# Carbon stock modelling of transition forests

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# Summary

## Introduction

- The Parliamentary Commissioner for the Environment contracted Manaaki Whenua-Landcare Research to estimate the carbon storage consequences of various transition forest (forests managed for transition from exotic forestry plantations to native forest) management scenarios.

## Background

- There is considerable uncertainty about carbon stocks in transition forests.
- An almost total lack of relevant quantitative, empirical data means that fit-for-purpose forest growth models are required to provide preliminary estimates of potential carbon stock changes, while clearly stating the assumptions and caveats associated with the models.
- We applied two separate models that have already been parameterised for New Zealand conditions, Physiological Processes Predicting Growth (3-PG) and Perfect Plasticity Approximation (PPA), to simulate, respectively, exotic and native carbon pools under a variety of transition forest scenarios.

## Objectives

- To apply the 3-PG model (for the exotic plantation component of transition forests) and the PPA model (for the native component) to assess the consequences of different transition forest scenarios on native and total (native + exotic) carbon stocks.
- To explore the effect of interactions between transition forest management choices (deliberate exotic canopy disturbance, identity of exotic canopy species, planting of native canopy dominant) and site variables (climate, slope, and amount of native forest in the surrounding landscape) on native and total carbon stocks.

## Methods

- A balanced sample of 100 sites on which to perform simulations was selected from within the potential distribution of *Pinus radiata* and *Eucalyptus fastigata* in New Zealand.
- Native, exotic, and total (native + exotic) carbon stocks were simulated over 100 years for various (but not factorial) combinations of exotic canopy species (*P. radiata* or *E. fastigata*), exotic canopy disturbance (none, coupe, early intervention, and simultaneous disturbance of the whole exotic canopy), native reforestation (natural colonisation, natural colonisation + replacement of killed exotic trees by planting native canopy-dominant species, and natural colonisation + dense planting of mānuka/kānuka).
- Carbon stocks were expressed either as the integral of carbon stocks (the sum of carbon stocks across years) or the carbon stock at selected stand ages (25, 50, 75, and 100 years).
- *Post hoc* tests within linear mixed-effects models were used to test for significant differences between transition forest scenarios.

- Extreme gradient-boosted regression trees were used to explore the effect of management and site variables (and interactions between them) on the integral of native and total carbon stocks.

## Conclusions

- Achieving native tree dominance in transition forests comes at the cost of reducing total carbon stocks, because native carbon stocks are enhanced by disturbance of the exotic canopy, while reducing total carbon stocks.
- Replacement of exotic trees killed during deliberate canopy disturbance by planting native canopy-dominant species enhances native carbon stocks when disturbance and planting occur earlier rather than later.
- The positive effect of deliberate exotic canopy disturbance on native tree carbon is moderated by the identity of the exotic plantation species (with the effect being larger under *P. radiata* than under *E. fastigata*) and climate (with the effect being larger at warmer temperatures).
- The difference in total carbon stocks between exotic plantation species (higher for *P. radiata* than for *E. fastigata*) was moderated by climate (with the difference being greater at cooler temperatures). The negative effect of disturbance on total carbon stocks was also moderated by climate (with the effect being stronger at higher temperatures).

## Recommendations

- Policies for incentivising transition forests within the Emissions Trading Scheme should consider how to assist landowners with the potential liability of surrendering carbon credits due to the deliberate exotic canopy disturbance required to promote native dominance.
- A representative network of permanent forest survey plots tracking native species composition and demographic rates in exotic plantation forests should be established.
- This should be complemented by targeted plots aligned to experimentally applied transition forest scenarios.

# 1 Background

Many parts of the world have experienced net reforestation in recent decades (Meyfroidt & Lambin 2011). This has multiple drivers, but it mainly involves replacing pastoral/arable agriculture on marginal land by either natural or plantation forests. However, there is concern that reforestation may lead to adverse environmental, biodiversity, and socioeconomic outcomes, particularly where top-down policy incentives and economic drivers promote the widespread establishment of low-diversity plantation forests (Lambin & Meyfroidt 2010).

Transitional forestry management has emerged as a framework which

> articulates a holistic re-evaluation of forest landscape design and management, primarily centred on forest purpose. This model involves an ongoing multi-decadal process of change from 'business-as-usual' forest management … to integrated future systems of forest landscape management, embedded across a continuum of new forest types optimised for a range of multiple-purpose outcomes (Jones et al. 2023).

In the New Zealand context there is concern that the vast majority of newly established forests are single-species exotic plantations (mainly *Pinus radiata*), while new indigenous forest plantings cover a much smaller area (Jones et al. 2023). In part this is due to the perceived greater potential carbon gain for exotic plantation forests, along with the higher difficulty and cost of planting native forests. An emerging strategy for establishing native forests at scale is to plant dense stands of fast-growing exotic tree species with a view to transitioning to native forest (Forbes 2021). The assumptions are that:

- thanks to industrial plantation forestry developments over many decades, seedlings of exotic plantation species are inexpensive and hardy, permitting the establishment of high planting densities over large areas
- the high density and fast growth rate of exotic tree species provides rapid canopy closure, thus suppressing light-demanding weeds
- rapid carbon sequestration by exotics provides a potential income stream through the Emissions Trading Scheme, which can support management to promote native forest species colonisation or planting (Jones et al. 2023).

Further, there are large areas of exotic plantation forest in New Zealand on land unsuitable for timber harvest. Many owners of such forests do not wish to retain the non-productive exotic forests, preferring instead a transition to permanent native forest (Forbes 2021).

The uncertainty about transitioning the long-term carbon stock of new or existing exotic forestry plantations to native forest (henceforth termed transition forests) is considerable. An almost total lack of relevant quantitative, empirical data means fit-for-purpose forest growth models are required to provide preliminary estimates of potential carbon stock changes, while clearly stating the assumptions and caveats associated with the models.

A variety of well-established forest growth-modelling tools are available for New Zealand's forests, but relatively few can simulate multi-cohort, mixed-species forests. Interactions among species and cohorts greatly influence forest stand dynamics, and simpler single-cohort or single-species forest models provide erroneous estimates of carbon stock changes for more complex forests. However, using and adapting existing models capable of simulating multi-cohort, mixed-species forests provides an opportunity to rapidly generate carbon stock change estimates for transition forests.

A limited number of studies have investigated changes in species composition – but not carbon – during transitions from exotic plantation to native forests in New Zealand (Norton 1998; Forbes 2017, 2021; Forbes et al. 2019; Forbes et al. 2021; Forbes et al. 2015; Forbes et al. 2016). A greater number of international studies use a range of methods, including harvesting or thinning of exotic canopies, fire, and planting of native tree species (Deng et al. 2020; Marshall et al. 2023; Matusick et al. 2022; Meng et al. 2014), which could inform transition forest scenarios analysed using forest growth models. However, we are not aware of any precedents in New Zealand for the application of forest growth models to transition forests. Consequently, it is unlikely to be practicable to apply forest growth models to the full range of potential management scenarios or to a wide range of exotic forestry species in the immediate term.

In this study we employ two existing forest growth models:

- Perfect Plasticity Approximation (PPA, Coomes et al. 2012; Purves et al. 2008)
- Physiological Processes Predicting Growth (3-PG, Landsberg & Waring 1997)

to estimate carbon stock change during transition from exotic to native forest through natural succession, leading to mixed-species native forests, potentially aided by supplementary planting, under various canopy disturbance scenarios.

There is a lack of spatially explicit forest models to simulate spatially heterogenous interventions (e.g. harvesting of coupes leaving the surrounding canopy intact) parameterised for the New Zealand context. Parameterisation of such models would require considerable investment in quantitative data collection and model development. For instance, the site-specific non-generalisable SORTIE-NZ model (Forsyth et al. 2015) took more than a decade of sustained field observations and subsequent analyses to parameterise. We selected the PPA and 3-PG models because they have already been parameterised for New Zealand forest tree species and require relatively minor adjustments to simulate transition forests. Further, while both are stand-level models, they have disparate model structures and provide differing insights into natural succession and planting, respectively.

