Native understory of pine plantation stands in Tairāwhiti, New Zealand

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Abstract

Aotearoa New Zealand faces dual crises of biodiversity loss and climate change. Clearfell exotic radiata pine (*Pinus radiata*) plantations were historically established in Tairāwhiti/East Coast to address erosion issues, but many plantations are now proving environmentally risky and uneconomic to harvest. Transitioning unharvested pine stands to permanent native forest may offer a sustainable long-term land-use option. This study investigated understory regeneration across 45 plots in 24 mature pine stands aged 21–63 years to evaluate transition potential and limiting factors.

Results show understory vegetation is overwhelmingly native comprising 98% of both stem number and understory carbon, dominated by secondary colonising species like twiggy coprosma, kawakawa and māhoe. However, understory carbon was only a small component of total forest carbon, including the pine canopy, averaging 22.5 t CO_2/ha or 1.6 % of total carbon. Understory carbon, stem density and species richness increased significantly with stand age and decreasing pine canopy density. Neither elevation nor distance to native seed sources significantly impacted overall metrics.

The native dominant understory height plateaued around 7 m beneath intact pine canopies and late-successional tall canopy species comprised only 1.8% of stems. Biodiversity and structural development are currently constrained by canopy shade, seed availability and widespread browsing pressure. These results suggest that successful long-term transition (>100 years) to diverse native broadleaved forest is likely to depend on active pest management, effective recruitment of native canopy species and ongoing canopy senescence.

Introduction

Aotearoa New Zealand faces the dual pressure of biodiversity loss and climate change. In Tairāwhiti, steep terrain and sedimentary geology combined with clearfell forestry and farming has led to unsustainable soil erosion (Stats NZ, 2024). Increasingly frequent storm events are further degrading freshwater and coastal ecosystems and threatening downstream communities and infrastructure.

Radiata pine (*Pinus radiata*) dominates plantation forestry in Tairāwhiti. Recent storms have exposed the limitations of clearfell exotic forestry on steep erosion-prone land and highlighted the need for changes in forest harvesting practices and alternative land-use approaches.

There is a growing interest in the potential for some exotic plantations in the region to remain unharvested and transition long term towards permanent native forest. The composition and development of native understory within pine plantations may indicate the transition potential of these forests.

This research investigates whether native understory regeneration within Tairāwhiti pine plantations is influenced by stand age, pine stem density and proximity to native seed sources. It also examines whether these understory communities indicate early stages of a transition toward native forest, and what factors may be limiting this process. The study contributes to wider research aimed at supporting the transition of unharvested exotic plantations to permanent native forest.

Methods

The study was conducted in older radiata pine stands (>20 years) across the Tairāwhiti region selected in consultation with forestry managers. Selection focused on including both inland and coastal stands, a range of distances from native forest seed sources, and a wide geographic distribution from northern to southern Tairāwhiti. Site selection was constrained by the availability of suitable older stands and by operational access and safety considerations. A total of 45 Permanent Sample Plots (PSPs) were established in 24 stands between February 2023 and August 2024 (Figure 1).

PSP establishment and measurement followed standard methods similar to those described by Kimberley et al. (2026b), with the addition of a 5.64 m radius subplot at each plot centre for sapling and seedling measurements. Stems were classified as trees (diameter at breast height or DBH ≥2.5 cm), saplings (DBH <2.5 cm and height ≥1.35 m) or seedlings (height <1.35 m). Within the main plots, all trees were recorded by species and measured for DBH and height. Within the subplots, saplings were recorded by species and height, while seedlings were counted by species within five height classes.

Understory carbon stocks, stand metrics, species richness and Shannon diversity indices were calculated using the methods described by Kimberley et al. (2026b). Carbon in saplings and seedlings was estimated from stem height (m) using the following non-linear regression model fitted to the tree data using the R nls function: Carbon (kg) = $0.00835 \times \text{Height}^{3.611}$. Relationships between understory carbon, stem density and diversity measures and stand characteristics (age, density, elevation and distance to native seed source) were analysed using Generalised Additive Mixed Models (GAMMs) with plots nested within stands (R gamm function).

