

Transitioning Exotic Forest to Native Bioclimatic Survey Report



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Fibre Futures Fund**

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Author:

Dr. Adam Forbes
Principal Ecologist
Forbes Ecology Limited

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Cover photograph:

Mahoe and fern regeneration in a mature radiata pine plantation.

1. INTRODUCTION

1.1 Introduction

This work forms part of the wider MPI SFFF Transitioning Exotic Forest to Native project. This workstream aims to examine whether the understory vegetation composition and structure of mature stands of plantation radiata pine vary spatially, and if so, what are the drivers of variation? Ultimately, if possible, the work aims to identify thresholds in variables that could be useful for making broad management decisions about appropriateness of transitional forestry in particular biotic and abiotic circumstances.

1.2 Objectives

The workstream has the following main objectives:

1. Undertake a nationwide survey of representative exotic conifer plantation forests to assess and understand key biotic and abiotic factors and regional variations that affect regeneration of native species within such forests.
2. Examine spatial gradients and patterns at a landscape scale (e.g., relationships between regeneration and proximity to existing native forest seed sources, etc.) and stand level variables (e.g., stand structure, canopy density).
3. Empirically define management thresholds regarding levels of regeneration to understand where and why adequate regeneration is attained without specific interventions.

1.3 Limitations

Seed source data used in the analysis were LCDB v5 Indigenous Forest class. These data lack floristic detail of actual seed source composition and seed source ecology is a topic requiring more detailed study.

2 METHODS

2.1 Study area

The survey involved sampling 80 plots distributed across the following regions of mainland New Zealand (Fig. 1):

- Northland (4 plots),
- Gisborne (7 plots),
- Waikato (25 plots),
- Bay of Plenty (6 plots),
- Wellington (10 plots),
- Marlborough (12 plots),
- West Coast (6 plots),
- Otago (10 plots).

The forests surveyed were all commercially owned and rotationally managed for timber by a total of four different forestry companies. All compartments surveyed were >20-years-old.

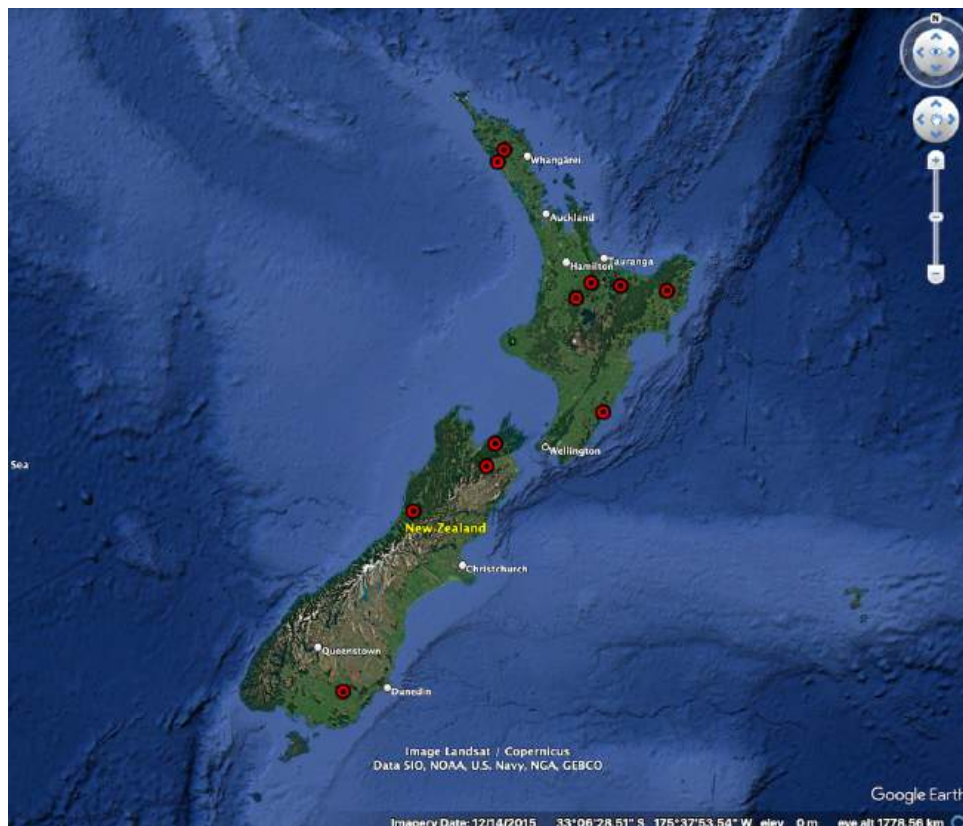


Figure 1. Generalised locations of field survey plots.

Summary statistics for the explanatory variables measured in the survey are shown in Tables 1 and 2. As described below, the survey was designed to sample along gradients of key biotic and abiotic explanatory variables. For instance, surveys were conducted across elevations from 52 to 805 m.a.s.l and across annual rainfall depths from 638 to 3252 mm/year (Table 1). Note, the LCDB5 refers to the New Zealand Land Cover Database (LCDB) classes, including five maps corresponding to five survey periods in 1996 - 2019. The LCDB5 provides a snapshot of land cover at different points in time, allowing for tracking of changes.

Table 1. Continuous explanatory variables.

Variable code	Variable	Unit	Mean	Min, Max
MN ANN WS	Mean annual wind speed	(m/s)	3.5	1.9, 4.7
JAN MEAN SRAD	January mean solar radiation	(W/m ²)	22.2	20, 23.4
JULY MEAN SRAD	July mean solar radiation	(W/m ²)	6.3	4.8, 7.7
JAN MEANT	January mean temperature	(°C)	15.9	13.5, 18.9
JULY MEANT	July mean temperature	(°C)	7.1	4.4, 11.6
T ANN PRECIP	Total annual precipitation	(mm)	1431	638, 3252
Area 5 km	LCDB5 native area within 5 km of plot centre*	(ha)	1197.7	0, 4203.2
Perc 5 km	LCDB5 native percentage within 5 km of plot centre*	(%)	15.3	0, 53.5
Area 100 m	LCDB5 native area within 100 m of plot centre*	(ha)	0	0, 0.7
Perc 100 m	LCDB5 native percentage within 100 m of plot centre*	(%)	0.6	0, 22.4
Elevation	Metres above sea level	(m.a.s.l)	370	52, 805
Slope	Slope	(°)	15	0, 41
Meso	Meso-topographic shelter index	(°)	11	1, 26
Top height	Canopy top height	(m)	28.4	15, 42.2
Pine stems	Plantation stem density	(stems/ha)	463	258, 633
Canopy cover	Canopy cover above breast height	(%)	80	40, 100

Table 2. Categorical explanatory variables.

