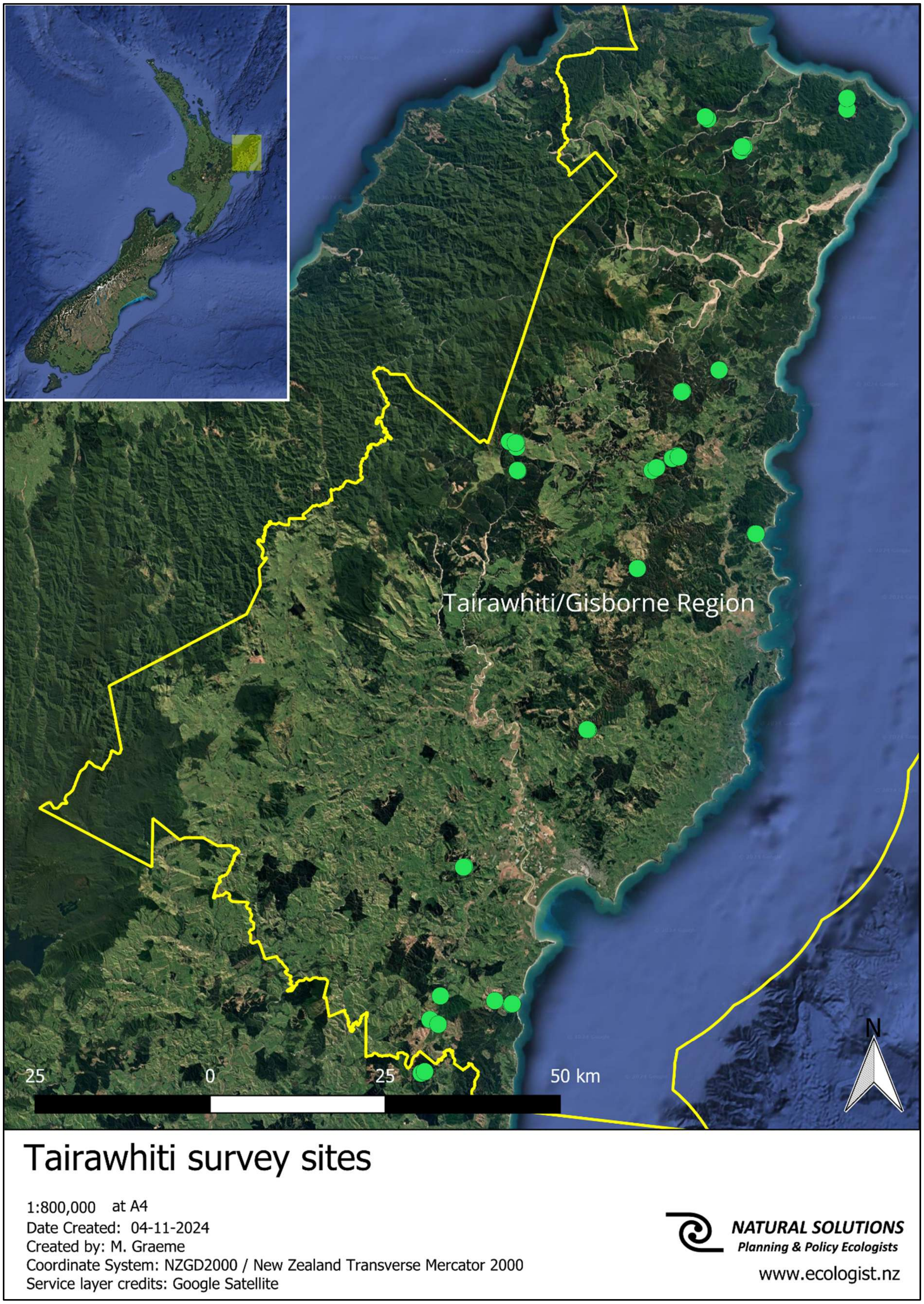


Figure 1: Survey sites in the Tairāwhiti/Gisborne region

3 Results

3.1 Characteristics of pine canopy trees and understory.

Characteristics of the surveyed Tairāwhiti plots are summarised in Table 1. A total of 45 plots at 24 sites were measured from just south of the southern regional boundary near Mōrere to Te Araroa, spanning some 150km of latitude. Elevation averaged 378 m and covered a wide range from 73 to 983 m. The study targeted older radiata pine stands as evidenced by the average age of 37 years with an age range of 21 to 63 years. Stand density of the radiata pine plantation trees averaged 310 stems/ha, and mean top height (MTH) averaged 42 m with a range from 28 to 53 m. On average, the radiata pine stand trees stored 1,353 t CO_2/ha.

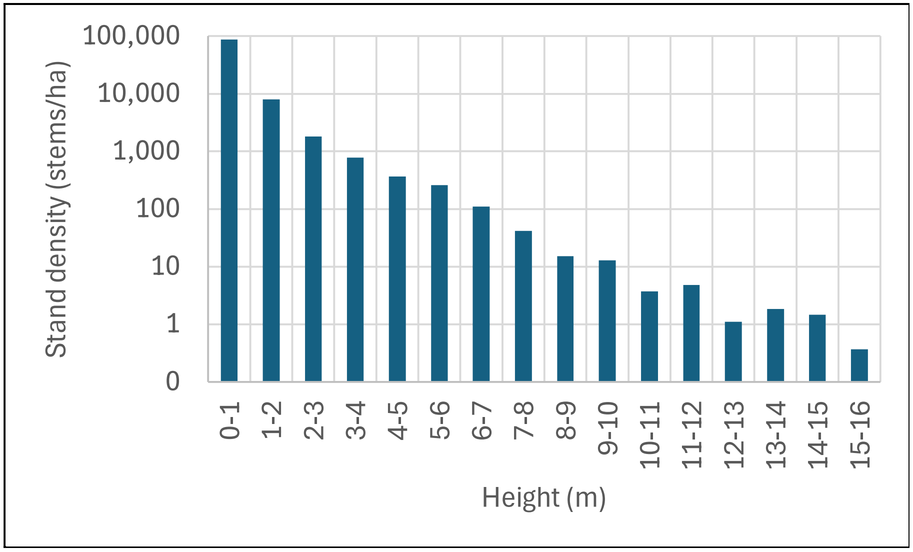
Species in the understory were overwhelmingly native, with natives comprising 98.2 percent of the stems and storing 98 percent of the understory carbon. As found in other studies (e.g. Kimberley et al., in prep, a), understory carbon was only a small percentage of total carbon, averaging 22.5 t CO_2/ha which was only 1.3 % of total carbon including pine stand trees.

Table 1: Summary of data from 45 Tairāwhiti plots showing means, standard deviations and ranges of various metrics of the pine stand and understory.

Variable		**Units**	**Mean ± Std. dev.**	**Range**
Stand age		years	37.1 ± 7.5	21 - 63
Elevation		m	378 ± 237	73 - 983
Distance to native seed source		m	633 ± 511	65 - 1,900
Browse score			1.47 ± 0.50	1 - 2
Pine stems	Stand density	stems/ha	310 ± 97	133 - 467
	Carbon	t CO_2/ha	1,353 ± 361	705 - 2,162
	Basal area	m^2/ha	83.4 ± 21.5	37.9 - 141.7
	Mean top height	m	41.6 ± 5.2	27.7 - 53.1
All understory stems	Stand density	stems/ha	99,208 ± 84,262	5,200 - 414,032
	Carbon	t CO_2/ha	22.1 ± 26.7	0.0 - 110.6
	Basal area	m^2/ha	3.6 ± 4.8	0.0 - 19.4
	Shannon diversity index		1.2 ± 0.5	0.2 - 2.2
	Number of species	N/plot	11.4 ± 4.3	2 - 23
	Carbon in native species	%	98.0 ± 7.1	56 - 100
	Stand density in native stems	%	98.2 ± 5.7	64 - 100
Understory stems ≥ 2.5 cm DBH	Stand density	stems/ha	924 ± 1,260	0 - 4,600
	Carbon	t CO_2/ha	17.1 ± 24.9	0.0 - 104.3
	Basal area	m^2/ha	3.6 ± 4.8	0.0 - 19.4
	Mean top height	m	6.7 ± 1.9	3.7 - 10.8
	Shannon diversity index		0.8 ± 0.6	0.0 - 2.3
	Number of species	N/plot	4.1 ± 3.7	0 - 14
	Carbon in native species	%	96.7 ± 11.0	46 - 100
	Stand density in native stems	%	97.2 ± 10.4	50 - 100
Understory stems < 2.5 cm DBH	Stand density	stems/ha	98,284 ± 83,907	5,200 - 414,000
	Carbon	t CO_2/ha	5.0 ± 0.6	0.0 - 26.7
	Shannon diversity index		1.2 ± 0.5	0.2 - 2.3
	Number of species	N/plot	9.8 ± 3.6	2 - 17
	Carbon in native species	%	98.8 ± 5.8	62 - 100
	Stand density in native stems	%	98.2 ± 5.7	64 - 100

Heights of understory stems followed an inverse J-shaped distribution with very large numbers of small stems and fewer larger stems (Figure 2a). Some 88.6% of stems were less than 1 m tall, and 96.6% less than 2 m tall. However, most of the understory carbon was stored in stems in the mid-range of the size distribution with 79.7% stored in 2-8 m tall stems, 14.9% in stems taller than 8 m, and only 5.4% in stems less than 2 m (Figure 2b).

(a)



(b)

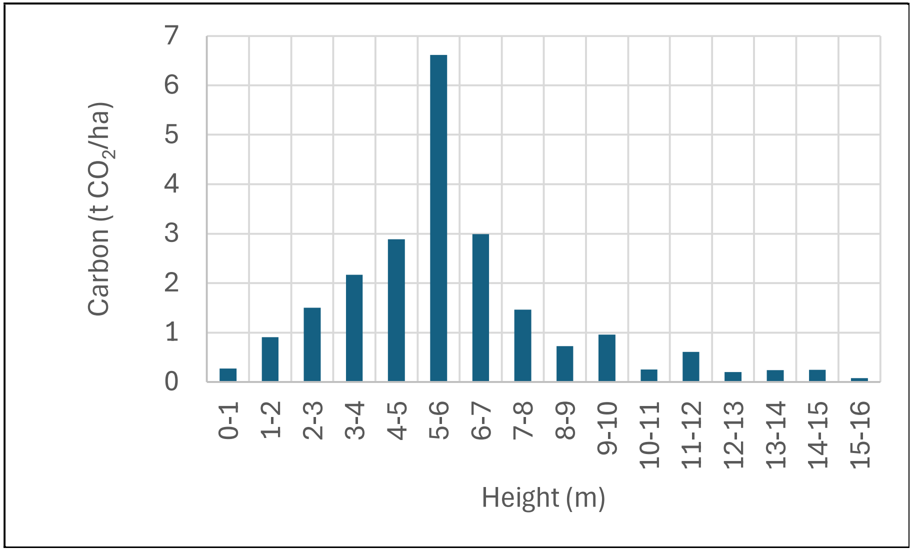


Figure 2: Height distribution of understory stems showing (a) stand density (stems/ha) by height class, and (b) carbon (t CO_2/ha) by height class.