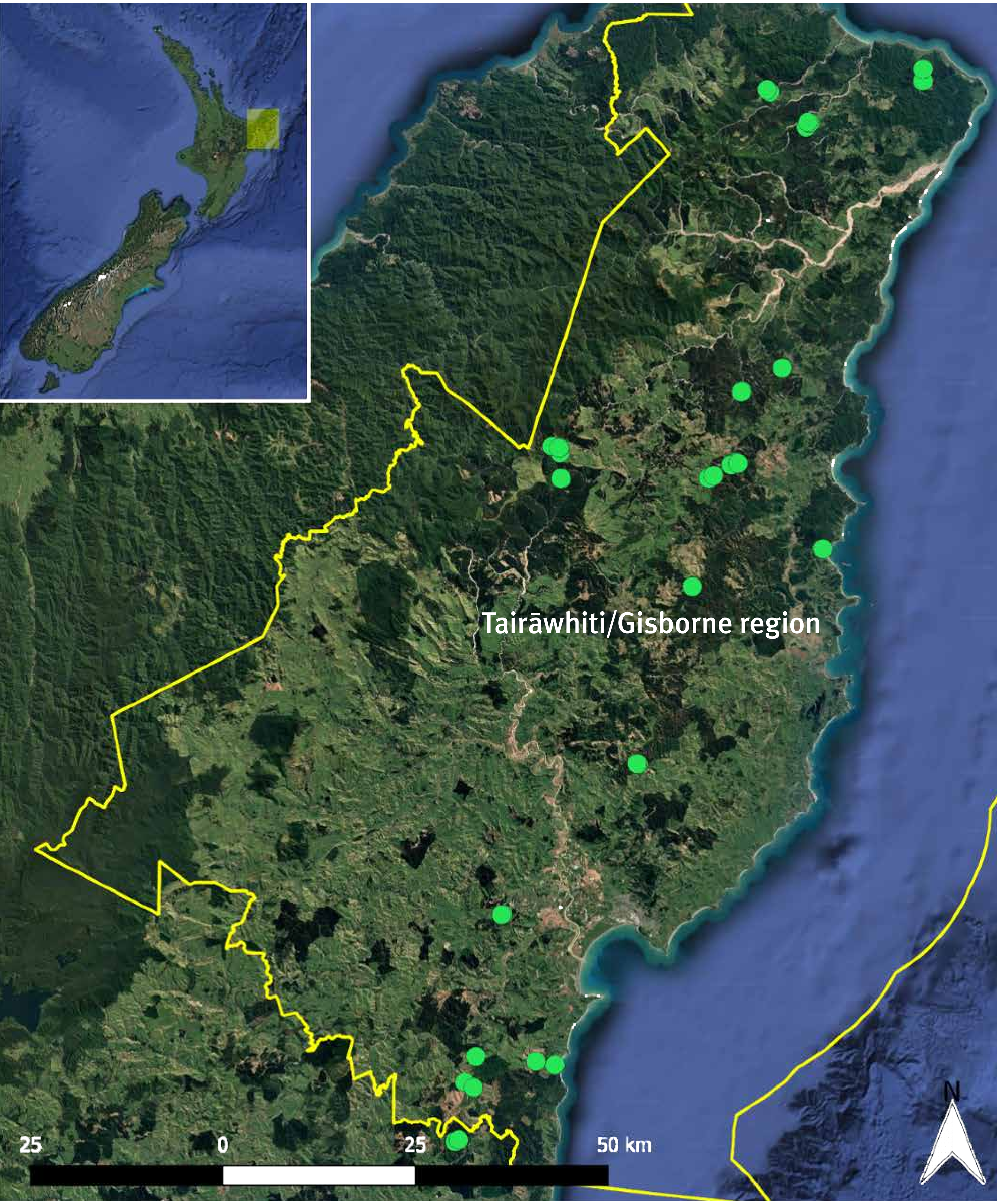

Figure 1: Survey sites in the Tairāwhiti/Gisborne region. Photo courtesy of Google Satellite