Variable code	Description	Unit	# plots
Aspect	Dominant slope direction	(Card.dir)	N : 9
			NE :13
			E : 8
			SE : 6
			S : 5
			SW : 2
			W :15
			NW :14
			Flat : 8
Physiography	Landform units	(Landform unit)	face : 64
			gully : 3
			ridge : 7
			terrace : 6

Note: *made up of LCDB.v5 Indigenous Forest class.

2.2 Organisms studied

The focus of the survey were woody species (native and exotic) in the understories of mature *Pinus radiata* (radiata pine) plantations. Some key non-woody weed species, e.g., *Rubus fruticosus* (blackberry) were also recorded given their effect on forest regeneration and succession.

2.3 Sampling design

Vegetation sampling was conducted along elevation gradients coinciding with areas of climate gradients (as mapped by the Chappell, n.d. NIWA report series) to capture variability in climate, native seed source proximity, and a variety of other site factors (e.g., Table 1). Gradients were located based on broad areas of suitable plantation age classes, gradients of mean annual rainfall (Chappell, n.d.), and elevation contours. Along a given gradient, a subjectively located position on a contour line served as a start point from which two or three vegetation plot (10 × 10 m) locations were randomly generated. Each plot was located at the randomly generated point using a hand-held GPS unit (Garmin GPSmap 62s). Plot clusters were located at consecutive vertical separations and between 50-150 m horizontal distance from one another to achieve independence among plots without varying too far from the nominated elevation for sampling. Plot locations were excluded within 30 m of a forest edge to avoid edge effects.

Within each 10 × 10 m plot, all exotic and indigenous woody species were identified to species level and counted within specific height classes. Stem counts were assigned to height classes. Seedlings were either <15 cm (a presence/absence record made), 16-45 cm, 46-75 cm, 76-105 cm, 106-135 cm. Saplings were >135 cm and less than 2.5 cm diameter at

breast height (DBH, 1.35 m above ground level). Trees were >135 cm and >2.5 cm DBH. Trees were measured for DBH and height.

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

A set of site factors was measured at each plot. Topographic exposure (McNab, 1993) was measured at each plot centre, which required measurement of eight equidistant slope to horizon measurements. Also measured at each plot were slope aspect, slope, physiography, drainage, shape, the nature of ground cover and the percentage of canopy cover (both above and below 1.35 m above ground level). Plot elevation (m a.s.l) was determined using the hand-held GPS unit. Distance to mature indigenous forest was a desktop measure from each plot centre-point to the outside boundary of the nearest LCDB.v5 Indigenous Forest area. Area of native forest was calculated by summing the area of LCDB.v5 Indigenous Forest class within 100 and 5,000 m radiuses. Stand age, size, location and identity data were obtained from the respective forest owners.

The radiata pine overstorey was surveyed based on a 13.8 m radius circular-plot centred on each 10 × 10 m plot. The 13.8 m radius was a slope-corrected measurement determined using a range finder (Nikon Forestry Pro). Within each circular plot, radiata pine basal area was estimated using a factor 5 basal area prism. Mean radiata pine canopy height was calculated from the mean of the six tallest trees within the plot. Tree heights were measured using a Nikon Forestry Pro range finder.

Sampling yielded a number of response and explanatory variables for analysis (Tables 1 & 2).

2.4 Data analyses

Slope aspect (predominant aspect in degrees, translated into the cardinal directions: N = 337.5–22.5, NE = 22.6–67.5, E = 67.6–112.5, SE = 112.6–157.5, S = 157.6–202.5, SW = 202.6–247.5, W = 247.6–292.5, NW = 292.6–337.5, sites of $<5^\circ$ slope were assigned to the class, flat).

Native woody species stem density data were calculated by summing the number of each woody species >15 cm tall in each plot and converted to stems ha^{-1} . Where given, error terms are one standard error of the mean which were calculated in R (R Core Team 2023) using the plotrix package (Lemon et al., 2006).

The cover-abundance data for the classes: radiata pine, native woody species, tree ferns, tall old-growth species¹ and exotic species were each transformed to one importance value IV as a response variable (Allen et al., 1995). The IVs were calculated from the sum of the above cover-abundance classes with the following weighting applied to the percent cover classes: 1 = $<1\%$, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%. Therefore, IVs, integrated both horizontal and vertical dimensions of vegetation structure, with the weighting applied to express the varying degrees of cover occurring for each IV class in height tiers.

Principal Components Analysis (PCA1) was undertaken in R for the variables listed below using functions from the following packages: ggplot2 (Wickham et al., 2016), ggrepel (Slowikowski et al., 2018), devtools (Wickham et al., 2022), usethis (Wickham et al., 2023), and factoextra (Kassambara & Mundt, 2017). Eigenvalues of site scores were extracted from the PCA1 and used as a response variable in subsequent Boosted Regression Tree (BRT) analysis.

- Pine_IV
- TF_IV
- Native_IV
- TalLOG_IV
- Exotic_IV
- Total_native_stems
- Total_exotic_stems
- Native_S
- Exotic_S

¹ Tall old-growth species were miro (*Prumnopitys ferruginea*), hinau (*Elaeocarpus dentatus*), kamahi (*Weinmannia racemosa*), rimu (*Dacrydium cupressinum*), totara (*Podocarpus totara*), tawa (*Beilschmiedia tawa*), and titoki (*Alectryon excelsus*).

The BRT output provided (1) relative measures of strength of association (% contribution/relative influence; RI) between the response and predictor variables in the model, (2) a non-linear response curve (in the form of partial dependence plots²), and (3) a measure of performance from the prediction to withheld sites, calculated using k-fold cross validation (CV)³, using the `gbm.step` function of the `gbm` package (Ridgeway et al., 2013). Model optimisation involved systematically tuning the number of trees (*nt*), learning rate (*lr*), and tree complexity (*tc*) (Elith & Leathwick, 2017). Optimal model selection resulted from a combination of *tc* and *lr*, which provided >1 000 *nt*, and returned the lowest predictive deviance from the CV (mean and SE; Elith et al., 2008).

Tree ferns were included in estimates of cover but excluded from stem density counts as their inclusion would potentially overestimate the density of stems contributing to successional development.

² Partial dependence plots show how a response variable changes in relation to changes in a given predictor variable accounting for the average effects of all other variables in the model (Elith et al., 2008). Note that the partial dependence plot y-axes are not in the units of the response variable.

³ In BRT modelling, cross validation (CV) is a diagnostic technique used for model development and/or evaluation, which provides a means of testing the model on withheld portions of data (Elith et al., 2008). For a given model, the model CV (and SE) expresses the mean change in predictive deviance calculated over all stages in the stepwise model building process (Elith et al., 2008).

3 RESULTS

3.1 Response variable summary statistics

Summary statistics for the response variables measured in the survey are shown in Table 3.