More than three quarters of understory stems belonged to shrub species with most of the remainder being subcanopy tree species and only a small percentage being canopy tree species and tree ferns (Figure 3a). However, only 20% of carbon was stored in shrub species with 42% in subcanopy tree species, 8% in canopy tree species, and 30% in tree ferns despite these comprising only 0.1% of stems (Figure 3b).

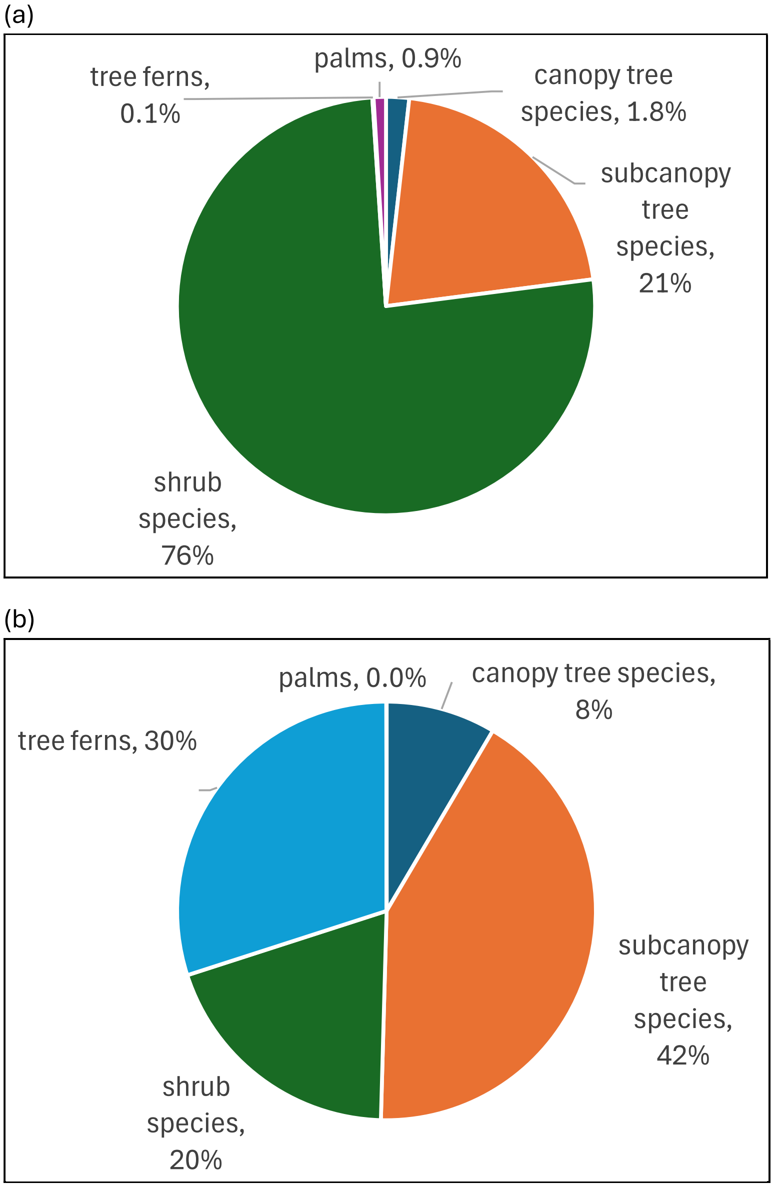


Figure 3: Growth habits of understory stems showing (a) percentage stems by growth habit, and (b) carbon by percentage growth habit.

Table 2 lists the 40 most important understory species based on carbon and with associated stem densities. The most common native species in terms of stem numbers was *Coprosma rhamnoides* followed by kawakawa (*Piper excelsum* subsp. *excelsum*), mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*) and Hangehange (*Geniostoma ligustrifolium* var. *ligustrifolium*). Only 3 species (Radiata pine, lilly pilly and Chinese privet) were exotic out of the 40 most important species.

In terms of carbon stock, the most important species were mamaku (*Sphaeropteris medullaris*), mahoe, ponga/silver fern (*Alsophila dealbata*) and makomako (*Aristotelia serrata*). While *Coprosma rhamnoides* is common and often dominates where browsers are common, the presence of species preferred by browsers indicates that the browsing pressure is not always high enough to exclude these species.

Table 2: The 40 most important understory species in terms of carbon with associated stand density.

Māori / common name	**Scientific name**	**Biostatus**	**Growth habit**	**Carbon (tCO_2/ha)**	**Stand density (stems/ha)**
Mamaku	*Sphaeropteris medullaris*	Indigenous	tree fern	3.76	25
Māhoe	*Melicytus ramiflorus*	Indigenous	subcanopy tree	3.72	8,253
Ponga/silver fern	*Alsophila dealbata*	Indigenous	tree fern	1.90	14
Makomako	*Aristotelia serrata*	Indigenous	subcanopy tree	1.83	1,503
Kawakawa	*Piper excelsum*	Indigenous	shrub	1.53	10,696
Putaputawētā	*Carpodetus serratus*	Indigenous	subcanopy tree	1.30	4,083
Mingimingi	*Leucopogon fasciculatus*	Indigenous	shrub	1.07	1,530
Wheki	*Dicksonia squarrosa*	Indigenous	tree fern	0.81	41
Kānuka	*Kunzea robusta*	Indigenous	subcanopy tree	0.77	79
Kamahi	*Pterophylla racemosa*	Indigenous	canopy tree	0.76	40
Radiata pine	*Pinus radiata*	Exotic	canopy tree	0.57	408
Twiggy coprosma	*Coprosma rhamnoides*	Indigenous	shrub	0.45	50,658
Kōhūhū	*Pittosporum tenuifolium*	Indigenous	subcanopy tree	0.44	1,240
Red mapau	*Myrsine australis*	Indigenous	subcanopy tree	0.34	918
Tutu	*Coriaria arborea*	Indigenous	shrub	0.34	4
Kaikōmako	*Pennantia corymbosa*	Indigenous	shrub	0.30	651
Pūriri	*Vitex lucens*	Indigenous	canopy tree	0.23	114
Titoki	*Alectryon excelsus*	Indigenous	subcanopy tree	0.20	476
Hangehange	*Geniostoma ligustrifolium*	Indigenous	shrub	0.19	6,173
Kanono	*Coprosma autumnalis*	Indigenous	shrub	0.18	2,576
Kohekohe	*Didymocheton spectabilis*	Indigenous	canopy tree	0.18	370
Kōtukutuku	*Fuchsia excorticata*	Indigenous	subcanopy tree	0.14	519
Long-leaved lacebark	*Hoheria sexstylosa*	Indigenous	subcanopy tree	0.14	117
Rewarewa	*Knightia excelsa*	Indigenous	canopy tree	0.13	72
Patē	*Schefflera digitata*	Indigenous	subcanopy tree	0.12	500
Porokaiwhiri	*Hedycarya arborea*	Indigenous	subcanopy tree	0.11	1,752
Kātoe	*Alsophila smithii*	Indigenous	tree fern	0.10	3
Mānuka	*Leptospermum scoparium*	Indigenous	shrub	0.08	1
Thin-leaved coprosma	*Coprosma areolata*	Indigenous	shrub	0.06	118
Horoeka	*Pseudopanax crassifolius*	Indigenous	subcanopy tree	0.05	243
wheki-ponga	*Dicksonia fibrosa*	Indigenous	tree fern	0.05	2
Rangiora	*Brachyglottis repanda*	Indigenous	shrub	0.04	723
Heketara	*Olearia rani var. colorata*	Indigenous	subcanopy tree	0.05	108
Lilly pilly	*Syzygium smithii*	Exotic	subcanopy tree	0.04	9
Hells bells	*Helichrysum lanceolatum*	Indigenous	shrub	0.03	800
karamū	*Coprosma lucida*	Indigenous	shrub	0.03	332
red horopito	*Pseudowintera colorata*	Indigenous	subcanopy tree	0.02	580
Round-leaved coprosma	*Coprosma rotundifolia*	Indigenous	shrub	0.02	71
tī kōuka / cabbage tree	*Cordyline australis*	Indigenous	cabbage tree	0.02	28
All other species				0.03	3,477

3.2 Correlations among and between site and stand characteristics and understory metrics

Table 4 shows correlations (Pearson correlation coefficients) between site and stand characteristics including pine stand and understory metrics. Among the site variables, elevation was positively correlated with distance from native seed source. This made it difficult to separate the effects of these two variables in the subsequent analysis. Stand age was positively correlated with understory carbon, stand density and number of species. Neither elevation nor distance to native seed source was significantly correlated with any understory characteristic except for a negative correlation between understory MTH and distance to native seed source. However, as these two variables were themselves highly correlated, they were included in the subsequent multivariable analysis to determine whether their combined effect could explain any understory variable. Browse score was also not significantly correlated with any understory metric and was excluded from subsequent analysis. Among the pine stand metrics, pine stand density was significantly negatively correlated with understory carbon, Shannon Diversity, and number of species, and this variable was therefore included in the subsequent multivariable analysis.

*Table 3: Pearson correlations among site characteristics and stand metrics of the pine stand and understory stems. Statistically significant correlations (α=0.05) are **bolded**.*

	Age	**Dist**	**Elev**	**Browse**	**Pine stock**	**Pine MTH**	**Pine carbon**	**Und stems**	**Und MTH**	**Und carbon**	**Shan**	**No. sp**
Age	1.00											
Dist. to native	0.14	1.00										
Elevation	0.24	**0.65**	1.00									
Browse score	0.24	0.02	-0.18	1.00								
Pine stocking	-0.10	**0.42**	**0.43**	-0.22	1.00							
Pine MTH	-0.04	-0.09	-0.08	**0.31**	**-0.45**	1.00						
Pine carbon	**0.41**	**0.42**	**0.55**	0.15	0.13	**0.40**	1.00					
Understory stems	**0.49**	-0.25	-0.20	0.11	0.01	-0.28	-0.12	1.00				
Understory MTH	0.25	**-0.30**	-0.20	-0.16	0.09	**-0.36**	-0.17	0.11	1.00			
Understory carbon	**0.54**	-0.32	-0.23	0.26	**-0.46**	0.12	0.01	0.29	**0.71**	1.00		
Shannon Diversity Index	0.14	-0.14	0.00	0.27	**-0.31**	**0.29**	0.07	-0.08	-0.25	**0.33**	1.00	
No. species	**0.54**	-0.23	-0.13	0.24	**-0.32**	0.13	0.12	**0.57**	0.19	**0.64**	**0.52**	1.00

3.3 Factors affecting understory stand metrics

Table 4 provides a summary of Generalised Linear Mixed Models (GLMM) testing relationships between understory stand metrics and four predictor variables (stand age, pine stand density, distance to native seed sources and elevation). The understory metrics included in these analyses were carbon, stem density, species richness and diversity.