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
Pine stems	Stand density	stems/ha	310 ± 97	133–467
	Carbon	t CO_2/ha	1,353 ± 361	705–2,162
	Basal area	m²/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	m²/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	m²/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 89% being small stems <1 m tall and 97% being less than 2 m tall. However, most of the understory carbon was stored in stems 2–8 m tall (80%), with 15% stored in stems taller than 8 m and only 5% in stems less than 2 m. More than three-quarters of understory stems belonged to shrub species (76%), with most of the remainder being subcanopy tree species (21.2%) and only a small percentage being canopy tree species (1.8%), tree ferns (0.1%) and palms (0.9%).

Results

Characteristics of pine canopy trees and understory

Characteristics of the surveyed Tairāwhiti plots are summarised in Table 1. Pine stand age averaged 37 years, with an average stand density of 310 stems/ha and mean top height (MTH) of 42 m. On average, the radiata pine stands stored 1,353 t CO_2/ha. Species in the understory were overwhelmingly native, with natives comprising 98% of the stems and storing 98% of the understory carbon. Understory carbon was only a small percentage of total carbon, averaging 22.5 t CO_2/ha or 1.63 % of total carbon including pine trees.

Table 2 lists important understory species based on carbon, while Table 3 lists species in terms of stem numbers. For carbon, the most important species groups were tree ferns and subcanopy trees. For stem numbers, the most prevalent native species were common shrub species (e.g. *Coprosma rhamnoides*), with only three species – radiata pine, lilly pilly and Chinese privet – being exotic. The unpalatable *C. rhamnoides* was common, although the presence of more palatable species indicates that browsing pressure is not always high enough to totally exclude these species.

The most common canopy tree seedlings present were tawa, radiata pine, kohekohe, kahikatea and pūriri (Table 3). The only canopy species in the understory that had reached the measurable DBH size were radiata pine, pūriri, kohekohe, kamahi and rewarewa.

While the total number of native tree species per hectare averaged nearly 100,000 stems, most were highly vulnerable small seedlings and the distribution and abundance varied between forests. Many forest seedlings, particularly stems <15 cm, do not survive to reach higher vegetation tiers. However, species composition of seedling stems indicates the diversity of nearby seed sources available for future understory development should conditions favour germination and growth. The current understory community is dominated by secondary colonising species, with relatively few later successional tall canopy species as yet represented in the taller sapling and upper subcanopy stems.

Factors affecting understory stand metrics

Table 4 summarises Generalised Linear Mixed Models (GLLMs) testing relationships between understory stand metrics (carbon, stem density, Shannon diversity and species richness) and four predictor variables (stand age, pine stem density, distance to native seed sources and elevation). Predictions from these models are shown in Figure 2.

The most important stand characteristic affecting the understory was stand age with understory carbon, stem density and number of species increasing significantly with age (Figures 2a and 2b). Further GAMM models fitted but not shown in Table 4 indicated that understory basal area also increased significantly with age of pines. However, MTH did not change significantly with age, with heights of taller understory stems tending to stabilise at about 7 m in older radiata pine stands.

Pine stand density also significantly influenced the understory with understory carbon increasing with reducing stand density (Figure 2c). There was also a significant negative relationship between pine stand density and the number of species per plot for understory stems ≥2.5 cm DBH. There was an unexplained positive relationship between pine stand density and understory stem density (Table 4).

Neither distance to native seed source nor elevation were significantly related to any understory characteristic shown in Table 4 or Figure 2. However, analysis of sapling data indicated that plots closer than 1,000 m from a native seed source had a significantly higher species diversity in understory saplings.