We apply these models within a small number of management scenarios that manipulate exotic forest cover to promote native species establishment under two common, fast-growing exotic forestry species, *Pinus radiata* and *Eucalyptus fastigata*, with contrasting physiology and canopy characteristics (Table 1). Both models are spatially implicit, meaning they are not suited to interventions such as removing groups of trees (e.g. coupe felling) that create high levels of spatial heterogeneity in the density of the forest canopy. However, it is possible to model spatially heterogenous management by modelling stands receiving different management treatments within a forest separately, using conservative assumptions and aggregating results to produce forest-level carbon change estimates.

**Table 1. Ecological traits of exotic forest cover species.**

| Ecological traits | *E. fastigata* | *P. radiata* |
|---|---|---|
| Max age (years) [a] | 35 | 114 |
| Potential lifespan (years)[c] | >80 | >150 |
| Mean height (m) [a] | 19 | 22 |
| Mean DBH (cm) [a] | 23 | 28 |
| Wood basic density (kg/m$^3$) | 480 | 350 |
| Temperature range for growth (°C) | 6–35 | 0–33 |
| Mean plot BA at age 30 (m$^2$/ha, 95% CI in parentheses) [b] | 38.0 (34.1–42.0) | 55.3 (52.4–58.1) |

[a] Derived from the permanent sample plot database.

[b] Modelling outputs generated using 3-PG in this study.

[c] Burns et al. 1990; Lindsay 1937; Sudworth 1908; Miller et al. 2000.

Notes: DBH = diameter at breast height; BA = basal area

We apply these models to a range of environmental contexts with differences in climate and surrounding vegetation to explore the effect of these factors on the establishment and growth of native species and carbon stock changes. These analyses will provide the first carbon estimates for transition forests based on explicitly stated ecological processes, data sources, and assumptions.

## 2 Objectives

- To apply the 3-PG and PPA models to assess the consequences of different transition forest scenarios on native and total (native + exotic) carbon stocks.
- To explore the effect of interactions between transition forest management choices (deliberate exotic canopy disturbance, identity of exotic canopy species, planting of native canopy dominant), and site variables (climate, slope, and amount of native forest in the surrounding landscape) on native and total carbon stocks.

## 3 Methods

### 3.1 Focal site selection

We selected 100 locations within the potential distribution of *Pinus radiata* as focal sites for modelling the carbon stock change of transition forest. All but four of the sites were also within the potential distribution of *E. fastigata*. The selection excluded areas not available for transition forests (national parks [consistent with current efforts to estimate reforestation potential on public conservation land], water bodies, native forests, areas with Land Use Capability class ≤ 4 (Lynn et al. 2009) , and areas higher than 1,210 m altitude). Sites were selected using a balanced sampling approach (Chauvet & Tillé 2006, Grafström et al. 2011), which selects an evenly spaced sample of locations within a multivariate sampling space (i.e. using two or more site attributes) encompassing the potential distribution of each exotic forestry species. The attributes used to define the sampling space were latitude and longitude, mean annual rainfall, mean annual temperature, altitude, slope, and amount of native forest in the surrounding landscape (within a 4 km radius). (See Appendix 1 for specific details.)

From the 100 sites selected, 60 were in the North Island and 40 in the South Island (Figure 1).

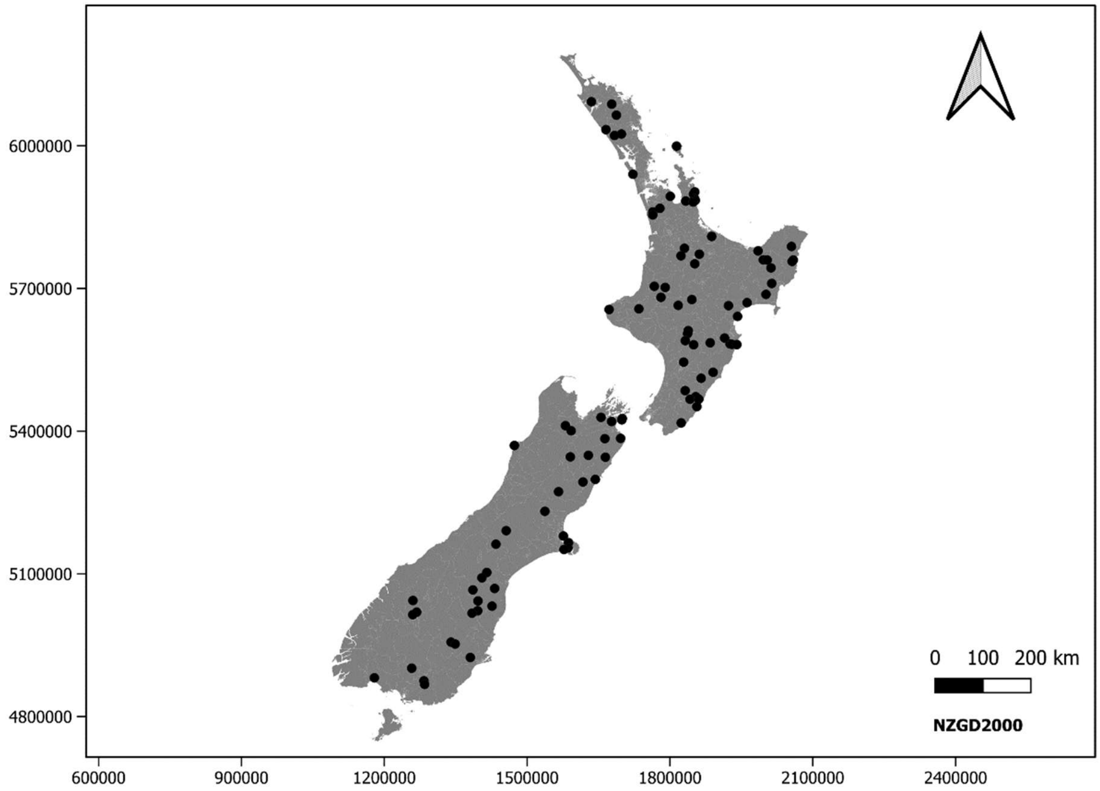

**Figure 1. Map showing the plots selected using the balanced sampling approach.**

## 3.2 Scenario definition

To design the management scenarios we drew on the expert opinions of Dr Adam Forbes and Te Kapunga Dewes. Based on their input we developed 17 separate scenarios for newly planted transition forests and pre-1990 forests managed for transition to native forest.

The scenarios comprise two types of activities related to transition forests: reforestation methods and plantation management interventions, for both new forests and pre-1990 forests. A detailed description of each scenario is included in the next section (3.3 Modelling scenarios). In that section we include the following information for each scenario:

- the exotic plantation species (*Pinus radiata* or *Eucalyptus fastigata*)
- the exotic planting density and other relevant silvicultural management actions (e.g. thinning)
- interventions to disturb the exotic canopy (early intervention, coupe, and whole-stand disturbance)

- native reforestation scenarios (natural succession, supplementary planting of a native canopy-dominant species or dense plantings of mānuka/kānuka)
- modelling approaches used to simulate scenarios (3-PG for exotic canopy plantations and PPA for native reforestation).

The scenarios do not follow a full factorial design because not all native reforestation options are applied to every exotic plantation management or canopy disturbance option. Further, some exotic plantation interventions are only applied to new forests and not to pre-1990 forests. It is important to note that all forest management scenarios assumed adequate weed and mammal pest control (including wilding individuals of exotic forestry nurse crop species) to limit the influence of these exotic invasive species on the regenerating native forest. In addition, it is assumed that natural dispersal mechanisms are in place (e.g. biotic seed dispersal) to allow natural colonisation by native tree species (see Appendix 2).

## 3.3 Modelling scenarios

In this section we describe the different scenarios modelled, including densities, types of intervention, and the frequency of interventions (summarised in Figure 2). In all simulations 3-PG was used to model exotic plantation tree growth and mortality, as well as carbon storage in live stems and coarse woody debris. The PPA model was used to simulate recruitment, growth and mortality of native stems, as well as carbon storage in live stems and the coarse woody debris of native species.