Predictions from these models of all understory stems are shown in Figure 4 and Figure 5. Similar predictions for understory stems ≥2.5cm and ≤2.5cm are shown in Appendix A. Several understory metrics were strongly related and are discussed further below.

Table 4: Results of Generalised Linear Mixed Models predicting characteristics of the understory for all understory stems, stems ≥ 2.5 cm DBH, and stems < 2.5 cm DBH. Dependent variables modelled were carbon, stand density, Shannon Diversity Index and number of species per plot. Independent variables included in all models were pine stand age, canopy stand density, distance to native seed source, and elevation. The table shows the F value and significance of each independent variable, and the percentage variance explained by each model

Understory component	**Dependent variable**	**F value**				**Adjusted R^2**
		Plantation Stand age	**Plantation stand density**	**Distance to natives**	**Elevation**	
All stems	Carbon	9.17**	8.72**	0.62	0.24	0.48
	Stem density	19.31**	4.16*	2.56	3.28	0.38
	Shannon Diversity	0.02	3.82	2.02	0.76	0.11
	No. species	19.07**	1.31	0.81	3.17	0.45
Stems ≥ 2.5 cm DBH	Mean top height	0.67	3.11	4.27	0.00	0.26
	Basal area	10.32**	9.73**	0.13	0.49	0.42
	Carbon	10.23**	8.83**	0.03	0.84	0.51
	Stem density	3.07	6.81*	0.00	0.04	0.21
	Shannon Diversity	4.53*	3.83	10.57**	0.06	0.50
	No. species	12.63**	16.76**	2.18	0.02	0.54
Stems < 2.5 cm DBH	Carbon	0.12	0.28	1.91	0.33	0.00
	Stem density	19.08**	4.32*	2.58	3.26	0.38
	Shannon Diversity	0.01	3.48	1.85	0.77	0.09
	No. species	12.99**	0.07	0.82	4.76*	0.32

* Significant at p=0.05, ** Significant at p=0.01

3.4 Effect of pine stand age on understory

Understory stem density of all stems (Figure 4B) and especially seedlings (Figure A4-B) increased with age of the pine canopy.

Basal area also increased with age of pines (Figure A1-B), and although there was a tendency for MTH to increase with age (Figure A1-A), this effect was not statistically significant suggesting that heights of understory stems tend to stabilise at about 7 m in older radiata pine stands.

Carbon stored in the understory increased significantly with pine stand age (Figure 4A), as did carbon stored in stems ≥ 2.5 cm DBH (Figure A2-A), but not carbon stored in the smaller stems (Figure A4-A).

The number of understory species (richness) also increased significantly with pine stand age for all stems, including saplings and seedlings (Figures 5B, A3-B and A5-B). The Shannon diversity index of saplings was also higher in older plots (Figure A2-A).

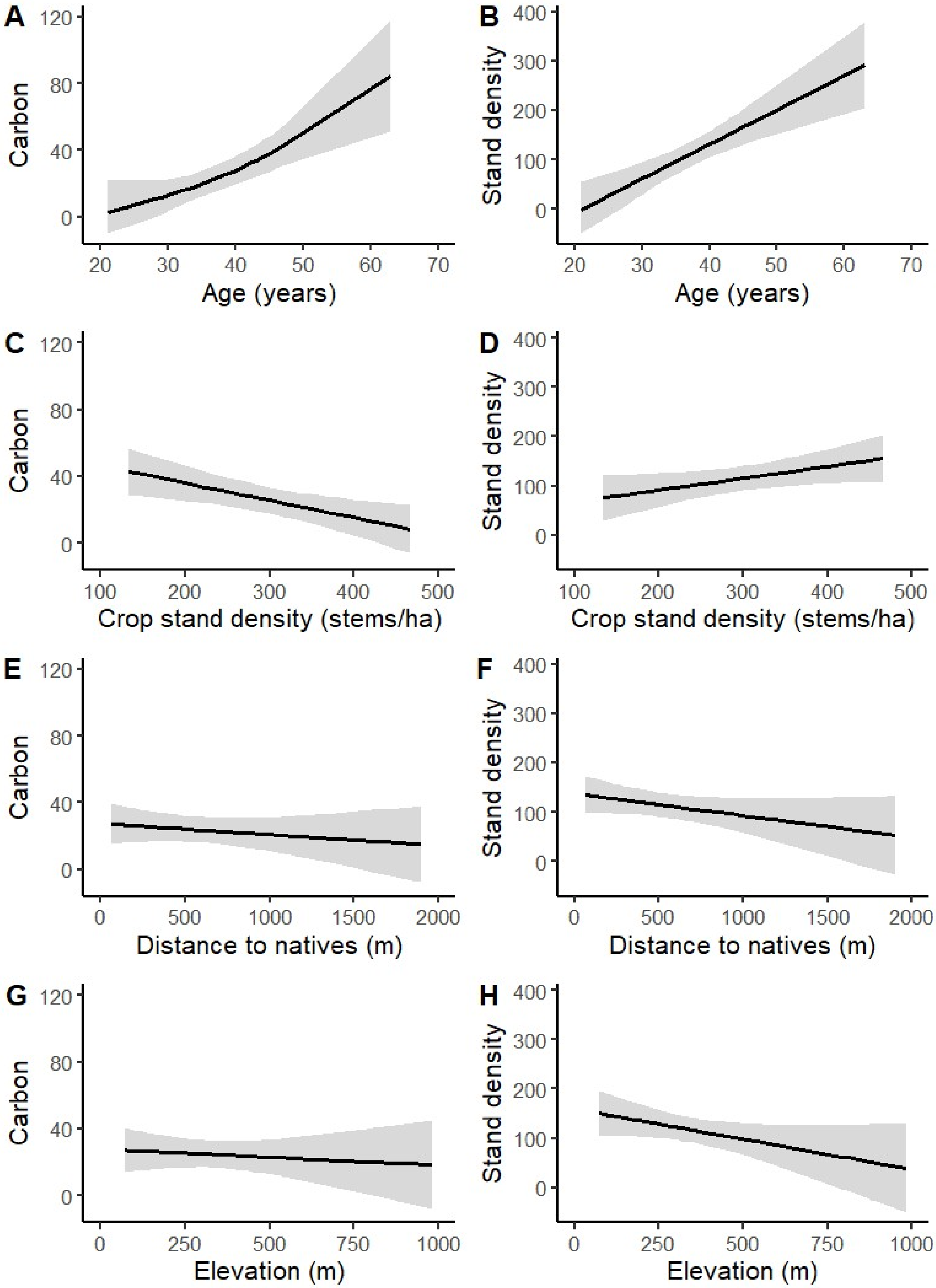


Figure 4: Predictions from Generalised Linear Mixed Models (GLMMs) of understory carbon (t CO2/ha) and understory stand density (1000 × stems/ha). Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.

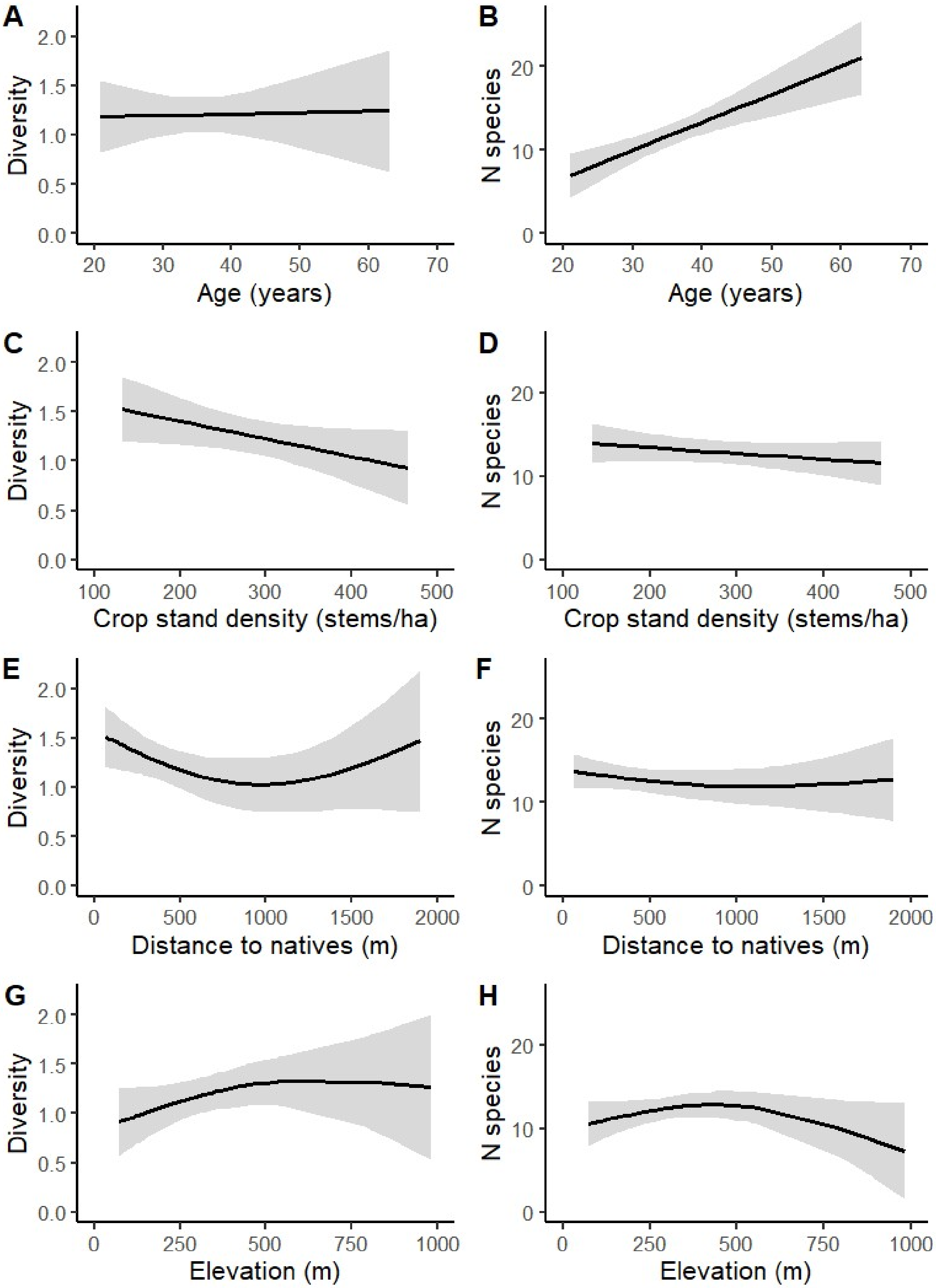


Figure 5: Predictions from Generalised Linear Mixed Models (GLMMs) of Shannon diversity index and number of species per plot of understory stems. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.