Table 3. Summary statistics for response variables

	Pine IV	TF IV	Native IV	Tall OG IV	Exotic IV	Total native stems	Total exotic stems	Native S	Exotic S	PCA1	Browse
	(IV)	(IV)	(IV)	(IV)	(IV)	(stems/ha)	(stems/ha)	(S)	(S)		#plots (%)
Min	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-4.9	bare : 6 (7.5)
1st Qu	7.8	0.0	5.5	0.0	0.0	600	0.0	4.0	0.0	-1.4	none : 6 (7.5)
Median	10.0	3.0	11.0	0.0	1.0	2350	0.0	6.0	1.0	-0.1	light : 6 (7.5)
Mean	9.4	4.0	12.8	0.5	2.3	3945	225	6.2	0.8	0.0	medium : 7 (8.5)
3rd Qu	11.0	6.0	20.3	0.0	4.0	6625	0.0	8.0	1.0	1.3	heavy : 55 (69)
Max	19.0	17.0	33.0	8.0	13.0	18600	5000	19.0	5.0	4.1	

3.2 Associations among continuous explanatory variables

Associations among continuous explanatory variables are shown in Figure 2. Of note are the significant associations between:

- July mean solar radiation and July mean temperature ($r = 0.57$, $p = <0.01$),
- Total annual precipitation and area of native cover within a 5 km radius ($r = 0.72$, $p = <0.01$),
- July mean annual temperature was negatively associated with elevation ($r = -0.47$, $p = <0.01$).

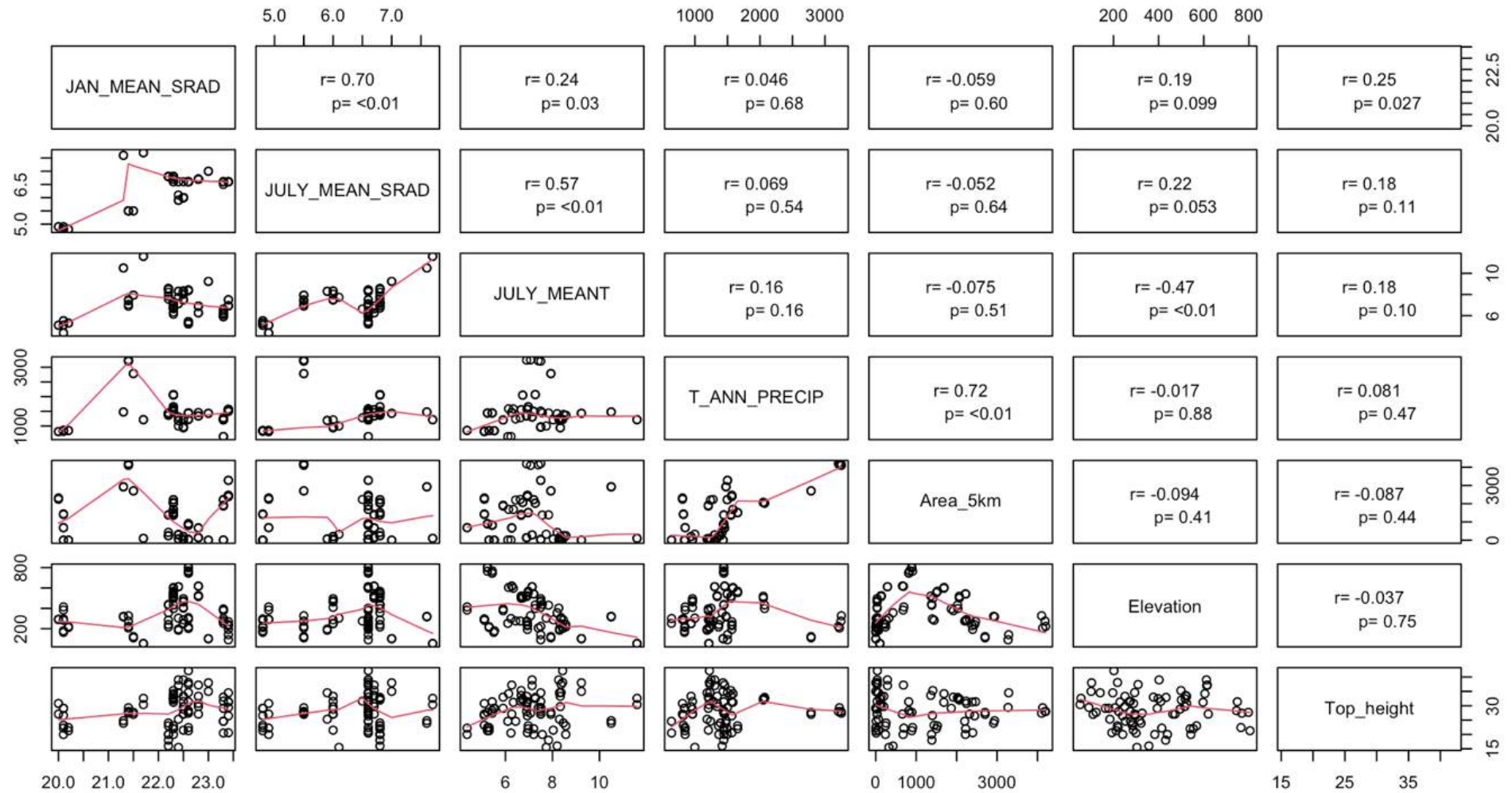


Figure 2. Associations among continuous explanatory variables.

3.3 Principal Component Analysis Ordination

Principal components 1, 2 and 3 explained 35%, 19% and 14% of the variation, respectively (Fig. 3).

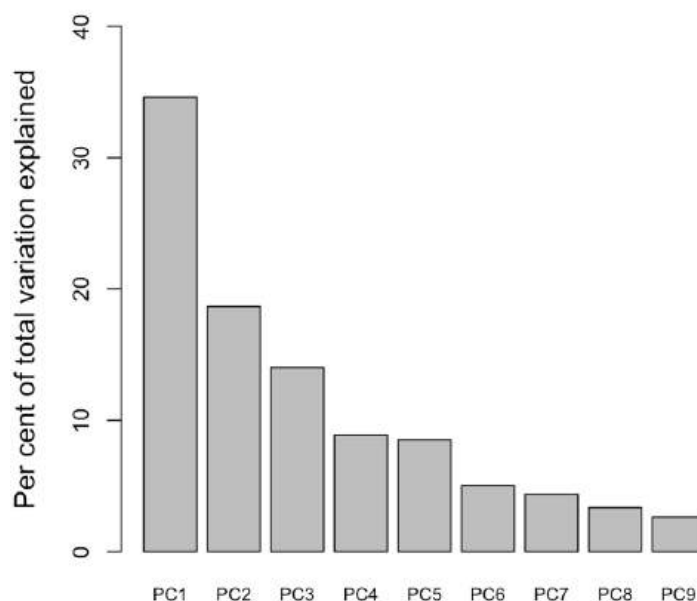


Figure 3. Percentage variation explained by each dimension of the PCA ordination.