The exotic canopy influences native species' recruitment, growth, and mortality via a parameter termed the Canopy Area Index (CAI), which expresses the total canopy area of a stand of trees (above a given height) as a ratio of the area occupied by the stand. Details of 3-PG and PPA model parameterisation and implementation are provided in subsequent sections. All the exotic plantation canopy disturbance interventions proposed in the scenarios below can be implemented with minimal impact on the understorey.

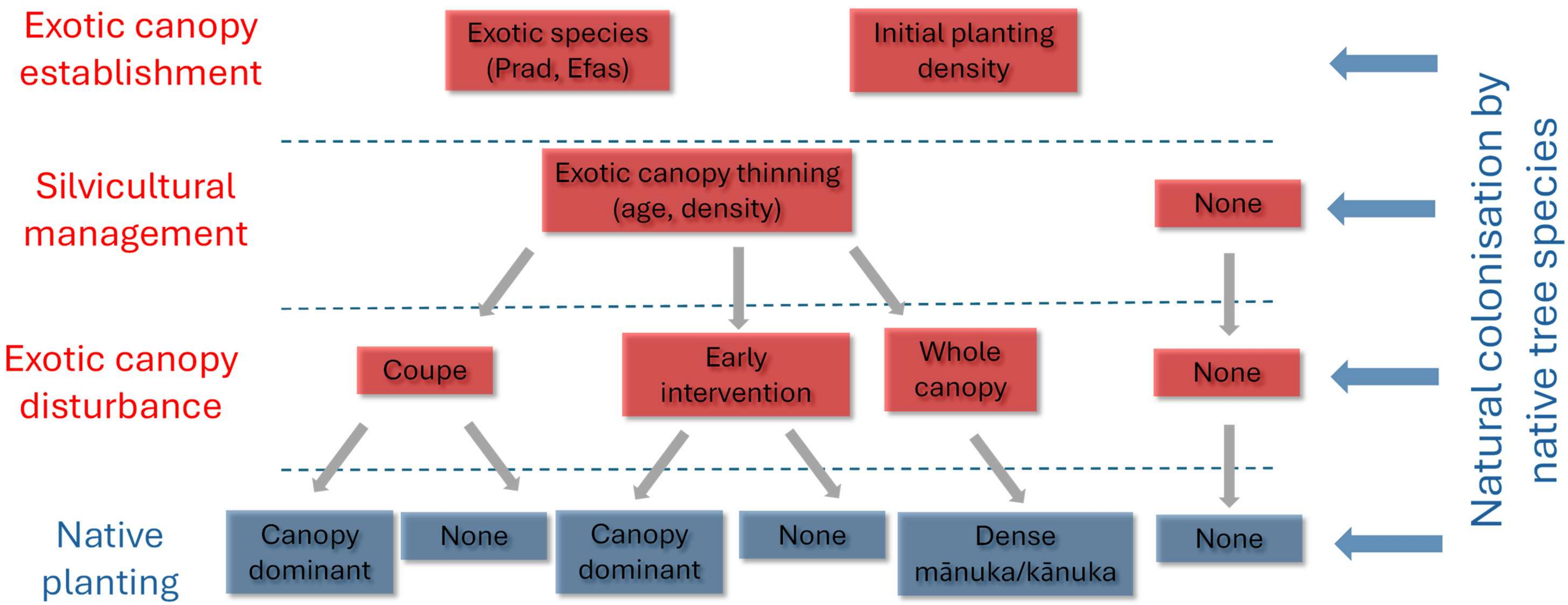

**Figure 2. Schematic representation of modelling scenarios.**

**Notes: Red shading indicate choices that directly affect exotic carbon stocks, while blue shading indicates choices and processes that directly affect native carbon stocks. Scenarios cover different choices at successive stages of the simulation process, from exotic plantation establishment to silvicultural management, exotic canopy disturbance, and native planting following exotic canopy disturbance. Natural colonisation by native tree species occurs at all stages of the simulation process. Prad = Pinus radiata; Efas = Eucalyptus fastigata.**

### 3.3.1 Newly planted transition forests

An emerging strategy for establishing native forests at scale is to plant dense stands of fast-growing exotic tree species with a view to transitioning to native forest. The logic is:

- seedlings of exotic plantation species are cheap, permitting high planting densities over large areas
- the high density and fast growth rate of exotics lead to rapid canopy closure, reducing problems from light-demanding weeds
- rapid carbon sequestration by exotics provides an income stream through the Emissions Trading Scheme, which can support management to promote native forest species colonisation or planting.

We aim to use our models to determine the consequences of different management options for carbon storage and native forest species establishment (especially canopy dominants) in newly planted transition forests.

#### *Whole-stand disturbance and dense restoration planting*

In this scenario we used the 3-PG model to simulate the stand-level growth of two different exotic forest plantation species, Pinus radiata and Eucalyptus fastigata, each planted at a density of 833 stems per hectare (sph). The first intervention occurred when the stand was 9 years old (the average age of canopy closure) and involved homogeneous thinning to 600 sph. The second intervention involved killing all exotic plantation trees, with dead tress left standing rather than being felled or harvested. Natural recruitment of native species was simulated using the PPA model from the year the exotic plantations were planted. Following this, we simulated the planting of native species (50% each of mānuka and kānuka) at a density of 1,100 sph, in addition to any naturally recruited native individuals, with subsequent succession occurring through natural recruitment.

#### *Early canopy intervention*

We simulated scenarios for newly planted transition forests with a density of 1,000 sph for *P. radiata* and *E. fastigata*. The first intervention was scheduled at a stand age of 9 years, which represents the average age of canopy closure, and involved a homogeneous thinning of 33% of the stems per hectare (i.e. every third row). This intervention was repeated every 5 years until the density of exotic species reached zero (stand age 19 years). To this exotic canopy disturbance scenario we applied two native reforestation options: one with only natural recruitment (using probability of occurrence and dispersal potential), and the other with natural recruitment plus supplemental planting of an ecologically appropriate native canopy-dominant tree species (i.e. the species from the following list with the highest predicted occurrence probability: miro (*Pectinopitys ferruginea*), mataī (*Prumnopitys taxifolia*), rimu (*Dacrydium cupressinum*), tōtara (*Podocarpus totara*), kahikatea (*Dacrycarpus dacrydioides*), beech species, and tawa (*Beilschmiedia tawa*) (see Appendix 2 for details). This provided four scenarios in total: two for each exotic plantation species. Native planting was implemented at a rate of one native tree planted for every two exotic plantation trees killed.

#### *Thinning with coupe ring-barking/poisoning*

We simulated an exotic forest of *P. radiata* and *E. fastigata* with an initial density of 833 sph. The forest underwent one thinning at a stand age of 9 years, harvesting 333 sph. After 25 years we implemented a coupe harvesting of 20% of the total stems in the stand every 10 years, continuing this process for 40 years until all stems were harvested. We applied the same two native reforestation options as for the early intervention exotic canopy disturbance scenario: one with only natural recruitment (using probability of occurrence and dispersal potential), and the other with natural recruitment plus supplemental planting of an ecologically appropriate native canopy dominant tree species (following the definition provided for 'early canopy intervention' above), thus providing four scenarios in total – two for each exotic plantation species.

#### *No interventions*

We also included scenarios without any exotic canopy or reforestation interventions (do nothing) but allowing natural recruitment of native individuals. This covered four scenarios in total, two each for each exotic canopy species, with initial planting densities set to match either that used in the early canopy intervention scenarios (1,000 sph) or coupe disturbance scenarios (833 sph).

### 3.3.2 Pre-1990 forests

Large areas of pre-1990 exotic plantation forestry occur on steep, erosion-prone land where harvesting is no longer an option. For many landowners a future of landscapes dominated by exotic plantation forest that provides no or minimal economic returns is highly undesirable. There is a high degree of interest in how these forests might be transitioned to native forests. While the consequences for carbon storage may be less of an issue here (as long as the land is still classed as forest, no penalties for carbon storage declines apply), there is still interest in how management interventions affect native dominance and long-term carbon storage. While pre-1990 forest lands may contain relatively young forests due to replanting post-harvest, we focus on forests established before 1990.