Table shows simple linear regression models fitted for predicting carbon stock and stand density as functions of stand age for each of the 40 most important understory species. Although most species showed an increase with age in both carbon and stand density (positive slope coefficient), in only a few species was this increase statistically significant. This was presumably because at the individual species level, the variability is too high to accurately determine individual growth rates in carbon or stand density. Species that showed significant increases in carbon with age were kamahi, kōhūhū, kanono, rewarewa, and pate. No species decreased significantly with age.

A significant portion of forest seedlings, particularly in the <15cm tier, commonly do not survive. However, species composition of the lower vegetation tiers provides an indication of the diversity of nearby seed sources availability for understory development if conditions are conducive to germination and establishment. Table shows the stem density of the 40 most common understory species. The current understory community is dominated by secondary colonising species, with few later successional mature phase tall canopy species as yet entering the higher sapling and tree tiers.

*Table 5: Simple linear regression models for predicting carbon stock (tCO2/ha) and stand density (stems/ha) as linear functions of stand age (years) for the 40 most important understory species. Statistically significant (α=0.05) slope coefficients are **bolded**.*

Common name	Scientific name	Carbon stock (tCO_2/ha)		Stand density (stems/ha)	
		Intercept	Slope	Intercept	Slope
Mamaku	*Sphaeropteris medullaris*	-9.1	0.35	-14	1
Māhoe	*Melicytus ramiflorus*	-7.9	**0.31**	937	191
Ponga/silver fern	*Alsophila dealbata*	-1.9	0.10	-14	1
Makomako	*Aristotelia serrata*	-1.2	0.09	1304	17
Kawakawa	*Piper excelsum*	0.0	0.04	-7034	465
Putaputawētā	*Carpodetus serratus*	-0.6	0.05	-3127	194
Mingimingi	*Leucopogon fasciculatus*	-2.2	0.08	-713	54
Wheki	*Dicksonia squarrosa*	0.6	0.01	-68	3
Kānuka	*Kunzea robusta*	-0.7	0.04	-98	4
Kamahi	*Pterophylla racemosa*	-17.4	**0.50**	-148	**5**
Radiata pine	*Pinus radiata*	-2.9	0.09	50	10
Twiggy coprosma	*Coprosma rhamnoides*	0.1	0.01	-12354	1656
Kōhūhū	*Pittosporum tenuifolium*	-1.7	**0.06**	-264	42
Red mapau	*Myrsine australis*	-0.2	0.01	391	13
Tutu	*Coriaria arborea*	-1.9	0.06	-21	1
Kaikōmako	*Pennantia corymbosa*	0.9	-0.01	1025	-10
Pūriri	*Vitex lucens*	1.1	-0.02	-7	3
Titoki	*Alectryon excelsus*	-0.1	0.01	419	2
Hangehange	*Geniostoma ligustrifolium*	-0.2	0.01	-3062	248
Kanono	*Coprosma autumnalis*	-2.6	**0.08**	-41071	**1200**
Kohekohe	*Didymocheton spectabilis*	0.0	0.00	111	6
Kōtukutuku	*Fuchsia excorticata*	-0.7	0.03	-328	26
Long-leaved lacebark	*Hoheria sexstylosa*	-0.1	0.01	-197	8
Rewarewa	*Knightia excelsa*	-1.1	**0.03**	-499	**15**
Patē	*Schefflera digitata*	-2.4	**0.07**	-4038	**123**
Porokaiwhiri	*Hedycarya arborea*	-0.1	0.01	-16974	**516**

Kātoe	*Alsophila smithii*	0.2	-0.00	10	-0
Mānuka	*Leptospermum scoparium*	0.1	-0.01	-3	0
Thin-leaved coprosma	*Coprosma areolata*	0.3	-0.01	638	-14
Horoeka	*Pseudopanax crassifolius*	-0.1	0.00	-54	8
wheki-ponga	*Dicksonia fibrosa*	1.0	-0.02	22	-0
Rangiora	*Brachyglottis repanda*	-0.1	0.00	813	-2
Heketara	*Olearia rani var. colorata*	-0.0	0.00	-1	0
Lilly pilly	*Syzygium smithii*	-0.0	0.00	-2	0
Hells bells	*Helichrysum lanceolatum*	-0.0	0.00	-960	43
karamū	*Coprosma lucida*	0.1	-0.00	904	-15
red horopito	*Pseudowintera colorata*	-0.1	0.00	-2468	88
Round-leaved coprosma	*Coprosma rotundifolia*	0.1	-0.00	273	-5
tī kōuka / cabbage tree	*Cordyline australis*	-0.0	0.00	-62	2

Table 6: Mean density in stems per hectare of each developmental stage for the 40 most common species present in the understory of all surveyed plots

Common name	Species	Growth form	Stem density (stems/ha)			**Total**
			Seedlings	Saplings	Trees	
Twiggy coprosma	*Coprosma rhamnoides*	Shrub	49,449	1,209	0	**50,658**
Kawakawa	*Piper excelsum*	shrub	9,938	596	162	**10,696**
Mahoe	*Melicytus ramiflorus*	subcanopy tree	6,542	1,413	298	**8,253**
Hangehange	*Geniostoma ligustrifolium*	shrub	5,947	213	13	**6,173**
Putaputawētā	*Carpodetus serratus*	subcanopy tree	3,529	498	56	**4,083**
Kanono	*Coprosma autumnalis*	shrub	2,542	27	7	**2,576**
Porokaiwhiri	*Hedycarya arborea*	subcanopy tree	1,618	133	1	**1,752**
Mingimingi	*Leucopogon fasciculatus*	shrub	1,111	311	108	**1,530**
Makomako	*Aristotelia serrata*	subcanopy tree	907	542	54	**1,503**
Kōhūhū	*Pittosporum tenuifolium*	subcanopy tree	1,129	89	22	**1,240**
Nīkau	*Rhopalostylis sapida*	palm	933	9	0	**942**
Red mapau	*Myrsine australis*	subcanopy tree	756	142	20	**918**
Hells bells	*Helichrysum lanceolatum*	shrub	649	151	0	**800**
Rangiora	*Brachyglottis repanda*	shrub	676	44	3	**723**
Kaikōmako	*Pennantia corymbosa*	shrub	373	267	11	**651**
red horopito	*Pseudowintera colorata*	subcanopy tree	533	44	2	**580**
Kōtukutuku	*Fuchsia excorticata*	subcanopy tree	489	18	12	**519**
Patē	*Schefflera digitata*	subcanopy tree	489	9	2	**500**
Titoki	*Alectryon excelsus*	subcanopy tree	329	142	5	**476**
Tawa	*Beilschmiedia tawa*	canopy tree	444	0	0	**444**
Radiata pine	*Pinus radiata*	canopy tree	391	9	8	**408**
Kohekohe	*Didymocheton spectabilis*	canopy tree	231	133	5	**370**
Shining karamū	*Coprosma lucida*	shrub	329	0	3	**332**
Chinese privet	*Ligustrum sinense*	subcanopy tree	302	18	0	**320**
Glossy karamū	*Coprosma robusta*	shrub	302	0	0	**303**
Poroporo	*Solanum laciniatum*	shrub	293	0	0	**293**
Horoeka	*Pseudopanax crassifolius*	subcanopy tree	213	27	3	**243**
Kahikatea	*Dacrycarpus dacrydioides*	canopy tree	231	0	0	**231**
Whauwhaupaku	*Pseudopanax arboreus*	subcanopy tree	196	9	0	**204**

Long-leaved lacebark	*Hoheria sexstylosa*	subcanopy tree	62	53	1	**117**
Thin-leaved coprosma	*Coprosma areolata*	shrub	71	44	3	**118**
Ngaio	*Myoporum laetum*	shrub	116	0	0	**116**
Pūriri	*Vitex lucens*	canopy tree	62	44	8	**114**
Heketara	*Olearia rani*	subcanopy tree	89	18	2	**108**
Bush snowberry	*Gaultheria antipoda*	shrub	71	18	0	**89**
Kānuka	*Kunzea robusta*	subcanopy tree	18	27	34	**79**
Rewarewa	*Knightia excelsa*	canopy tree	53	18	1	**72**
Round-leaved coprosma	*Coprosma rotundifolia*	shrub	27	44	0	**71**
Kakawariki	*Coprosma grandifolia*	shrub	62	0	0	**62**
Other species			438	27	77	**542**
		Totals	**91,938**	**6,347**	**924**	**99,208**

3.5 *Effect of radiata pine stand density*

There was a significant relationship between pine stand density and carbon (Figure 4C). Carbon increased with decreasing pine stand density for larger sapling understory stems (Figure A2-C), but not for smaller seedling stems (Figure A4-C).

Understory stem density of saplings also increased with reducing pine stand densities (Figures A2-D). Lower pine stand density was also associated with higher sapling basal area (Figure A1-D), but although lower stocked plots tended to have taller understory stems (Figure A1-C), this effect was not significantly affect (Table 4:).

Finally, there were significant negative relationships between pine stand density and the number of species per plot (Figure A3-D) for understory stems ≥ 2.5 cm DBH.

3.6 *Combined effect of pine stand age and density on understory carbon*

Table gives details of a linear mixed model fitted to the data that can be used to predict understory carbon as a function of stand age and pine stand density. Pine stand density has been standardised by subtracting 300 and dividing by 100. The model predicts that, on average at a pine stand density of 300 stems/ha, understory carbon increases by 1.47 t CO_2/ha/year. The increase is greater by 0.84 for every 100 stems/ha reduction in pine stand density. Therefore, at pine density of 200 stems/ha, carbon is predicted to increase by 2.71 t CO_2/ha/year. Conversely, at 400 stems/ha, carbon is predicted to increase by only 0.63 t CO_2/ha/year. The model should only be applied over the range covered by the data, i.e., for pine stand density in the range 130-470 stems/ha, and age in the range 20-60 years.