Positive differences along PC1 are driven by native IV (0.81), native S (0.78) and total native woody stems (0.73; Table 4). These three variables are highly positively correlated in multivariate space (Fig. 4A). Exotic IV (-0.58) and Exotic S (-0.62) are negatively correlated along PC1. These groupings of native separate from exotic response variables indicate a level of organisation regarding native versus exotic dominance in plantation understories (Fig. 4A). Principle Component 2 (Fig. 4B) is dominated by total exotic stems (0.72) and PC3 is dominated by Pine IV (0.78; Fig. 4C).

Table 4. PCA loadings indicating the strength of correlation of response variables with a given PCA axis

Response variables	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9
Pine_IV	0.09752841	-0.4345525	0.77903797	-0.2431898	0.14876303	-0.2696039	-0.0954424	0.13980834	-0.1101753
TF_IV	0.5429334	0.4899414	-0.3054652	-0.1994669	-0.3814343	-0.4064107	0.05622669	0.05398515	-0.123883
Native_IV	0.80498699	0.2744907	0.13918538	0.06165067	0.12974715	0.33312347	0.17619247	0.14989216	-0.2686268
Tall OG_IV	0.47683753	-0.1334006	0.38557039	0.58414114	-0.4982681	0.01148343	-0.1176757	-0.0360372	0.0373585
Exotic_IV	-0.5756949	0.4543669	0.26290191	-0.3242292	-0.3875503	0.24340919	-0.1208199	0.23507044	0.09265739
Total_native_stems	0.72989973	0.3829359	-0.0269225	-0.1228921	0.22924894	0.0568246	-0.4834014	-0.1173512	0.03933021
Total_exotic_stems	-0.260186	0.7167645	0.1761834	0.41006949	0.35746421	-0.199517	0.05138663	0.18923108	0.11540223
Native_S	0.78383561	0.1426997	0.34452627	-0.2535547	0.00651157	0.02439623	0.28656502	-0.1322842	0.28634594
Exotic_S	-0.6226383	0.5207912	0.41635315	-0.0197999	-0.0372555	-0.0014956	0.05606808	-0.3653562	-0.1712805

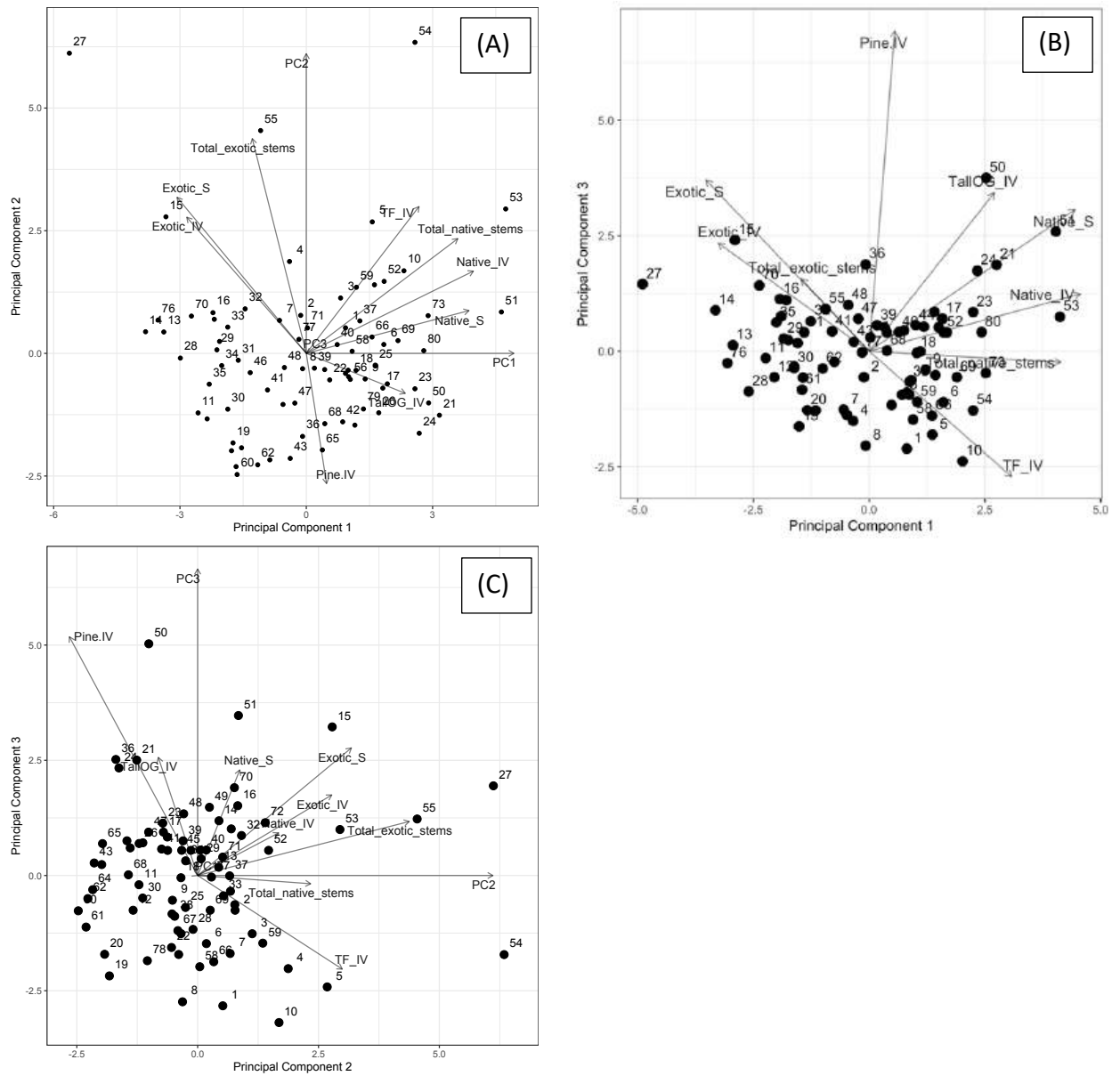


Figure 4 A-C. PCA ordination plots for (A) PC1 and 2, (B) PC1 and 3, and (C) PC2 and 3.

3.4 BRT modelling

Relative influence of explanatory variables

The explanatory variables showing the greatest influence (i.e., $\geq 20\%$ relative influence) in explaining variation in the response variables were total annual precipitation, elevation, and aspect (Table 5). Other explanatory variables of elevated importance (10 to 19%) were top height, mean annual wind speed, and January mean solar radiation (Table 5). Remaining explanatory variables were of relatively less influence (i.e., all $< 10\%$) over the response variables.