#### *Thinning with coupe ring-barking/poisoning*

For this scenario we simulated a *P. radiata* plantation with an initial density of 1,250 sph. The intervention included only an intensive thinning at a stand age of 10 years, reducing the number of stems per hectare to 370. This reflects standard pre-1990 forest management practice. At age 40 we simulated coupe disturbance, killing 20% of the total stems per stand every 10 years until all stems were harvested, which occurred at a stand age of approximately 80 years. We added two variations to this scenario: one that included natural recruitment of native tree species and the other with natural recruitment plus supplemental planting of ecologically appropriate canopy-dominant species (at a rate of one native planted for every two exotic plantation trees removed). We also simulated a *P. radiata* plantation with a density of 1,250 sph where no intervention was done, allowing only for natural regeneration to establish.

## 3.4 Model implementation and parameterisation

### 3.4.1 3-PG model

Physiological Processes Predicting Growth (commonly known as 3-PG) is a simple, stand-scale, process-based forest growth model that has been widely used in research and industry across the globe, and that has been well validated (Landsberg et al. 2003; Gupta & Sharma 2019). The 3-PG model consists of five simple sub-models in a causal chain, starting with light absorption and assimilation, and ending with the conversion of biomass into output variables of interest to forest managers (Figure 3). Initially, 3-PG was developed for even-aged monocultures, but over time it has been expanded and can, with appropriate parameterisation, be used to investigate spatial variation in forest growth (3PG-SPATIAL; Tickle et al. 2001), remotely sensed data (3-PGS; Coops et al.1998; Coops & Waring 2001), and mixed-species forest dynamics at monthly or yearly time-steps (3-PG$_{\mathrm{mix}}$; Forrester & Tang 2016).

The 3-PG model and its variants estimate net primary productivity, transpiration, respiration, and growth by calculating the absorbed photosynthetically active radiation (APAR) from the photosynthetically active radiation and leaf area index. The portion of APAR that is actually used (APARu) is determined by a set of modifiers that range from 0 (complete limitation) to 1 (no limitation), which account for limitations due to extreme temperatures, vapour pressure deficit, poor soil fertility, and low available soil water.

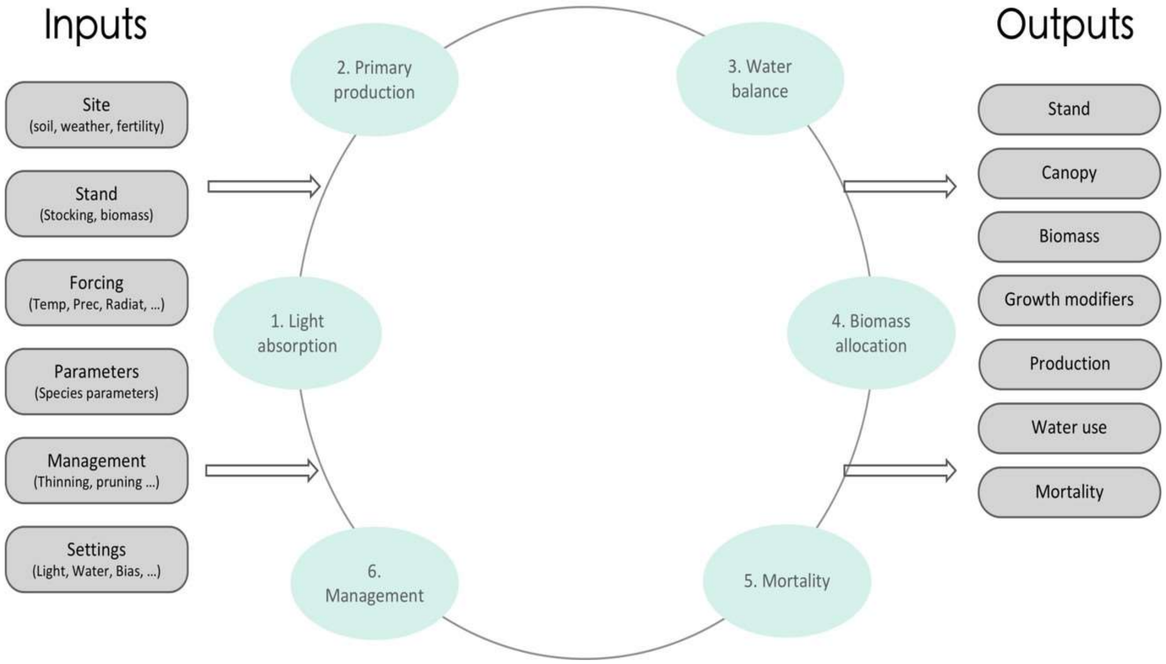

**Figure 3. A schematic representation of 3-PG's six sub-models, and the inputs and outputs from the model. (Source: adapted from Trotsiuk et al. 2020)**

Over time almost all the major New Zealand plantation forest tree species have been parameterised, calibrated, and tested to simulate with 3-PG (version 2.7 pjs, which is not spatially explicit), including both *P. radiata* and *E. fastigata* (Meason & Mason 2014; Salekin et al. 2024).

For the purposes of this study, 3-PG was used to model the growth, mortality, and carbon stocks of the exotic component of the forest over time. Forest structure parameters required to model the native forest component using PPA, such as CAI, were calculated based on the 3-PG outputs (described below). The parameters used in this study are identical to those presented for *P. radiata* and *E. fasiculata* by Salekin et al. (2024, Supplementary Table 1).

The 3-PG model was developed to simulate the impacts of silvicultural treatments, and therefore is able to model the influence of thinning on subsequent forest growth. However, it does not include specific options for ring-barking techniques or herbicide applications (i.e. 'chemical thinning'); therefore, we modelled these treatments as thinning, with the assumptions that tree mortality would occur within a year and the treatments would be 100% effective.

The 3-PG model does not track biomass or carbon in coarse woody debris (i.e. dead wood), so we tracked this biomass manually outside of the model. As trees in the simulation died, their biomass was added to the dead wood pool cumulatively. In addition, constant annual decay rates of 53% and 44% mass loss were applied to the dead wood pool for *P. radiata* and *E. fastigata*, respectively (Mackensen et al. 2003).

### 3.4.2 PPA model

The PPA model uses 'perfect plasticity approximation' (PPA) to model neighbourhood light competition and simulate individual tree dynamics at the stand level (Purves et al. 2008). Tree demographic rates (i.e. growth, mortality, and recruitment) are modelled as functions of a CAI, which represents the total canopy area of trees within a stand taller than the target tree's height, minus a fraction (h) of the target tree's canopy depth (Caspersen et al. 2011). We set h = 0.25 for both growth and mortality to maintain model consistency with observed data, following Coomes et al. (2012). The PPA model is implemented at the default plot scale of a 0.04 ha stand (20 × 20 m), aligning with standard forest plot sizes in New Zealand (Hurst & Allen 2007).

The model systematically simulates the diameter at breast height (DBH) and species composition of trees within a stand, conducting various operations annually (e.g. stem diameter growth), based on species-specific functions incorporating CAI, tree size, and environmental variables (e.g. temperature, rainfall, altitude, and slope). The PPA model accounts for individual uncertainty and temporal autocorrelation in tree growth, constraining our values below the 95th percentile of predicted growth values to minimise the effect of outliers.

#### *Growth rate parameterisation*

Growth rates were parameterised using data from repeatedly measured permanent plots from New Zealand's National Vegetation survey (NVS) databank for 30 common tree species found in natural forests in New Zealand. Species-specific annual stem diameter growth ($G$) between the first census (T1) and the subsequent census (T2) was then fitted using a functional form with a gamma error structure to address the positive asymmetric distribution of growth rates (Coomes et al. 2014):

$$G = \frac{g_0 {DBH_{T1}}^{g_1}(1 + g_4 MAT)(1 + g_6 MAP)e^{g_5 DBH_{T1}}}{1 + \frac{g_0}{g_2} e^{g_3 CAI}}$$

where MAT represents mean annual temperature and MAP denotes mean annual precipitation. The estimated parameters ($g_{0\,-\,6}$) were incorporated in the growth function in the PPA model.

For tree species without species-level parameters, we used the parameters of kānuka (*Kunzea ericoides*).