Table 7: Coefficients estimates with standard errors and test statistics for a linear mixed model predicting understory carbon (t CO_2/ha) as a function of pine stand age (years) and density (stems/ha),

Coefficient	**Value**	**Std. Error**	**t-value**	**p-value**
Intercept	-31.7	16.9	-1.87	0.074
Pine stand age	1.47	0.44	3.36	0.003
(pine stand density – 300)/100	0.20	0.14	1.42	0.17
Age × (pine stand density – 300)/100	-0.84	0.35	-2.40	0.027

3.7 *Effect of distance from native seed source*

Understory characteristics were assessed against distance to native seed source to determine whether this has a measurable effect on the native understory development. Distances to seed sources varied from 65m – 1,900m. Distance to native seed source was not significantly related to any understory characteristic other than Shannon diversity index for saplings (Table 4:). Plots closer than 1000 m from a native seed source tended to have a higher species diversity in these larger stems (Figure A5-E).

3.8 *Effect of elevation*

The study plots covered a wide range of elevation from 70 to nearly 1000 m (Table 1) but understory characteristics were mostly fairly uniform across this range. The only exception was number of species per plot in seedlings (stems < 2.5 cm DBH) (Table 4:). Numbers of species tended to drop above 750m elevations (Figure 10H). This could potentially reflect the more remote locations and hence lower browser control pressure, rather than vegetation growth preferences.

3.9 *Canopy tree species characteristics in the understory*

The most common native canopy tree species present in surveyed pine understory plots were tawa, radiata pine, kohekohe, kahikatea, and pūriri (Table). While most of these species were found throughout the survey plots, kohekohe and pūriri where characteristic of coastal lowland plots. The only canopy species that were found under the surveyed pine canopy that had reached the large stem ‘tree tier’ were radiata pine, pūriri, kohekohe, kamahi and rewarewa.

Table 8: Mean density in stems per hectare of each developmental stage for canopy tree species in the understory of all surveyed plots

Common name	Species	Biostatus	Stand density (stems/ha)			Total
			Seedlings	Saplings	Trees	
Radiata pine	*Pinus radiata*	Exotic	391	9	8	**408**
Pūriri	*Vitex lucens*	Indigenous	62	44	8	**114**
Kohekohe	*Didymocheton spectabilis*	Indigenous	231	133	5	**370**
Kamahi	*Pterophylla racemosa*	Indigenous	36	0	4	**40**
Rewarewa	*Knightia excelsa*	Indigenous	53	18	1	**72**
Tawa	*Beilschmiedia tawa*	Indigenous	444	0	0	**444**
Karaka	*Corynocarpus laevigatus*	Indigenous	53	0	0	**53**
Kahikatea	*Dacrycarpus dacrydioides*	Indigenous	231	0	0	**231**
Tōtara	*Podocarpus totara*	Indigenous	18	0	0	**18**
		Totals	**1519**	**204**	**26**	**1750**

The coastal Waipare block potentially benefited from more favourable growing conditions and/or less browser pressure as pūriri and kohekohe were common in the sapling and tree tiers in these plots. Natural pine wind fall may have contributed to this by providing greater overhead light and/or restrictions to browser access. Good native seed sources were also nearby.

Pine regeneration was negligible in a closed canopy pine forest. The majority of the naturally regenerating pine were in the seedling tiers and the majority of these were <15cm. Half of the sites with pine seedlings present had a north-westerly aspect but there was no correlation evident between presence of pine seedlings and pine stand density. One pine was recorded in the sapling vegetation height, and 11 in the tree vegetation height (4 sites with the majority having a northerly slope aspect).

3.10 Effects of browsing

Goat, deer and possum sign were commonly seen as well as scattered sign/sightings of cattle, pigs and cat. Some plots with tall dense understory had a significant occurrence of trees (predominantly māhoe) pushed over by either deer or cattle.

There was a significant negative relationship between browse score and understory carbon, with plots containing higher levels of understory carbon having greater evidence of browsing. However, analysis found a positive correlation with Shannon diversity index and browse pressure, pine stand density and pine mean top height. Browse pressure was common throughout the stands surveyed. Even low browsing affected understory vegetation by hindering the growth of young plants through to a safe sapling/tree height.

3.11 Other general observations

Windthrow was commonly noted in the vicinity of the plots.

It was notable that there appeared to be a flush of early regeneration during the early pine stand development where a number of the saplings had managed to survive to grow out of deer browsing reach. Below these taller sapling/trees there was often a gap in the understory down to the lower seedling/sapling tiers. This may indicate a period of time when browsers such as deer and goats were at a much lower density compared with the present day, which allowed some of the early establishing understory to reach the upper sapling/tree tiers.

The only weed species noted were isolated patches of Kahali ginger, Taiwan cherry, banana passion fruit, lillypilly and Mexican daisy. These were generally associated with proximity to housing or roads.

Some of the older putaputawētā and pūriri understory regeneration had pūriri moth holes.

Sighting of whiteheads indicated the pine stands were providing good habitat for insectivorous birds that require relatively well-connected forest as they are rather poor long-distance fliers (Innes et al 2022). Also of note was one sighting of what appeared to be a tītitipounamu/rifleman. Other birds heard or seen included grey warbler, fantail, tomtit, tui, kererū, magpie, blackbird, pheasant, paradise duck, kingfisher, shining cuckoo, waxeye, bellbird and kāhu.

4 Discussion

The current study's site selection was heavily influenced by access constraints. Recent weather events, including Cyclone Gabrielle, cut off access to a significant portion of the forestry estate and made other areas unsafe or difficult to access easily. It was therefore impossible to standardise site characteristics such as aspect and slope.

4.1 Effects of early pine stand development

‘Nurse’ crops of fast growing indigenous or exotic species can be used to create a micro-environment that support the establishment of desired indigenous plants (Davis et al. 2009). Pine plantations have this potential, but because they are usually harvested by age 30 years the long-term development of plant and animal diversity within clearfell stands is usually interrupted. Brockerhoff et al. (2003) found that young pine forest effectively shades out initial ground vegetation. This is a useful trait as early regenerating vegetation often supports a high proportion of light-demanding exotic species that can outcompete native vegetation. The developing pine canopy then provides a suitable sheltered and shaded environment that supports the establishment of predominantly native ferns, shrub and tree species. The proportion of primary (shade tolerant) and secondary species with intermediate shade tolerance expanded with increasing pine stand age (Brockerhoff et al. 2003). Differences in stocking also appeared to affect the proportion of pioneer and later seral species suggesting that shade from the pine overstory is an important successional factor. High stocking at 16 years appeared to have a beneficial effect on preferencing secondary (e.g mahoe, ribbonwood, maire and mapou) species over pioneer species (e.g grasses, mānuka, poroporo, koromiko). Brockerhoff et al. (2003) concluded the ‘higher proportion of indigenous species in stands of higher canopy closure and the observation that such stands also have more later seral and shade-tolerant species indicates that the transition from pioneer to later seral species was accelerated in the higher stocked stands.’ Our results showed a predominance of secondary colonisers including kawakawa, māhoe, hangehange, putaputawētā, kanono, porokaiwhiri etc.

The pine crowns of mature pine trees growing in Tairāwhiti were generally relatively compact and, together with the significant pine height, meant light was able to penetrate through to the understory. Our analysis showed that there is a significant correlation between pine stand age and density, and the presence of understory vegetation gaining tree dimensions (≥ 2.5cm diameter at breast height 1.35m). This suggests that as the pine stand ages and thins it will support greater growth of understory shrub and tree species. However, the results also suggest that the understory height reaches a ‘maximum’ of ~7m under an intact pine canopy. Further height growth (for tree species) can be expected once the pine canopy senesces producing open ‘gap’ light environments.

4.2 Bioclimatic effects on succession

Studies have shown that successional changes are strongly influenced by geographic variations such as rainfall and temperature gradients (Leathwick & Rogers 1996, Leathwick et al. 1998, Brockerhoff et al. 2003, Forbes 2025). This bioclimatic variation is minimised to some extent in this research by concentrating study sites within the one region. However, Leathwick et al. (1998) also found that distance from intact forest, topography, slope and solar radiation, become important at local scales. This may become more pronounced with climate change. In some places it may become increasingly challenging to re-establish forests in a way that resembles their former character (PCE 2025). Utilising exotic nurse crops to facilitate native forest establishment to counter harsh establishment conditions may be one way of addressing this challenge (see Adaptive Management of Coastal Forestry Buffers). Other considerations include the impact of increased evapotranspiration, whereby over-storey nurse species can reduce the soil moisture available to the understory target species, and for this reason vigorous nurse crops tend to be least successful in dry areas (Davis et al, 2009). Conversely, the density of nurse crop shade and leaf litter may be a positive contribution to reducing soil moisture loss.

The results of this Tairāwhiti study show that for the larger stems ≥ 2.5 cm DBH, the mean understory stem density (924 ± 1,260 stems/ha), species richness (4.1 ± 3.7 no. sp/plot), Shannon diversity index (0.84 ± 0.61) and carbon (22 tonnes CO_2/ha) are all higher than the national mean found in LUCAS plots – 520 ± 108 stems/ha, 3.4 ± 0.4 no. sp/plot, 0.63 ± 0.09 and 6.3 tonnes CO_2/ha respectively (Kimberely et al, in prep, a). This greater understory regional growth will be influenced by local rainfall, wind and temperature conditions conducive to native forest succession.

4.3 Understory carbon

The carbon in the understory had a mean of 22t CO^2/ha (cf. 1,353t CO_2/ha for the pine stand). Three quarters of the understory carbon was held in the tree tier (DBH at 1.35m ≥ 2.5cm), and 98% of this carbon was in native species (mamaku, māhoe, ponga/silver fern, makomako, kawakawa). Most of the understory carbon was associated with subcanopy tree species, followed by tree ferns, then shrub species. Canopy tree species made up 8% of the understory carbon. As the vast proportion of carbon is stored in canopy trees, the presence and growth of native canopy species in the understory will determine the future carbon profile of the stand as the pine canopy trees senesce.

Analysis of understory carbon found a significant correlation with pine stand density and age, and a lesser correlation with distance to native seed source This indicates that as the mature pine canopy ages and thins, the understory carbon will increase but this increase may be influenced by the seeding species (both native and exotic) in the vicinity and browse pressure. Therefore, ensuring a diverse supply of local native seed and low browser pressure will be key to enhancing the likelihood of native canopy trees being able to germinate and grow into the upper understory tiers ready to fill gaps in the pine canopy over time. If these conditions are not present, the canopy gaps are likely to be either dominated by native shrub and sub-canopy species or, if a dense native subcanopy is missing and the ground is bare, wilding pine seedlings could establish. These various scenarios will have ramifications on the long-term carbon profile, and likelihood/timeframe of achieving a successful forest transition towards a sustainable mature native forest dominated by tall canopy tree species.