Table 5. Relative influences of explanatory variables on Boosted Regression Tree models for three main response variables

Native woody stem density		Native woody species richness		PCA1 score	
Variable	rel.inf (%)	Variable	rel.inf (%)	Variable	rel.inf (%)
T_ANN_PRECIP	20.1	Elevation	31.8	T_ANN_PRECIP	22.5
Top_height	16.8	Aspect	22.0	JAN_MEAN_SRAD	12.2
MN_ANN_WS	15.4	Top_height	12.4	Elevation	7.3
Aspect	14.7	Area_5km	6.7	JULY_MEANT	5.8
Browse	9.5	T_ANN_PRECIP	6.4	Area_5km	5.7
Elevation	7.1	JAN_MEANT	4.4	Top_height	5.0
JULY_MEANT	6.2	JULY_MEANT	4.3	MN_ANN_WS	3.7
JULY_MEAN_SRAD	5.9	Slope	4.1	JAN_MEANT	3.5
Area_5km	1.5	Pine_stems_ha	2.1	Pine_stems_ha	3.3
Slope	0.9	MN_ANN_WS	1.5	Slope	2.5
Pine_stems_ha	0.7	Meso	1.3	Canopy_cover	1.6
Meso	0.6	JAN_MEAN_SRAD	1.0	Meso	1.5
JAN_MEANT	0.6	Browse	0.7	JULY_MEAN_SRAD	1.3
JAN_MEAN_SRAD	0.0	Canopy_cover	0.6	Browse	1.0
Perc_5km	0.0	JULY_MEAN_SRAD	0.5	Perc_5km	0.3
Area_100m	0.0	Perc_5km	0.3	Physiography	0.1
Perc_100m	0.0	Physiography	0.0	Area_100m	0.0
Physiography	0.0	Area_100m	0.0	Perc_100m	0.0

Explanatory variable partial dependence response curves

All response variables responded positively to increases in total annual precipitation between approximately 1,200 and 1,500 mm, after which there was no additional influence of increasing precipitation on the response variables.

Response variables responded positively to increasing elevation between approximately 200 and 500 m.a.s.l, with optimum conditions ≥ 500 m.a.s.l.

Slope aspects ranging southeast through southwest were most favourable for all response variables. Response variables were least favourable on slope aspects west through north, and flat sites.

All response variables increased with increasing stand top height between heights of c. 25 and 35 m tall, with no additional influence of top height at heights above 35 m.

The native woody *S* and PCA1 response variables showed positive associations with increasing native cover in the landscape up to approximately 2,500 ha within a 5 km radius (7,854 ha area), which equates to increases in these response variables in landscapes ranging up to 32% native cover.

Native woody stem densities declined when wind speed exceeded c. 3 m/s.

Native woody *S* responded positively to increases in July mean solar radiation and July mean temperature from 6.5 to 7°C and 6 to 8°C, respectively.

Native woody stem densities were highest where browse was no more than light and lowest when subjected to heavy levels of browse.

The PCA1 response indicated a negative association with January mean solar radiation at values approximately >22.5 Watts/m².

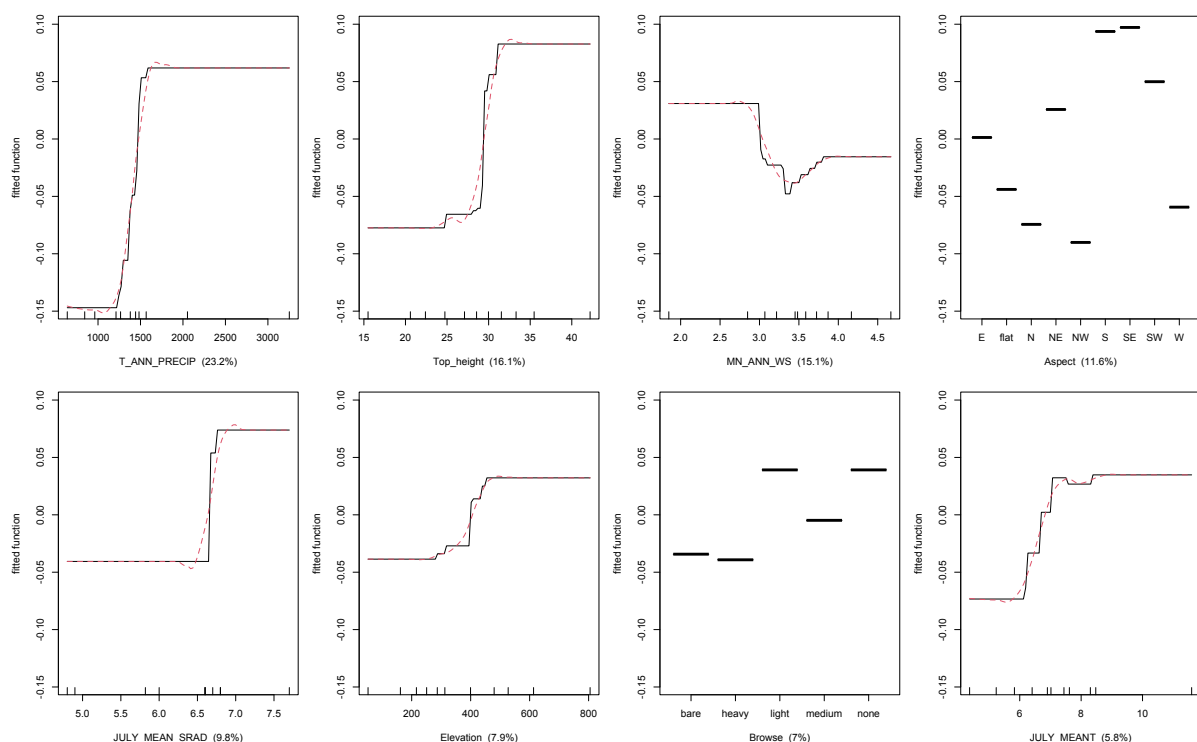


Figure 5. Partial dependence plots showing the relative influence of explanatory variables for the response variable native woody stem density.