### *Mortality rate parameterisation*

We used data from Land Use and Carbon Analysis System (LUCAS) plots to estimate mortality for native species coded in the model. We first filtered the data to include only stems that were alive at T1 and either alive or dead at T2. To parameterise the mortality rates per species, we fitted a mortality rate model, following Kohyama et al. (2018), incorporating stem size (DBH) and environmental variables (MAP and MAT). Specifically, we estimated the annual mortality probability of stem $M$ based on the census interval and the probability of mortality of the stem ($p$), which was related to the observed status of each stem found at T1 ($Obs$), whether it survived during the census interval (0) or not (1), using a Bernoulli distribution (Kohyama et al. 2018):

$$Obs = Bernoulli\ (p)$$

$$p = 1 - \ e^{-MT}$$

Then, we parameterised mortality rates for 111 species and for five growth forms (i.e. conifer, beech, tree fern, angiosperm tree, and other understorey trees) using the following model:

$$\ln(M) = m_0 + \ m_1 DBH + \ m_2 \log(DBH) + \ m_3 CAI + \ m_4 MAP + \ m_5 MAT + \ m_6 altitude$$

The estimated parameters ($m_{0-6}$) were incorporated in the mortality function the PPA model.

### *Recruitment rate parameterisation*

Recruitment for each species was modelled as a multi-step process:

1 define the pool of species available for recruitment

2 estimate the probability that a given species will produce any recruits

3 estimate the number of recruits produced for each species that produces recruits.

These steps are discussed in turn below.

1 Define the pool of species available for recruitment

Using distance-weighted species occurrence probabilities (described below), we performed a binomial draw to identify which species could be recruited; if the output was zero, recruitment was set to zero. The distance-weighted species occurrence probability was derived from species occurrence data for 109 species collected from LUCAS plots, along with environmental data from a comprehensive data set that included variables such as MAT, MAP, slope, and land cover. We used extreme gradient-boosted regression trees (xgb) with cross-validation to predict species occurrence probabilities.

For our modelling we selected 100 site locations (specifically *P. radiata* and *E. fastigata* plantations) and created a 4 km buffer around each site. Within these buffers we generated a grid of points to extract environmental data. These data were then used to predict species occurrence probabilities at each point based on models derived from the LUCAS plots. Finally, we calculated the distance from each point to the site location to estimate species colonisation probabilities, weighting these estimates using the inverse of the distance from the point to the site location. (More details are available in Appendix 1.)

2 Estimate the probability that a given species will produce any recruits

The probability of each site having new recruits of each species ($p_u$) was modelled, using tagged stem data from remeasured LUCAS plots, as a function of CAI and site attributes with species- ($p_{species}$, $p_4$) and site-specific parameters ($p_{1-3}$):

$$\mathrm{logit}\,(p_u) = p_0 + p_{species} + p_1 MAP + p_2 MAT + p_3 altitude - p_4 CAI$$

Whether or not a species produced any recruits ($u$) was determined by a random binomial (Bernoulli) draw

$$u \sim Bernoulli\,(p_u)$$

3 Estimate the number of recruits produced for each species that produces results

Our approach for estimating the number of recruits per species quantifies the recruitment rate at the individual stem and site level. The annual recruitment rate per stem ($R$) is modelled based on tagged stems in remeasured LUCAS plots, distinguishing between newly recruited stems and previously recorded stems from the prior census, with the same function as used in mortality probability with a Bernoulli distribution. To estimate species- ($r_{speci}$ , $r_4$) and site-specific parameters ($r_{1-3}$) for the recruitment rate, we modelled the annual recruitment rate as a function of CAI and site attributes, which include MAP, MAT, and the altitude of the plot location, using the following model:

$$\ln\,(R) = r_0 + r_{species} + r_1 MAP + r_2 MAT + r_3 altitude - r_4 \mathrm{C}AI$$

The recruitment number for species where new recruits are produced ($\lambda$) was modelled as a function of the recruitment rate estimated in the aforementioned recruitment rate model, the stem basal area of the species in the site, and the proportion of neighbouring native forests within a 4 km radius buffer area around the site (where 0 denotes no native forest within the 4 km radius buffer and 1 represents all surrounding areas within the 4 km radius being native forests).

$$\ln(\lambda) = l_0 + l_1 R + l_2 BA + l_3 Neighbouring\ native\ forest\ prevalence$$

The number of recruits (*RN*) was then simulated using a random Poisson process, with the mean defined as the product of $u$ and λ:

$$RN \sim Poisson\,(u\lambda)$$

To estimate species- and site-specific parameters for estimating $\lambda$, we employed a Poisson model. First, the annual count of new recruits was scaled by a factor of 100, rounded, and modelled using a Poisson distribution. The resulting fitted values of $\lambda$ were rescaled to their actual numbers.

### *Recruitment through native planting*

For whole-stand exotic canopy intervention, we modelled forest succession through both natural recruitment and dense planting (1,100 sph) of mānuka and kānuka (with planted stems shared evenly between them). This assumed that after clear-felling, weed species (including wilding individuals of exotic plantation species) are managed kānuka. While the species composition of pioneer woody communities varies markedly throughout New Zealand, most pioneering shrub and small tree species are not parameterised in the PPA model. A variety of native tree and shrub species are known to colonise intact exotic forestry stands (Allen et al. 1995; Brockerhoff et al. 2003; Ogden et al. 1997), and future work could examine initial stands of varying species composition.

In the other scenarios where native planting was implemented, we added supplemental plantings of the species with the highest predicted occurrence probability from a set of high carbon storage potential canopy dominants: miro (*Pectinopitys ferruginea*), mataī (*Prumnopitys taxifolia*), rimu (*Dacrydium cupressinum*), tōtara (*Podocarpus totara*), kahikatea (*Dacrycarpus dacrydioides*), various beech species, and tawa (*Beilschmiedia tawa*). Only one species was selected per site. For scenarios where interventions (such as thinning, early intervention, and coupe disturbance of exotic canopies) were simulated, we added one stem for every two exotic trees removed.

### *Incorporating CAI from 3-PG model for exotic plantations*

CAI values of exotic plantations were obtained from the outputs of the 3-PG model. We used the diameter–height allometric equations of Holdaway et al. (2014) to calculate the contribution of the exotic canopy to CAI values of each native stem. This information allowed us to track changes in CAI and report the development of exotic forest stands. We calculated the CAI of exotic species along the simulation years for each scenario that included interventions such as partial canopy removal (thinning or ring-barking) and incorporated this into the PPA model.

### *Biomass calculation*

For each time-step of the model, total above-ground biomass in live stems was calculated using an allometric function that incorporates DBH, height, and species-specific wood density, following Holdaway et al. (2017). The model also estimates the deadwood biomass pool by tracking the biomass transferred from the live stem pool to coarse woody debris for stems greater than 10 cm DBH, while modelling coarse woody debris decay over time using established species-specific decay functions (Beets et al. 2008). To estimate below-ground biomass, we multiplied the above-ground live stem biomass estimates by 1.25, assuming that 25% of the total biomass is below ground, as per Beets et al. 2012. This value was then combined with the coarse woody debris mass to obtain the total native biomass. The mean (across PPA simulations) native biomass for each scenario in each site in each year was used in subsequent analyses. Total (native + exotic) biomass for each scenario at each site in each year was estimated using 3-PG as the sum of the mean native biomass (across PPA simulations) and exotic biomass.

### *PPA simulation implementation*

PPA simulations were initiated at the same time as the establishment of exotic plantations, with 100 kānuka stems per hectare (equivalent to four stems per 20 m × 20 m plot). We performed 50 simulations for each scenario at each modelling location over a 100-year period. Since the PPA model is not spatially explicit, we simulated a coupe disturbance scenario by combining five sub-models with different whole-stand disturbance timings. The outputs from these sub-models were aggregated to produce the coupe disturbance simulation results. For the coupe disturbance scenarios, we ran 30 simulations over 100 years for each of the five sub-models.

### *Native species composition*

Species abundance was recorded as the mean live stem biomass across PPA simulations for each scenario at each site. Species were aggregated into three groups: mānuka and kānuka (all *Leptospermum* and *Kunzea* taxa), canopy dominants (as listed above), and 'other' (all other native tree species). The mean (across sites) absolute and relative (% of total native abundance) were calculated annually for each group.