4.4 Understory species abundance, richness and diversity

The mean number of species (richness) in the understory is 11 with the majority (85%) of these being in the lower tiers (<2.5 cm DBH). However, the spread of this species richness or relative abundance, as indicated by the Shannon Diversity index, shows that there is a more uneven distribution of species in the upper tiers (≥2.5cm DBH) than the lower tiers. This could indicate that seedlings in the lower tiers are establishing but not surviving either due to physical conditions under the pine canopy or a pressure unrelated to the pine canopy, such as browser density.

Similarly, analysis found a correlation with Shannon diversity index and browse pressure, pine stand density and pine mean top height. This suggests that the understory becomes more diverse with lower browse pressure and older and sparser pine canopy and therefore, achieving a diverse native forest transition will require time and pest control.

4.5 Predominance of canopy species in the understory tiers

As discussed above in relation to carbon stocks, the establishment and long-term dominance of native tall canopy trees affects the future carbon profile of the stand but also affects whether a sustainable forest is achieved. The sustainability of a forest can be indicated by its vegetation diversity and plant functional traits. While the number of tall canopy tree species in the seedling tier provides an indication of the potential for succession to tall forest (see Table 8), the presence of these species reaching the taller sapling and tree tiers provides more of an indication of the likelihood of succession to tall forest.

Canopy species whose seedlings are shade tolerant (e.g. tawa) are more likely to be present in shaded pine forest understory than shade intolerant species such as rimu. Field observations noted tawa as a common canopy species present in remnant native forest stands, while very little podocarp was observed, thus, together with shade preferences, it was not unexpected that podocarp regeneration was absent in our surveys.

Forbes (2021) found tall canopy species are currently poorly represented in the Waingaki regeneration phase, although this is expected as these species tend to enter forest successions several decades following disturbance (Carswell et al., 2012).

Cameron (1960) reports that in Whirinaki when good seed years and favourable climatic conditions are present, it takes 50 years of natural regeneration before the establishment of dense stockings of podocarp seedlings. A further 50 years is required before these seedlings develop into poles and saplings. However, climate change and reduced seed dispersal agents, are threatening the occurrence of favourable conditions conducive to podocarp establishment and growth.

Cameron (1960) noted that dense mānuka or kānuka canopy can delay or prohibit podocarp regeneration. It is likely that conifer recruitment will be restricted under closed canopies typical of regenerating broad-leaved angiosperm forests as conifer establishment requires specific conditions of light gaps and canopy openings, (McGlone et al. 2017). Broadleaved seedlings commonly outcompete podocarps in light gaps however, should a podocarp seedling gain an opportunity to dominate a light gap, it can then outlive the more common broadleaf canopy (see Heenan et al 2024). Current models of vegetation dynamics in mixed podocarp-hardwood forests in New Zealand incorporate disturbance as an integral factor which is vital for the long-term maintenance of podocarps (Ogden & Stewart 1995, Willems 1999). Different proposed regeneration modes include catastrophic regeneration (large scale disturbances >1000 m^2 such as mass windthrow, landslide, glaciation, vulcanism and flood, resulting in even-aged stands), gap-phase regeneration (generally single or small-group tree falls), or continuous regeneration (species regenerating continuously are generally shade-tolerant and have an all-aged population structure).

Therefore, it could be expected that as plantations age and thin, the environment becomes more suitable for native tall canopy species to establish via gap-phase or continuous regeneration. Other influences could include the time taken for birds and wind to disperse an adequate supply of seeds, coincidence of heavy seeding year and suitable climatic conditions (Cameron 1960) and fluctuations in exotic browser densities reducing the chances of seedling establishment (Cameron 1960, Hawcroft et al. 2024).

An alternative trajectory could be gap-phase or continuous regeneration is overtaken by a catastrophic disturbance to the pine stand which could favour, dependant on available seed sources, the establishment of an even-aged podocarp forest.

4.6 Seed supply

Distance to seed source was measured from the plot centre to the nearest native forest edge. This was based on known native vegetation (mapped layers) and local observations. This provided a generalised indication for distance to native seed source, noting however the limitation that species composition of the native vegetation was generally not well known. Additionally, field observations often found single or small groups of trees were providing the main local seed source and these small seed sources are not easily mapped without good local knowledge.

Seeds are spread either by wind, water, gravity, or animal dispersal, with birds playing a key role as pollinators and seed dispersers. Birds such as kererū and weka capable of dispersing larger seeds have reduced populations due to predation and food availability/forest quality (Carpenter et al. 2021, McEwen 1978; Wotton & Kelly 2012). While loss of forest habitat has been slowed, introduced mammals and changing climate need to be addressed to ensure bird populations and their associated seeding dispersing role are sustained (Lyver et al. 2008). To illustrate the disruption exotic mammals pose, a study by Carpenter et al. (2018) found 76% of hīnau seed was dispersed on islands (mainly by weka) compared with only 4% dispersal on the mainland; and seed dispersal improved with pest eradication in fenced ecosanctuaries (Iles & Kelly 2014; Bombaci et al. 2021).

Distance to native seed source can have important implications on seedling establishment. Forbes (2021) found native woody densities were greater within c. 80 m of existing native seed sources and old growth species were found in clearfells some kilometres from the nearest parent tree (e.g., rimu). Also, while Forbes (2025) did not find any significant correlation between pine understory characteristics and distance to mapped LCDB native forest, a correlation was found with percent cover of native forest within a 5-km radius of the understory survey site.

4.7 Exotic species pressure

Browser sign of deer, goats, possums and/or cattle was noted in all surveyed plot locations. The few sites where larger understory stems were absent were sites also used for stock browsing.

Herbivorous mammals can substantially alter forest composition, structure, and ecosystem function particularly on islands such as New Zealand where they were naturally absent (see Hawcroft et al. 2024). Apart from reduced biomass and palatable species diversity and recruitment, altered forest composition and structure can facilitate the expansion of non-native plants and increase forest's vulnerability to pathogens (see Hawcroft et al. 2024

Native species richness and abundance are altered through ungulate browse of the understory < 2.5cm DBH and brushtail possum browse causes increased mortality of mature stems (Wardle et al., 2001, Coomes et al., 2003a, Wright et al., 2012, Bellingham et al., 2016, Clout and Ericksen, 2000; Bellingham et al., 2020, Allen et al., 2023, Hawcroft et al. 2024, Bellingham et al., 2016; Husheer and Tanentzap, 2023; Waller et al., 2024). A number of studies on possum diet have shown marked diet preferences, with these varying according to species availability in the areas studied (e.g., Mason 1958; Fitzgerald et al. 1976, Fitzgerald & Wardle 1979; Coleman et al. 1985).

Peltzer & Nugent (2023) state that near-total reductions or eradications are likely to be needed to allow regeneration of the most preferred species, most of which have trivial contribution to carbon in old-growth forests but which could have key functional roles in succession. This highlights the importance of ensuring that forest restoration efforts are not confined to increasing carbon sequestration. Such a focus could lead to long-term loss of biodiversity and harm restoration benefits.

Other exotic species such as rats, possums and pigs potentially reduce recruitment through consumption of fruits and flowers (Nugent et al., 2000, Wilson et al., 2003). Predators of native seed dispersing animals such as birds can also reduce recruitment (Innes et al 2010, Carpenter et al 2018).

Weeds were absent or a minor component of the surveyed plot understories. Pine seedlings were noted where the native understory was absent or sparse and particularly on northern exposed aspects. Kimberley et al. (in prep, a) found that pine seedlings generally were shaded out by the planted pine stand over time. Other weeds that are shade tolerant are more of a concern as they are more likely to persist in the understory. Wild ginger and Taiwan cherry were the only other exotic weed species of concern noted in a few plots which were near housing or public road ends.

4.8 Potential succession scenario - conditional on successful pest control and proximity of seed sources

The establishment of juvenile trees plays a significant role in future canopy composition (Kobe, 1996; Pacala et al., 1996 – in Carswell et al. 2012). Key variables that can influence which species are present in the seedling tiers include forest microclimate, distance to seed source and browser pressure.

Historical land clearance ha severely affected the natural ability of regenerating forest to restore their biodiversity. For example, extensive deforestation by Polynesian fires and European farming have decimated the formerly dominant lowland conifer forests of the eastern North and South islands (Perry et al. 2012; McGlone et al. 2017; Heenan et al. 2024) which affects modern restoration initiatives due to an absence of seed sources (Carswell et al. 2007; Forbes et al.2020*)*. Hence there may be a need to plant 'seed islands' at strategic locations where mapping shows a lack of natural seed source.

Before starting any restoration or planting works, browsers need to be controlled (Norton et al, 2018).

Assuming that browser pressure is addressed and suitable seed sources are present, a maturing Tairāwhiti pine stand is likely to provide a suitable shaded, moist environment to encourage the establishment of regenerating forest species on a successional path towards a broadleaf forest. An effective transition will however take a long time (100+ years) and meanwhile the transition trajectory may be influenced by disturbance events with varying possible outcomes. This is explored further in an associated workstream modelling potential carbon and biodiversity outcomes over the long-term (Kimberley et al. in prep).

A change in land use on vulnerable steeplands from farmland and clearfell forestry to permanent forest could help address both the detrimental effects of elevated sedimentation and plantation debris on our freshwater and coastal biodiversity, local communities and infrastructure, as well as assist NZ meet its' international carbon emissions targets.

5 Conclusion

This study of *Pinus radiata* stands in Tairāwhiti surveyed stands ranging from 21 - 63 years old with a mean stand age of 37 years.

Our findings reflect those found in the associated LUCAS assessment of pine stand understory (Kimberley et al, in prep,a). Species in the understory were overwhelmingly native, with natives comprising 98.2 % of the understory stems and storing 98 % of the understory carbon. Understory carbon was only a small percentage of total carbon, averaging 22.5 tCO_2/ha which was 1.3 % of total carbon including pine canopy trees.

The Tairāwhiti understory metrics were higher than the national LUCAS metrics. This may reflect suitable biotic and abiotic conditions present in Tairāwhiti, despite the presence of browsers. Bioclimatic results indicate there are thresholds where understory growth is enhanced with optimal conditions of annual precipitation, elevation, slope aspect, seed source proximity, mean annual wind speed, mammal browse and January mean solar radiation (Forbes 2025).

The pine canopy density and age influenced a number of understory characteristics including carbon, plant species richness and diversity. Distance to native seed source also influenced seedling density and species richness. The lack of canopy species in the upper understory tiers may indicate that the forests need more time for greater plant diversity (including mature stage canopy species) to start establishing in significant numbers. Alternatively, it may indicate that appropriate seed sources are missing, that canopy understory conditions are unfavourable, or that browse pressure is not allowing native species to grow past browsing height.