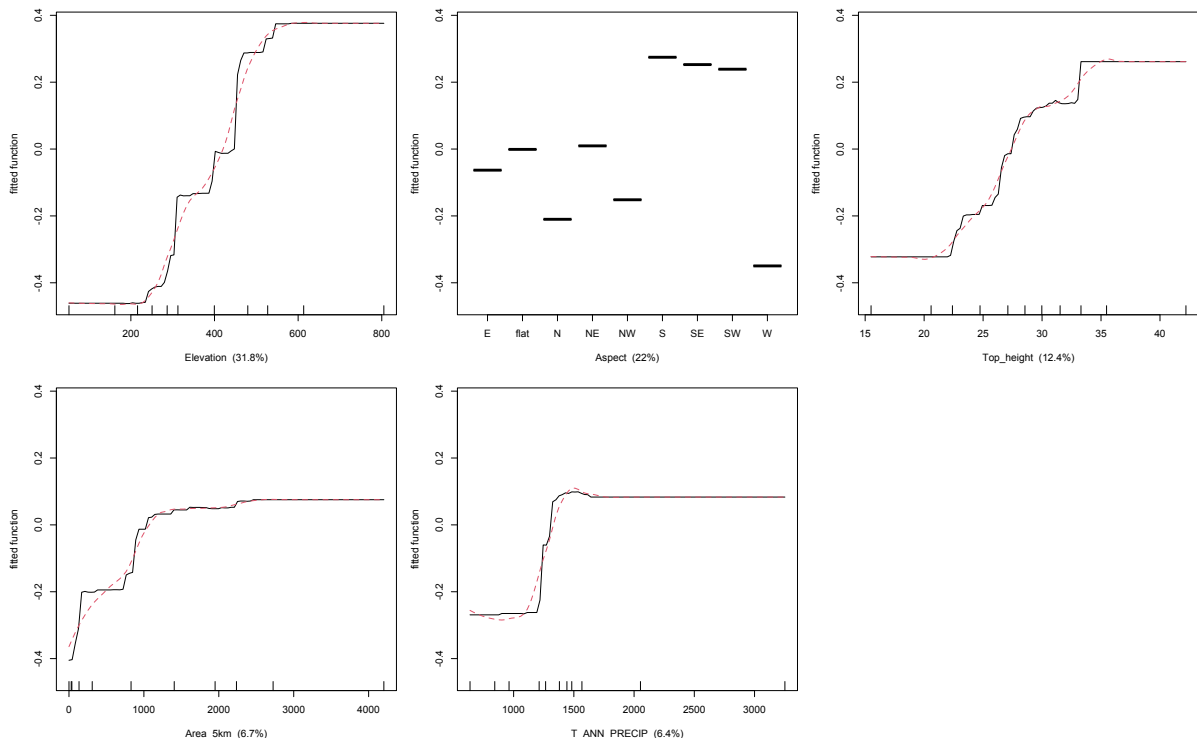


Figure 6. Partial dependence plots showing the relative influence of explanatory variables for the response variable native woody species richness.

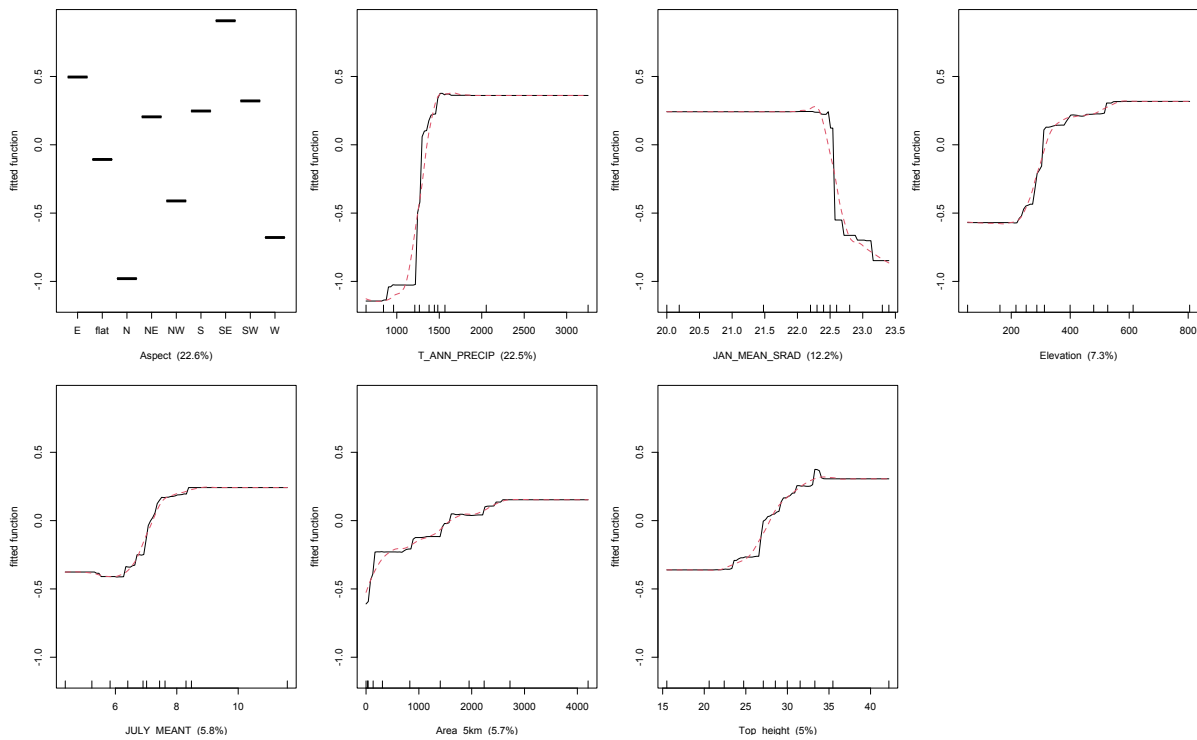


Figure 7. Partial dependence plots showing the relative influence of explanatory variables for the response variable PCA1 score.

BRT interactions

Models for total native woody stem density and native woody species richness had only minor interactions that are unlikely to be of consequence for interpretation of the model outputs. This is indicated by the magnitude of the interaction sizes listed for pairwise comparisons of explanatory variables for each of the three BRT models (Tables 6, 7, & 8).

The main interaction of interest was in the PCA model between the explanatory variables total annual precipitation and January mean solar radiation (Table 8; Fig. 8). At high levels of January solar radiation, total annual precipitation had much less effect on PCA scores compared to PCA scores in locations of less January solar radiation where increasing rainfall positively influenced PCA score. High levels of January solar radiation somewhat masked the influence of increasing total annual rainfall (Fig. 8).

Table 6. Pair-wise analysis of interactions among explanatory variables in the native woody stem density BRT model.

Variable #	Variable name	Variable #	Variable name	Interaction size
13	Aspect	6	T_ANN_PRECIP	0.63
16	Top_height	13	Aspect	0.36
11	Elevation	3	JULY_MEAN_SRAD	0.3
6	T_ANN_PRECIP	1	MN_ANN_WS	0.23
11	Elevation	7	Area_5km	0.15
19	Browse	1	MN_ANN_WS	0.13
19	Browse	13	Aspect	0.1
16	Top_height	6	T_ANN_PRECIP	0.1
7	Area_5km	3	JULY_MEAN_SRAD	0.1
6	T_ANN_PRECIP	5	JULY_MEANT	0.08
13	Aspect	1	MN_ANN_WS	0.06
19	Browse	11	Elevation	0.04
16	Top_height	7	Area_5km	0.04
16	Top_height	1	MN_ANN_WS	0.04
16	Top_height	5	JULY_MEANT	0.03
16	Top_height	3	JULY_MEAN_SRAD	0.03
5	JULY_MEANT	3	JULY_MEAN_SRAD	0.03
19	Browse	7	Area_5km	0.02

Table 7. Pair-wise analysis of interactions among explanatory variables in the native woody species richness BRT model.