## 3.4.3 Effect of management scenarios and management and site variables on carbon stocks

We used two types of metric to quantify native and total (native + exotic) carbon stocks for each scenario at each site. First, we used the integral of carbon stocks – simply the sum of carbon stocks across years. We chose this metric because it integrates variation in carbon stocks through time in response to exotic plantation stand development, exotic canopy disturbance, and native reforestation. The second type of metric we used was carbon stocks at selected stand age (25, 50, 75, and 100 years).

### *Effect of scenarios*

We tested for significant differences between scenarios in both types of carbon stock metric by fitting linear mixed-effects models of carbon stocks against scenario identity (fixed effect), with site as the random factor. We then applied the Tukey honest significant difference *post hoc* test to test for significant differences between all possible pairs of scenarios. Linear mixed-effects models were fitted using the *lme()* function from the nlme package in R. Tukey tests were performed using the *emmeans()* function in the emmeans package in R.

### *Effect of management and site variables*

Cross-validated extreme gradient-boosted regression trees (xgb, Chen & Guestrin 2016), a machine-learning approach to predictive modelling, were fitted to assess the relative influence of management and site variable on carbon stocks within the 'do nothing', coupe, and early intervention new forest scenarios. The integral values of native and total carbon stocks (either the integral or stocks at selected ages) were the response variables, and the integral values for each scenario at each site were treated as individual observations. Predictor variables were disturbance (0 = none, 1 = coupe, and 2 = early intervention), altitude, amount of native forest cover within a 4 km radius, MAP, MAT, native planting (0 = no planting and 1 = replacement planting of killed exotic trees with native canopy dominants), exotic canopy species (0 = Efas, 1 = Prad), and slope (derived from a 15 m digital elevation model).

Like many machine-learning approaches to predictive modelling, xgb requires separating data into training (used to fit the model) and validation (used to test the model's accuracy) subsets through a process known as cross-validation. We divided the data set into 10 subsets to provide 10-fold cross-validation (i.e. 10 xgb 'fold' models were fitted, each one excluding a different subset of the data used for model validation from the training data set). In fitting xgb models, site was used as a grouping variable to ensure all observations for a given site were assigned to the same subset of the data (i.e. to ensure observations from the same site were never in both the training and validation data sets). Cross-validated xgb models were fitted using the *xgb.cv()* function from the xgboost package in R.

Models were fitted by minimising the mean absolute error between predicted and observed values of the response variable. Model accuracy was assessed as the correlation between predicted and observed values. Predicted values for each observation were taken from the xgb fold model in which the observation was excluded from the training data set. This measure of model accuracy provides an indication of the accuracy of model predictions onto new data.

The influence of each predictor within each xgb models is quantified using three metrics:

- gain, the reduction in unexplained deviance when a predictor is used to make a split in the data set
- cover, the proportion of observations covered by splits in the data set involving each predictor
- frequency, the proportion of splits involving each predictor.

Variable importance was calculated for each xgb fold model using the *xgb.importance()* function from the xgboost package in R. Variable importance was visualised using simple bar graphs of the mean and the 95% confidence interval for each variable (across xgb fold models).

The independent effect of each predictor was assessed using partial dependence plots, which graph the marginal effect of individual predictors on the predicted outcome of a machine-learning model. They are a useful way of visualising the shape of relationship between a predictor and the response (e.g. linear, non-linear monotonic or unimodal). Partial dependence values for each predictor in each xgb fold model were estimated using the *partial_dep()* function from the pdp package in R. Partial dependencies for each predictor were visualised using simple bi-plots, showing partial dependence for each xgb fold model and the mean across fold models.

One advantage of regression tree models such as xgb is that they model interactions between predictors effectively without the user needing to specify which interactions to include in the model. Two-way interactions between variables were estimated for each xgb fold model using the *hstats()* function from the hstats package in R. Interactions were visualised using three-dimensional perspective plots.

# 4 Results

## 4.1 Newly planted transition forests

Below we present figures for time series of native, exotic, and total carbon pools for each new forest scenario. Where relevant we refer to *post hoc* analyses from linear mixed-effects models to assess statistical support for differences in **native** and **total** carbon stocks between scenarios in either (a) the integral of carbon stocks (annual stocks summed over the 100-year simulation period) or (b) carbon stocks at selected stand ages (25, 50, 75, and 100 years).

### 4.1.1 No intervention (do nothing scenarios)

*P. radiata* carbon reaches a steady state due to negligible natural mortality, although older stands may be susceptible to wind throw or other disturbances. In contrast, *E. fastigata* carbon decreases in older stands because natural mortality is larger. In all 'do nothing' scenarios, total carbon increases once exotic carbon stabilises or declines, due to an increase in native carbon pools. Despite the considerable variation in carbon stocks across sites there is evidence that the integral of native carbon stocks is significantly higher under the *E. fastigata* 'do nothing' scenarios compared to *P. radiata* (Figure 4; Table 2). By contrast, the integral of total carbon stocks was higher for the *P. radiata* 'do nothing' scenarios than for *E. fastigata* (Table 2).

Despite increasing throughout the simulation period, the native carbon pool still accounted for less than half of the total carbon pool by year 100 for the *P. radiata* scenarios (the end of the simulation period). By year 100, the end of the simulation period, the native carbon pool accounted for much of the total carbon pool in *E. fastigata* stands, but it was not until stand ages >75 years that native carbon was significantly greater under *E. fastigata* than under *P. radiata* (Table 4). By contrast, total carbon stocks were significantly higher for *P. radiata* 'do nothing' scenarios than for the corresponding *E. fastigata* scenarios at all the stand ages examined (Table 5).

**Table 2. Post hoc analyses of a linear mixed-effects (LME) model predicting the integral of native carbon stocks ("Carbon integral" summed across the 100 year simulation period) from management scenario**

| Scenario | Carbon integral (Mg C/ha) | SE | df | 2.75% | 97.5% | Group |
|---|---|---|---|---|---|---|
| Efas; coupe; no planting | 1,996 | 76.78 | 99 | 579 | 3,910 | f |
| Efas; coupe; planting | 1,806 | 76.78 | 99 | 401 | 2,929 | de |
| Efas; early; no planting | 1,601 | 76.78 | 99 | 424 | 2,530 | bc |
| Efas; early; planting | 1,952 | 76.78 | 99 | 639 | 4,363 | ef |
| Efas; do nothing; coupe density | 1,466 | 76.78 | 99 | 423 | 2,425 | b |
| Efas; do nothing; early density | 1,452 | 76.78 | 99 | 453 | 2,537 | b |
| Efas whole stand; mānuka/kānuka | 2,310 | 76.78 | 99 | 808 | 3,732 | g |
| Prad; coupe; no planting | 1,675 | 76.78 | 99 | 353 | 2,782 | cd |
| Prad; coupe; planting | 1,687 | 76.78 | 99 | 311 | 2,737 | cd |
| Prad; early; no planting | 1,675 | 76.78 | 99 | 353 | 2,782 | cd |
| Prad; early; planting | 2,261 | 76.78 | 99 | 650 | 5,872 | g |
| Prad; do nothing; coupe density | 1,244 | 76.78 | 99 | 269 | 2,162 | a |
| Prad; do nothing; early density | 1,267 | 76.78 | 99 | 353 | 2,318 | a |
| Prad whole stand; mānuka/kānuka | 2,352 | 76.78 | 99 | 720 | 3,855 | g |

Notes: 'Scenario' lists each combination of exotic species, disturbance, and planting. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 0.05. SE and df are, respectively, standard error and degrees of freedom in the LME model. 2.75% and 97.5% are the 95% confidence bounds of carbon values for each scenario across sites.