With time, an aging pine canopy could develop a diverse understory that reflected the diversity of native seed supply in the local vicinity. The understory would be dominated by the pine canopy until this canopy senesced to allow the native understory to grow and increase in carbon content. The understory may replace the pine canopy with native forest cover. However, whether the native understory is likely to replace the pine canopy in terms of carbon will be determined by the presence of tall canopy species in the understory. It is feasible that the resultant native forest lacks tall canopy species and only develops a forest characterised by shrubs and sub-canopy species.

This study did not find a clear correlation between understory characteristics and browsing pressure. This may be due to widespread browser presence in the region having a prevalent effect on the development of the understory. Planting trials associated with the wider transition project may be able to provide further insights on browsing effects. Also, the different long-term trajectories of a pine to native transitioning forest depending on availability of seeds, browse pressure, and disturbances will be explored further through modelling.

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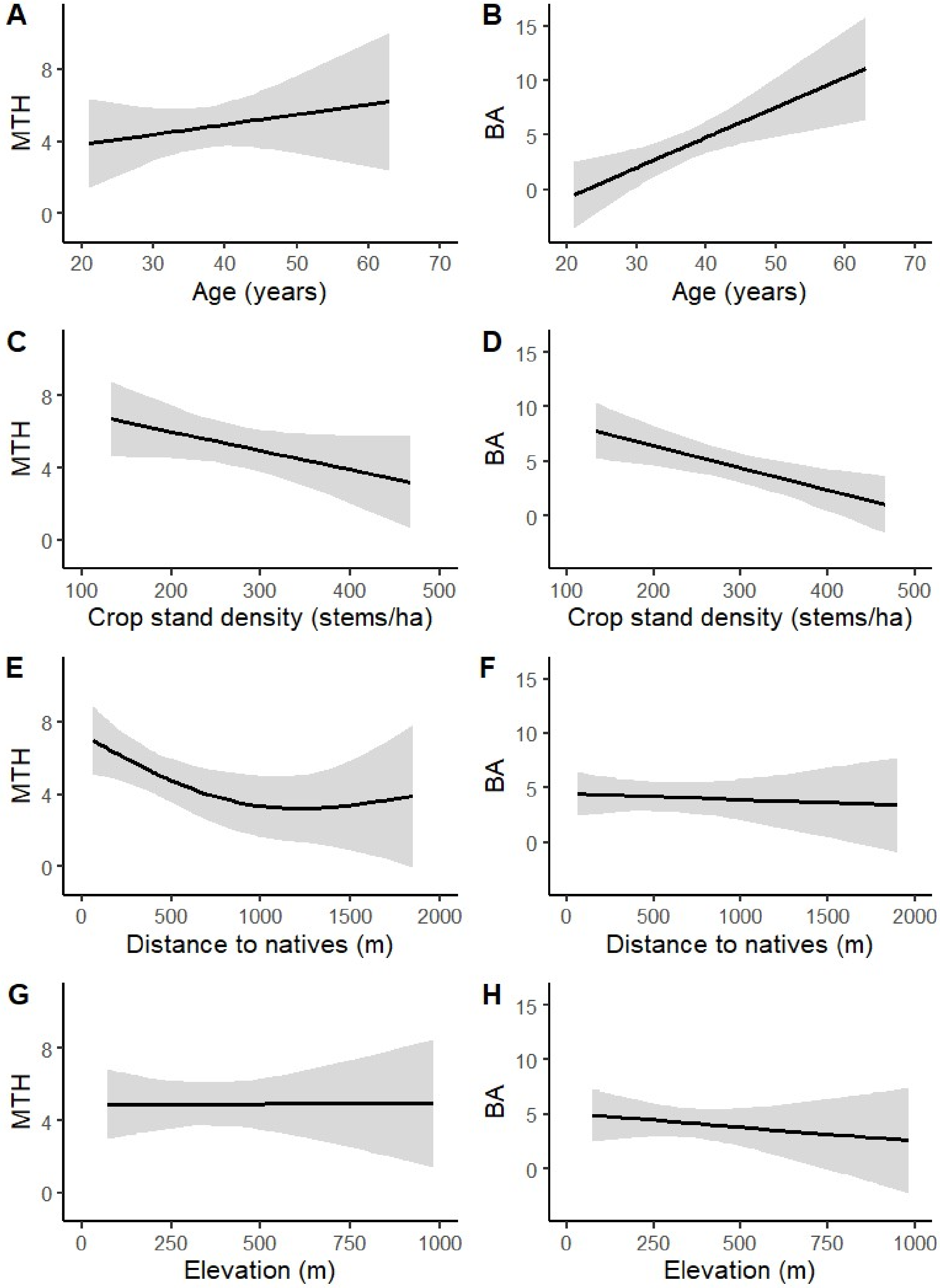
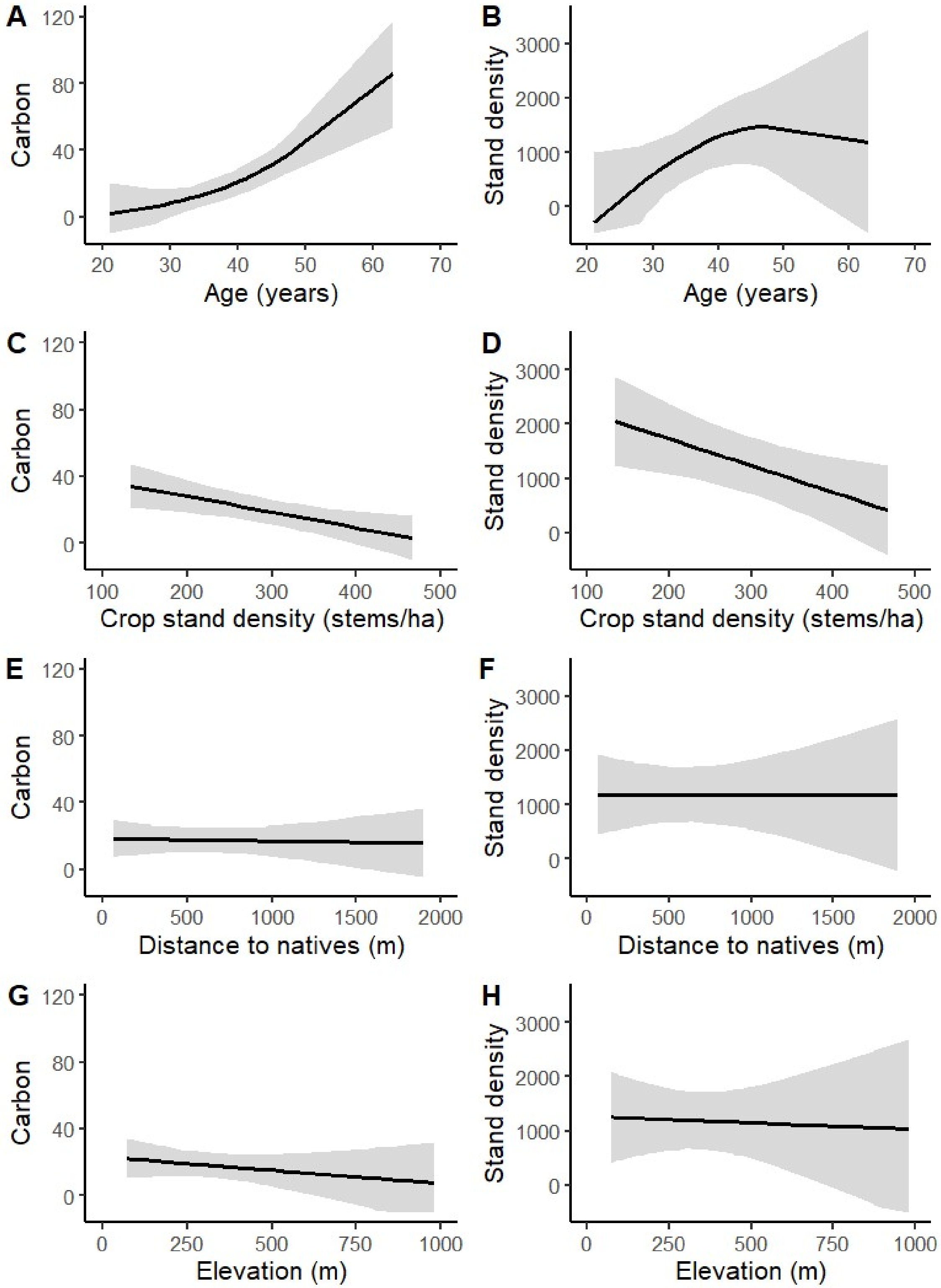
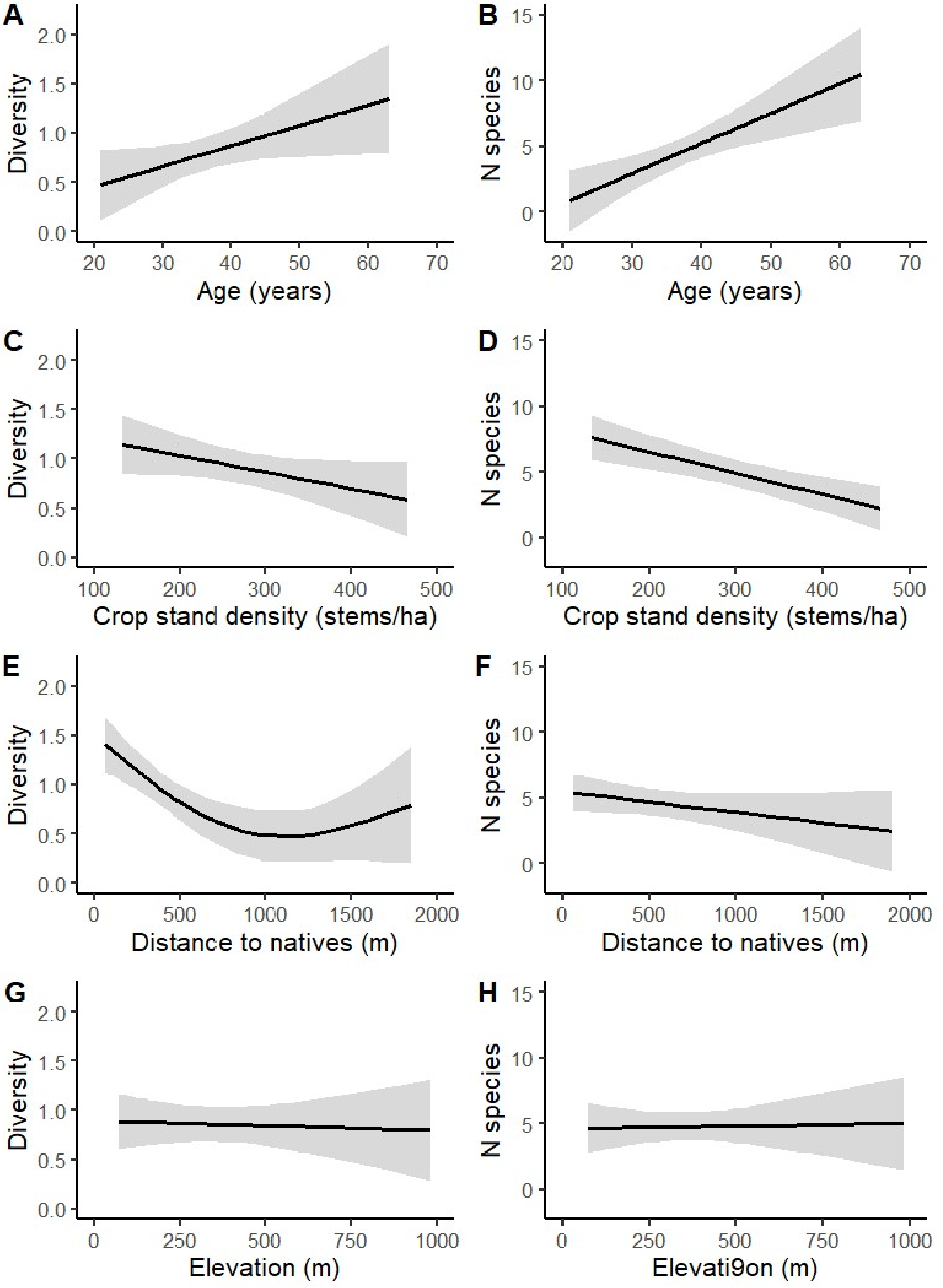
APPENDIX A: Predictions from GLMMs