Variable #	Variable name	Variable #	Variable name	Interaction size
13	Aspect	11	Elevation	4.46
11	Elevation	6	T_ANN_PRECIP	1.98
11	Elevation	7	Area_5km	1.3
13	Aspect	6	T_ANN_PRECIP	0.91
11	Elevation	5	JULY_MEANT	0.87
16	Top_height	13	Aspect	0.83
13	Aspect	7	Area_5km	0.7
11	Elevation	4	JAN_MEANT	0.68
16	Top_height	6	T_ANN_PRECIP	0.57
7	Area_5km	5	JULY_MEANT	0.52
14	Slope	11	Elevation	0.5
13	Aspect	5	JULY_MEANT	0.43
7	Area_5km	4	JAN_MEANT	0.42
13	Aspect	4	JAN_MEANT	0.38
6	T_ANN_PRECIP	1	MN_ANN_WS	0.23
16	Top_height	7	Area_5km	0.19
16	Top_height	11	Elevation	0.18
14	Slope	13	Aspect	0.17

Table 8. Pair-wise analysis of interactions among explanatory variables in the PCA1 BRT model.

Variable #	Variable name	Variable #	Variable name	Interaction size
6	T_ANN_PRECIP	2	JAN_MEAN_SRAD	15.32
13	Aspect	11	Elevation	12.75
17	Pine_stems_ha	13	Aspect	11.49
13	Aspect	6	T_ANN_PRECIP	9.46
6	T_ANN_PRECIP	1	MN_ANN_WS	6.65
13	Aspect	2	JAN_MEAN_SRAD	5.48
13	Aspect	4	JAN_MEANT	4.1
11	Elevation	5	JULY_MEANT	2.95
13	Aspect	7	Area_5km	2.7
16	Top_height	13	Aspect	2.29
13	Aspect	5	JULY_MEANT	2.22
16	Top_height	2	JAN_MEAN_SRAD	2.01
3	JULY_MEAN_SRAD	2	JAN_MEAN_SRAD	1.37
16	Top_height	6	T_ANN_PRECIP	1.35
6	T_ANN_PRECIP	3	JULY_MEAN_SRAD	1.24

17	Pine_stems_ha	2	JAN_MEAN_SRAD	1.1
16	Top_height	14	Slope	1.03
17	Pine_stems_ha	14	Slope	0.92

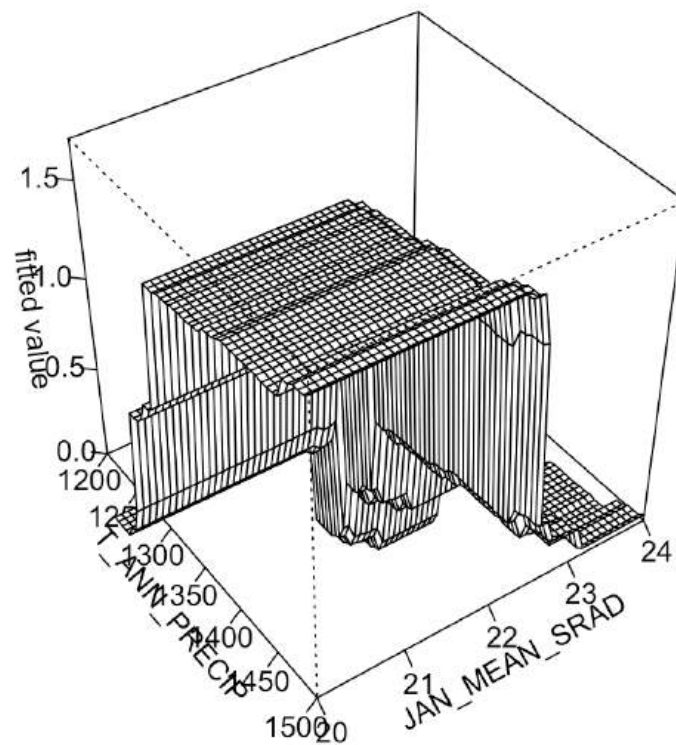


Figure 8. Boosted regression tree interaction plot illustrating the interaction between total annual precipitation and January mean solar radiation in the PCA1 model.

4 DISCUSSION

4.1 Factors shaping native understorey regeneration across New Zealand

Native understorey regeneration within mature radiata-pine plantations sampled in eight regions between Northland and Southland varied according to differences in climate, landscape-scale seed source availability, and physiographic site factors. The climate variables total annual precipitation, mean annual wind speed, and January mean solar radiation had most influence over native response variables. The site factors elevation and aspect had most influence, and plantation top height and the amount of indigenous forest located within a 5-km radius were both important biotic variables.

Climate has been demonstrated in other studies to strongly influence natural native tree establishment and native forest biomass (Mason et al., 2013; Mason et al., 2012). The results presented here suggest that the potential for adequate native understorey composition and structure will be limited at sites receiving less than approximately 1,200 mm/year of precipitation. The results show that understorey regeneration is indicated to respond positively with increasing rainfall amounts up to 1,500 mm/year, and beyond which, the benefit of increasing rainfall plateaus. Mason et al., (2013) had a similar finding for rainfall with the additional finding that the probability of tree establishment increased again at around 5,000 through to 8,000 mm/year precipitation.

Sites receiving high levels ($>c. 22.5 \text{ Watts/m}^2$) of solar radiation in summer and those that are more windy (annual wind speed $> c. 3 \text{ m/s}$) are indicated to be detrimental to the measures of native understorey regeneration. High levels of summertime solar radiation mask the beneficial effect of increasing rainfall rates. In their national assessment of the probability of natural tree establishment, Mason et al., (2013) found mean annual temperature, mean annual rainfall, and mean annual solar radiation to strongly influence predictions of tree establishment. The latter two variables are consistent with results presented here; however, collected data indicate temperature to be less important compared to other variables controlling understorey regeneration. Perhaps the less important role of temperature is due to the data being derived from the sheltered understories of existing forests whereas Mason et al., (2013) data were from non-forested (i.e., less buffered) land areas.

The strong influence of both elevation and aspect over native forest regeneration is consistent with the existing literature (Forbes et al., 2021; Murphy et al., 2015; Dong et al., 2018; Wilson, 1994; Wardle, 1964). Our results indicate that native understorey regeneration will be limited below 200 m.a.s.l, and will increase with increasing elevation up to 600 m.a.s.l, above which no further benefit of increasing elevation is indicated. The

finding of more favourable conditions for native understorey development on slope aspects ranging southeast through southwest (and least favourable from north through western aspects, and on flat sites) is consistent with existing knowledge over the effects of slope aspect on microclimate conditions and the resulting effect on forest regeneration processes.