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

Table 2: The 20 understory species with the highest carbon stocks

Māori/common name	Scientific name	Biostatus	Growth habit	Carbon (t CO_2 ha^{-1})
Mamaku	*Sphaeropteris medullaris*	Indigenous	Tree fern	3.76
Māhoe	*Melicytus ramiflorus*	Indigenous	Subcanopy tree	3.72
Ponga/silver fern	*Alsophila dealbata*	Indigenous	Tree fern	1.90
Makomako	*Aristotelia serrata*	Indigenous	Subcanopy tree	1.83
Kawakawa	*Piper excelsum*	Indigenous	Shrub	1.53
Putaputawētā	*Carpodetus serratus*	Indigenous	Subcanopy tree	1.30
Mingimingi	*Leucopogon fasciculatus*	Indigenous	Shrub	1.07
Wheki	*Dicksonia squarrosa*	Indigenous	Tree fern	0.81
Kānuka	*Kunzea robusta*	Indigenous	Subcanopy tree	0.77
Kamahi	*Pterophylla racemosa*	Indigenous	Canopy tree	0.76
Radiata pine	*Pinus radiata*	Exotic	Canopy tree	0.57
Twiggy coprosma	*Coprosma rhamnoides*	Indigenous	Shrub	0.45
Kōhūhū	*Pittosporum tenuifolium*	Indigenous	Subcanopy tree	0.44
Mapou	*Myrsine australis*	Indigenous	Subcanopy tree	0.34
Tutu	*Coriaria arborea*	Indigenous	Shrub	0.34
Kaikōmako	*Pennantia corymbosa*	Indigenous	Shrub	0.30
Pūriri	*Vitex lucens*	Indigenous	Canopy tree	0.23
Titoki	*Alectryon excelsus*	Indigenous	Subcanopy tree	0.20
Hangehange	*Geniostoma ligustrifolium*	Indigenous	Shrub	0.19
Kohekohe	*Didymocheton spectabilis*	Indigenous	Canopy tree	0.18
All other species				1.41

Table 3: Mean density in stems/ha 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)			
			Seedlings	Saplings	Trees	Total
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**
Mapou	*Myrsine australis*	Subcanopy tree	756	142	20	**918**
Niniaobells	*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**
Raurekau	*Coprosma grandifolia*	Shrub	62	0	0	**62**
Karaka	*Corynocarpus laevigatus*	Canopy tree	53	0	0	**53**
Other species			385	27	77	**489**
		Totals	**91,938**	**6,347**	**924**	**99,208**

Table 4: Results of Generalised Linear Mixed Models (GLLMs) predicting characteristics of the understory

Dependent variable	F value				Adjusted R^2
	Plantation stand age	Plantation stand density	Distance to natives	Elevation	
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

* Significant at p=0.05; ** Significant at p=0.01

Note: 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.