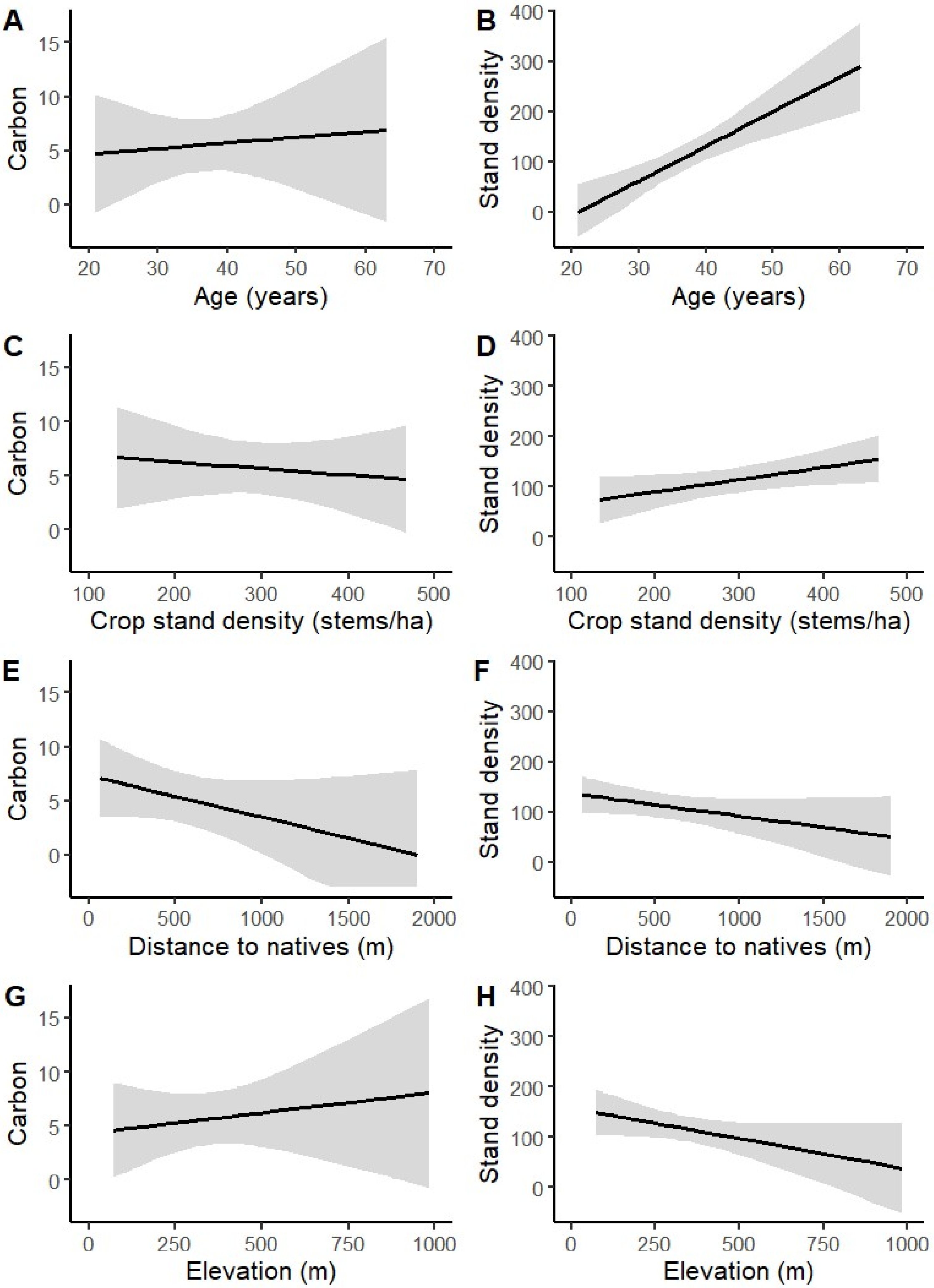
A1 *Figure A3: Predictions from Generalised Linear Mixed Models (GLMMs) of mean top height (m) and basal area (m2/ha) of understory stems ≥ 2.5 cm DBH. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.*



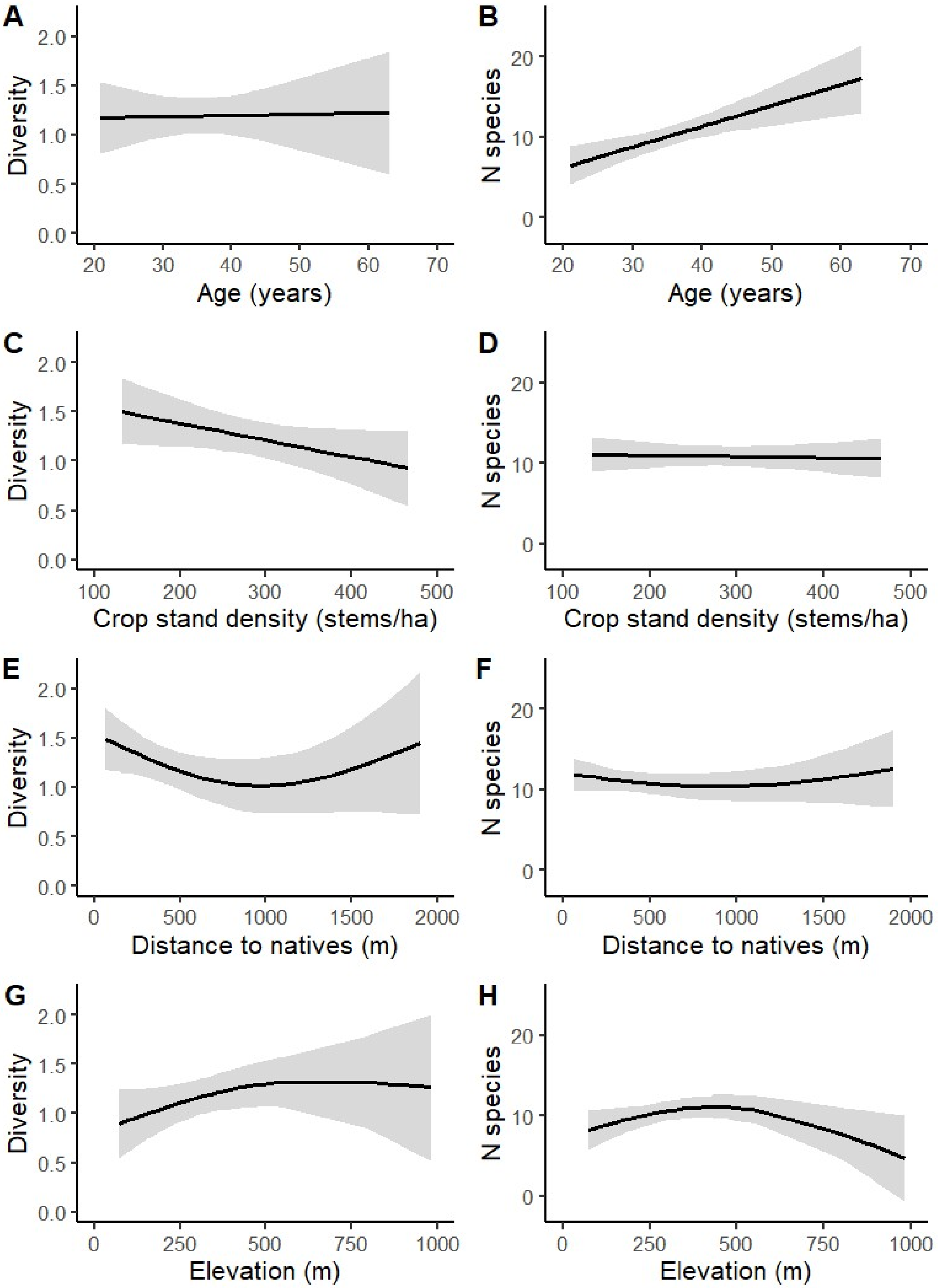
A2 *Figure A4: Predictions from Generalised Linear Mixed Models (GLMMs) of carbon (t CO2/ha) and stand density (stems/ha) in understory stems ≥ 2.5 cm DBH. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.*



A3 *Figure A5: Predictions from Generalised Linear Mixed Models (GLMMs) of Shannon diversity index and number of species per plot for understory stems ≥ 2.5 cm DBH. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.*



A4 Figure A6: Predictions from Generalised Linear Mixed Models (GLMMs) of carbon (t CO2/ha) and stand density (1000 × stems/ha) for understory stems < 2.5 cm DBH. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.



A5 Figure A7: Predictions from Generalised Linear Mixed Models (GLMMs) of Shannon diversity index and number of species per plot for understory stems < 2.5 cm DBH. Predictions are shown for each of the four independent variables with shaded areas showing 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values.