Plantation stand structure has long been demonstrated to have strong influences over plantation understorey composition and structure through its control over forest microclimate conditions, in particular the degree of light transmission (Forbes et al., 2019; Brockerhoff et al., 2003; Ogden et al., 1997). Presented data show plantation mean top height to have some influence over understorey regeneration. The actual cause of this influence is not clear from these data; however, it may be due to age (i.e., taller trees being older; older forests having more time for understorey development) or factors limiting pine tree growth (e.g., climate or soil limitations) also being expressed in limitation of the plantation understorey development.

The role of seed source amount (ha) has been assessed at two scales and the larger-scale measure was of most influence over understorey regeneration. The apparently limited importance of nearby seed sources is strongly inconsistent with the existing literature (Canham et al., 2014; Wotton & Kelly, 2012) and is probably due to there being few nearby (within 100 m of each survey plot) seed sources around the plot locations. This work highlights this as a limiting characteristic of commercial scale, radiata-pine plantations where native understorey development is an objective. Because commercial plantations are often extensive in area, it will be common to have few opportunities for close proximity seed sources.

The data indicate that native understorey regeneration will be more diverse when the surrounding landscape within a 5 km radius of the given location is covered in more than 30% native forest cover. This value aligns with ecological theory (species-area relationship; Gleason, 1922) and Land Environment classification (Walker, 2006) and resulting policy (e.g., MfE, n.d) of New Zealand's land area based on the percentage of native cover remaining with areas less than 20% in native cover being most threatened and ecologically dysfunctional (i.e., Acutely and Chronically Threatened Environments). The data on the role of native seed sources at the landscape scale furthers our understanding of how seed sources function at large scales as sources of propagules for regeneration and succession in New Zealand's exotic plantations. As there is often no immediate seed source in an exotic conifer plantation (and often no proximal seed source), the dynamics of dispersal are critical and are undoubtedly a limiting factor on understorey composition and structure. This is further supported by these results.

Browse by introduced mammalian herbivores (mainly possums, deer, goats, pigs, and domestic stock) is well known to be detrimental to native regeneration and succession

(Wright et al., 2012). This is through the effects of preferential browsing and the resulting filtering of forest compositions and through the direct disturbance to forest understoreys, especially to the seedling and sapling tiers from browsing mammals (Wardle et al., 2001). The results are consistent with the existing literature in this regard. Anything more than light levels of browse adversely affected native understorey response variables. Exotic plantations tend to provide very favourable refuge for feral deer, especially in landscapes near pasture where deer can readily emerge from the plantation to graze. This means exotic plantations would require particular effort in culling programmes if exotic mammal populations are to be effectively controlled.

4.2 Application for transitional forestry

The presented results show that native understorey regeneration structure and composition is organised along gradients of key biotic and abiotic variables that operate at multiple scales. Where a forestry approach is reliant on natural forest establishment, some locations, based on their biotic and abiotic characteristics, will perform better than others. These results also show that browsing mammals have the potential to curtail native regeneration in the understorey of an exotic tree plantation, which is concerning given the high and, in some cases, growing populations of browsing mammals currently in New Zealand (Moloney et al., 2021).

The results provide a strong indication that transitional forests are unlikely to be successful in many locations (based on factors such as climate, topographic factors, stand age and structure, the amount of native forest within a 5-km radius). Success will also be unlikely in any location where browsing mammal populations are impacting native understorey vegetation.

Optimal conditions for the explanatory variables included in the BRT modelling regeneration are listed in Table 9. At this point these variables can be used to identify optimum conditions for transitional forestry. A next step would be to attempt mapping of a revised version of the BRT models⁴ to provide a spatial representation of response variable performance at the landscape scale. For instance, how do the BRT predictions of woody native stem density or woody native species richness vary spatially when applied to actual landscapes?

⁴ Models would need to be confined to only include variables that can be predicted from existing datasets. For example, there is no quantitative spatial data layer for browse intensity so it would need to be removed from the model.

Table 9. Indicative optimal conditions for native response variables modelled through this study

Explanatory variable	Unit of measurement	Indicative optimal value
Total annual precipitation	mm/year	≥ 1,500
Elevation	m.a.s.l	≥ 500
Slope aspect	Cardinal direction	SE to SW
Seed source proximity	% cover native forest within 5-km radius	≥ 30
Mean annual wind speed	m/s	< 3
Mammal browse	REECE browse categories	≤ Light
January mean solar radiation	Watts/m ²	< 22

The bigger and more challenging question yet to be resolved is what level of understorey regeneration will be adequate to achieve sufficient native understorey to enable a reliable transition to native forest? This is a question on which there is currently no consensus view, but it is an important topic needing scientific data and interpretation.

Currently, assessments of regeneration potential/resilience are based on site-specific assessments of site abiotic conditions, land use history (level of degradation), biotic interactions (competition, disturbance by browsers), landscape context (surrounding matrix), coupled with an element of judgement of native stem densities occurring and the composition of the seedling bank (e.g., Forbes, 2021a; Forbes, 2021b; Forbes et al., 2021; Prach et al., 2020; Holl & Aide, 2011). Considerations over levels of competition with environmental weeds and other management factors such as browser control will always need to be site-based observations. Even with thresholds developed, site-specific assessment and validation will be essential.

The data show that measures of native understorey development will vary even within sites (e.g., north facing slopes and ridges vs. sheltered gullies and lower south-facing slopes), so thresholds would need to accommodate this level of variability. Which measure(s) (e.g., native woody stem density, native species richness, canopy cover, life forms) and at what quantities are critical questions needing to be addressed to fully resolve the question over management thresholds to inform decisions over the appropriateness of a site for transitional forestry.

5 CONCLUSIONS AND RECOMMENDATIONS

5.1 Conclusions

Sampling mature radiata-pine plantation understories along elevation gradients in eight regions between Northland and Southland revealed relationships among native understory response variables and a collection of biotic and abiotic explanatory variables. Response curves presented in partial dependence plots show the shapes of relationships in terms of the contribution of individual explanatory variables to response variables. Interpretation of these curves, with support from other analyses presented herein, provide an indication of optimal conditions for transitional forestry. What is not known is whether, in those optimal conditions, regeneration would be adequate to secure a transition from exotic to native forest.

5.2 Recommendations

Recommendations are made below for further work:

- Undertake mapping of a version of the BRT models to apply the predictions across digital elevation models (DEMs) and ground truth the predictions to check their accuracy. This should be undertaken at multiple sites and scales.
- Undertake further work on determining the level and characteristics of regeneration required to secure a transition from exotic to native forest.

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