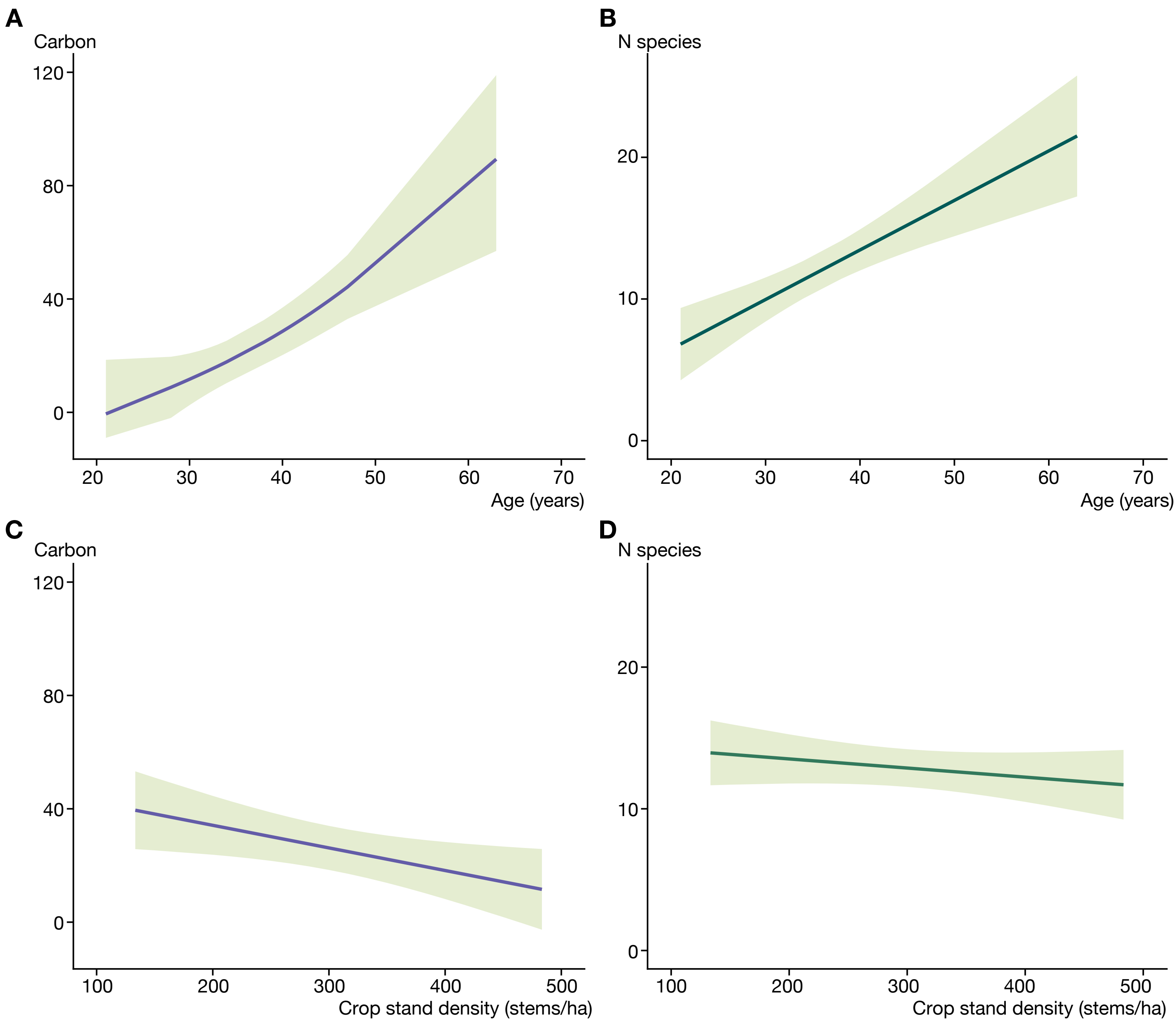

Figure 2: Predictions from GLMMs of understory carbon (t CO_2/ha) and number of understory species per plot vs crop age and stand density. Shaded areas show 95% confidence intervals. For each independent variable, predictions are made with values of other independent variables set to their mean values

Table 5: Coefficients estimates with standard errors and test statistics for a linear mixed model predicting understory carbon (t CO2/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

Combined effect of pine stand age and density on understory carbon

Table 5 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 a pine density of 200 stems/ha understory carbon is predicted to increase by 2.31 t CO_2/ha/year. Conversely, at 400 stems/ha, understory carbon is predicted to increase by only 0.63 t CO_2/ha/year.

Discussion

Effect of exotic nurse crop

Fast-growing indigenous or exotic 'nurse' crops can create sheltered micro-environments that support indigenous plant establishment (Davis et al., 2009). Young pine stands suppress light-demanding weeds with higher pine stocking densities accelerating succession from pioneer species, such as grasses, mānuka, koromiko (*Veronica stricta* var. *stricta*), to shade-tolerant secondary species (Brockerhoff et al., 2003; Ogden et al., 1997). Our results confirm this trend, showing a dominance of shade-tolerant secondary colonisers like kawakawa, māhoe, hangehange, putaputawētā and kānono.

Statistical analysis showed significant relationships between both pine stand age and stand density, and understory development. Older and gradually thinning pine stands will support increased native understory growth. However, understory height plateaued around 7 m beneath intact pine canopies suggesting further growth requires time or canopy senescence to create light gaps.

The Tairāwhiti understory metrics exceeded national averages reported from LUCAS plots (Kimberley et al., 2026b), including stem density, species richness, Shannon diversity and carbon stocks, likely reflecting the older age of these stands and favourable regional climatic conditions.