**Table 3. Post hoc analyses of a linear mixed-effects (LME) model predicting the integral of total (native + exotic) carbon stocks (summed across the 100 year simulation period) against management scenario**

| Scenario | Carbon integral (Mg C/ha summed over 100 years) | SE | df | 2.75% | 97.5% | Group |
|---|---|---|---|---|---|---|
| Efas; coupe; no planting | 4,525 | 254 | 99 | 1,258 | 7,384 | d |
| Efas; coupe; planting | 4,335 | 254 | 99 | 1,157 | 6,977 | d |
| Efas; early; no planting | 2,313 | 254 | 99 | 614 | 3,605 | a |
| Efas; early; planting | 2,665 | 254 | 99 | 889 | 4,956 | a |
| Efas; do nothing; coupe density | 6,172 | 254 | 99 | 1,298 | 10,605 | e |
| Efas; do nothing; early density | 6,476 | 254 | 99 | 1,466 | 11,248 | e |
| Efas whole stand; mānuka/kānuka | 3,462 | 254 | 99 | 1,074 | 5,435 | bc |
| Prad; coupe; no planting | 5,937 | 254 | 99 | 2,210 | 9,241 | e |
| Prad; coupe; planting | 5,949 | 254 | 99 | 2,183 | 9,361 | e |
| Prad; early; no planting | 2,425 | 254 | 99 | 571 | 4,116 | a |
| Prad; early; planting | 3,010 | 254 | 99 | 864 | 6,576 | ab |
| Prad; do nothing; coupe density | 13,653 | 254 | 99 | 5,557 | 21,637 | f |
| Prad; do nothing; early density | 14,078 | 254 | 99 | 5,599 | 21,982 | f |
| Prad whole stand; mānuka/kānuka | 4,098 | 254 | 99 | 1,670 | 6,000 | cd |

Notes: 'Scenario' lists each combination of exotic species, disturbance, and planting. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 005. SE and df are, respectively, standard error and degrees of freedom in the LME model. 2.75% and 97.5% are the 95% confidence bounds of carbon values for each scenario across sites.

**Table 4. Post hoc analyses of linear mixed-effects (LME) models predicting native carbon stocks (Mg C/ha/year) from management scenario for stand ages 25, 50, 75, and 100 years**

| Scenario | Mean (95 CI) 25 | | Mean (95 CI) 50 | | Mean (95 CI) 75 | | Mean (95 CI) 100 | |
|---|---|---|---|---|---|---|---|---|
| Efas; coupe; no planting | 2.98 (1.02, 5.42) | c | 12.9 (3.75, 23) | de | 33.5 (9.68, 6.5) | g | 63.9 (18.1, 134) | ef |
| Efas; coupe; planting | 2.75 (0.779, 4.64) | bc | 11.8 (2.87, 19.7) | cd | 30.3 (6.61, 9.8) | ef | 57.5 (12.3, 95.6) | d |
| Efas; early; no planting | 2.63 (0.914, 4.29) | ab | 11.2 (2.88, 17.9) | bc | 26.9 (6.85, 2.9) | cd | 48.6 (12.8, 76.7) | bc |
| Efas; early; planting | 3.22 (1.36, 5.32) | d | 13.7 (4.68, 27.7) | e | 32.8 (10.3, 5.2) | fg | 59 (17.6, 139) | de |
| Efas; do nothing; coupe density | 2.51 (0.763, 4.57) | ab | 9.99 (2.89, 16.8) | ab | 24.4 (7.01, 0.6) | c | 45.7 (13.3, 3.8) | b |
| Efas; do nothing; early density | 2.52 (0.87, 4.66) | ab | 9.99 (3.24, 18.5) | ab | 24.1 (7.31, 2.3) | bc | 44.9 (13.1, 76.2) | b |
| Efas whole stand; mānuka/kānuka | 3.24 (1.59, 5.07) | d | 16 (6, 25.6) | f | 39.2 (13.3, 3.8) | h | 70.9 (21.8, 114) | g |
| Prad; coupe; no planting | 2.72 (0.745, 5) | b | 11.6 (2.69, 21.2) | c | 28.2 (5.64, 6.6) | de | 51.1 (10.4, 0.3) | c |
| Prad; coupe; planting | 2.59 (0.562, 4.66) | ab | 11 (2.02, 18.6) | bc | 28.2 (5.12, 6.2) | de | 53.7 (10.1, 6.9) | cd |
| Prad; early; no planting | 2.72 (0.745, 5) | b | 11.6 (2.69, 21.2) | c | 28.2 (5.64, 6.6) | de | 51.1 (10.4, 0.3) | c |
| Prad; early; planting | 3.64 (1.44, 6.54) | e | 16 (4.98, 39.7) | f | 38.2 (10.6, 102) | h | 67.8 (18.8, 180) | fg |
| Prad; do nothing; coupe density | 2.4 (0.571, 4.25) | a | 9.16 (1.97, 16.2) | a | 20.8 (4.37, 6.1) | a | 36.1 (8.57, 2.3) | a |
| Prad; do nothing; early density | 2.46 (0.697, 4.32) | a | 9.35 (2.74, 16.5) | a | 21.1 (5.62, 39) | ab | 36.7 (10.2, 6.8) | a |
| Prad whole stand; mānuka/kānuka | 3.28 (1.44, 5.13) | d | 16.4 (5.62, 26.2) | f | 40 (11.8, 6.2) | h | 72 (20.1, 118) | g |

Notes: 'Scenario' lists each combination of exotic species, disturbance and planting. Mean (95 CI) presents the mean and 95% confidence interval across sites for each scenario at each stand age. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 0.05.

**Table 5. Post hoc analyses of linear mixed-effects (LME) models predicting total (native + exotic) carbon stocks (Mg C/ha/year) from management scenario for stand ages 25, 50, 75, and 100 years**

| Scenario | Mean (95 CI) 25 | | Mean (95 CI) 50 | | Mean (95 CI) 75 | | Mean (95 CI) 100 | |
|---|---|---|---|---|---|---|---|---|
| Efas; coupe; no planting | 64.6<br>(7.96, 116) | b | 45.3<br>(9.92, 80) | b | 33.5<br>(9.68, 66.5) | abc | 63.9<br>(18.1, 134) | cde |
| Efas; coupe; planting | 64.4<br>(7.36, 116) | b | 44.3<br>(9.67, 78.3) | b | 30.3<br>(6.61, 49.8) | ab | 57.5<br>(12.3, 95.6) | abc |
| Efas; early; no planting | 2.64<br>(0.916, 4.3) | a | 11.2<br>(2.88, 17.9) | a | 26.9<br>(6.85, 42.9) | a | 48.6<br>(12.8, 76.7) | a |
| Efas; early; planting | 3.23<br>(1.36, 5.33) | a | 13.7<br>(4.68, 27.7) | a | 32.8<br>(10.3, 75.2) | abc | 59<br>(17.6, 139) | bcd |
| Efas; do nothing; coupe density | 69.4<br>(7.58, 124) | b | 62.4<br>(11.3, 114) | c | 66<br>(14.4, 116) | d | 78.4<br>(18.4, 132) | f |
| Efas; do nothing; early density | 74.1<br>(7.93, 134) | b | 66.4<br>(12, 124) | c | 68.8<br>(16.7, 122) | d | 80.1<br>(20.2, 134) | f |
| Efas whole stand; mānuka/kānuka | 64.8<br>(7.56, 116) | b | 16<br>(6, 25.6) | a | 39.2<br>(13.3, 63.8) | bc | 70.9<br>(21.8, 114) | ef |
| Prad; coupe; no planting | 111<br>(52.7, 198) | c | 65.5<br>(21.6, 123) | c | 28.2<br>(5.64, 46.6) | a | 51.1<br>(10.4, 80.3) | ab |
| Prad; coupe; planting | 111<br>(52.9, 198) | c | 65<br>(21.3, 121) | c | 28.2<br>(5.12, 46.2) | a | 53.7<br>(10.1, 86.9) | ab |
| Prad; early; no planting | 2.72 (0.746, 5) | a | 11.6<br>(2.69, 21.2) | a | 28.2<br>(5.64, 46.6) | a | 51.1 (10.4, 80.3) | ab |
| Prad; early; planting | 3.64<br>(1.44, 6.54) | a | 16<br>(4.98, 39.7) | a | 38.2<br>(10.6, 102) | bc | 67.8<br>(18.8, 180) | de |
| Prad; do nothing; coupe density | 131<br>(62.2, 241) | d | 151<br>(58.6, 251) | d | 160<br>(61, 258) | e | 175<br>(64.5, 282) | g |
| Prad; do nothing; early density | 137<br>(63.7, 241) | d | 156<br>(59.5, 255) | d | 165<br>(61.5, 264) | e | 180<br>(64.6, 291) | g |
| Prad whole stand; mānuka/kānuka | 112<br>(53.7, 199) | c | 16.4<br>(5.62, 26.2) | a | 40<br>(11.8, 66.2) | c | 72<br>(20.1, 118) | ef |

Notes: 'Scenario' lists each combination of exotic species, disturbance, and planting. Mean (95 CI) presents the mean and 95% confidence interval across sites for each scenario at each stand age. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 0.05.