Understory species abundance, richness and diversity

The Shannon diversity index revealed a more uneven species distribution in larger understory stems (≥2.5 cm DBH) than smaller stems, indicating that while seedlings establish, many fail to reach larger size classes. These results indicate that achieving a diverse native forest transition will require both time and effective pest animal control.

Most understory carbon was associated with subcanopy tree species, followed by tree ferns and shrubs with little in canopy tree species. Because much of the long-term carbon storage, structural complexity and biodiversity value of mature native forest is associated with large canopy trees, successful recruitment of these species within the understory is likely to be important as the pine canopy gradually senesces. Although lower in number and with low carbon component now, the long age/growth spans and larger size typically attained by many canopy tree species compared to indigenous shrub/subcanopy species is expected to result in an increase in proportion of carbon contained in indigenous canopy species trees over time should they establish and grow. The number of stems currently observed may be disproportionately important despite their low representation by number and carbon content at this stage of the PSP monitoring.

Browse pressure was widespread across sites, and these results suggest that although understory carbon increases as pine canopies age and thin, succession may be constrained by browsing as well as limited native seed supply and the presence of weeds. A diverse supply of local native seed, particularly canopy species, together with low browse pressure, will be important for enabling native canopy trees to establish and eventually occupy canopy gaps. Without these conditions, gaps may instead become dominated by native shrubs and subcanopy species, or light-demanding weeds and pines, affecting both long-term carbon storage and successful transition to mature native forest.

The only canopy species reaching the larger tree stem size apart from radiata pine were pūriri, kohekohe, kamahi (a component of Other Species in Table 3) and rewarewa. Tawa, radiata pine and kahikatea were found throughout the survey plots, while kohekohe and pūriri were characteristic of the coastal lowland plots. The surveyed coastal block potentially benefited from more favourable growing conditions and/or less browse pressure as pūriri and kohekohe were common in the sapling and tree stems in these plots. Good native seed sources were nearby and natural pine windfall contributed greater overhead light and often created a barrier to browser access.

Weeds were minor with most understory pine seedlings <15 cm and likely to be shaded out over time consistent with Kimberley et al. (2026b), although shade-tolerant wild ginger (*Hedychium gardnerianum*) and Taiwan cherry (*Prunus campanulata*) posed localised concerns near housing and road ends.

Ultimately, if browser pressure is managed and suitable native seed sources are present or introduced through approaches that involve supplementary planting of native species (e.g. seed islands), maturing pine stands in Tairāwhiti are likely to provide sheltered conditions favourable for native forest regeneration and succession towards a broadleaved forest as the pine canopy opens up. However, this transition is expected to be a long-term process (>100 years), providing both increased carbon sequestration and greater biodiversity. These likely long-term carbon and biodiversity trajectories are explored further by Mason et al. (2025) and Kimberley et al. (2026a).

Conclusions

This study demonstrates that mature radiata pine plantations in Tairāwhiti can support substantial native understory development on erosion-prone hill country where clearfell harvesting may no longer be environmentally or economically sustainable. Native species overwhelmingly dominated the understory, with understory carbon, stem density and species richness increasing as pine stands aged and thinned.

However, the understory in sampled stands remains dominated by early successional native shrubs and subcanopy species, with relatively few tall native canopy species established. Understory height also appeared to stabilise beneath intact pine canopies, suggesting that any transition toward mature native forest is still at an early stage if such succession continues. As the oldest pine stands surveyed have not yet reached widespread canopy senescence, further native forest development appears possible over the coming decades.

Reducing browsing pressure may be one of the most effective immediate management actions to encourage the establishment and progression of native canopy species. Where natural seed availability is limited, enrichment planting (including strategically located seed islands) and creation of canopy gaps/light wells may help accelerate native forest development.

Continued monitoring will be important to understand how canopy senescence, native understory recruitment, and pest animal management influence future forest succession, carbon dynamics and biodiversity outcomes in unharvested pine forests managed towards permanent native forest.

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