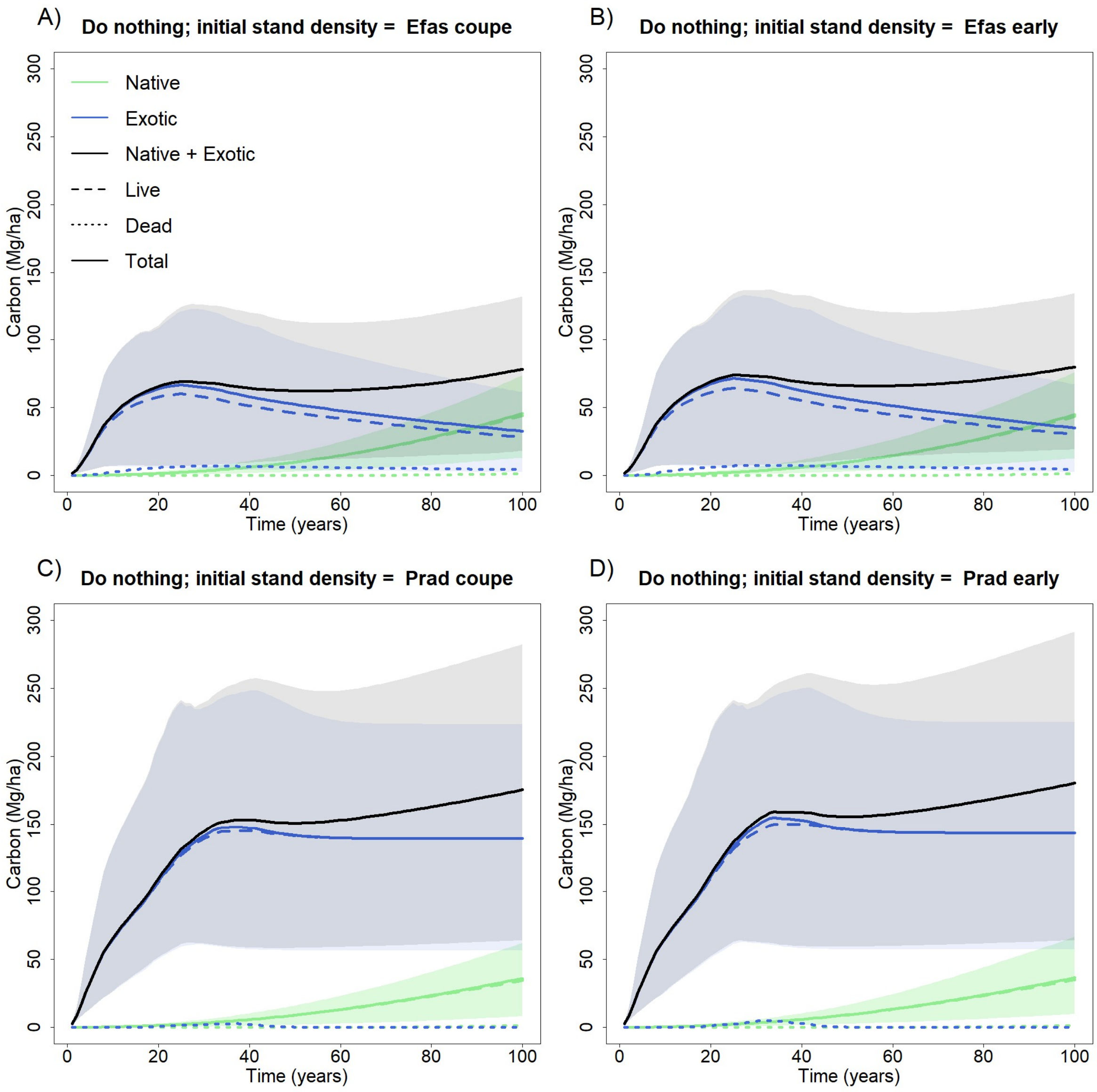

**Figure 4. Time series of live (dashed lines), dead (dotted lines), and total (live + dead, solid lines) native (green), exotic (blue), and native + exotic (black) carbon pools for the 'do nothing' new forest scenarios.**

Notes: Under these scenarios initial stand density is the same as for the corresponding species and disturbance scenario listed in the sub-figure titles, but no disturbance or native planting is applied. Shaded areas indicate 95% confidence bounds (across sites) for total native (green) and exotic (blue) and native + exotic (grey) carbon stocks. Native carbon values for each site represent the mean taken across PPA simulation runs, since the PPA is a stochastic model.

### *Whole-stand disturbance with dense restoration planting*

Almost all carbon stocks are lost following the removal of the exotic canopy. The total carbon stock for *E. fastigata* recovered to its pre-disturbance peak within 100 years, whereas *P. radiata* did not, because the pre-disturbance peak for *P. radiata* was much higher (Figure 5). The integral of native carbon is not significantly different between exotic species (Table 2), nor are native carbon stocks significantly different at any of the stand ages examined (Table 4). The integral of total carbon stocks was not significantly different between exotic canopy species (Table 3), and the only significant difference across the stand ages examined was at 25 years (Table 5).

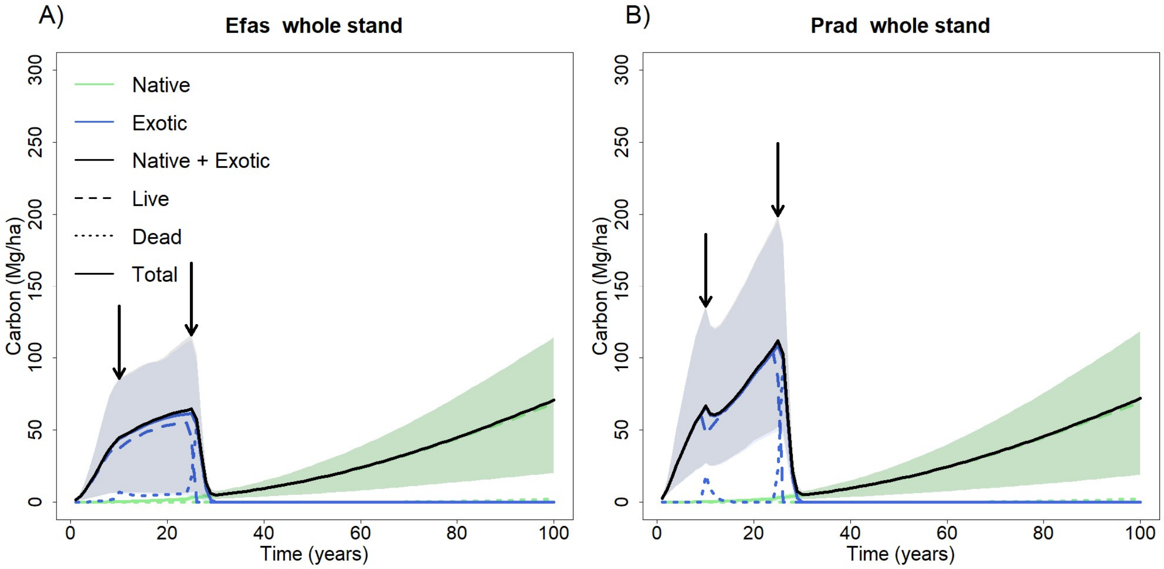

**Figure 5. Time series of live (dashed lines), dead (dotted lines), and total (live + dead, solid lines) native (green), exotic (blue), and native + exotic (black) carbon pools for the Eucalyptus fastigata (Efas) and Pinus radiata (Prad) new forest whole-stand disturbance scenarios with dense planting of mānuka and kānuka.**

**Notes: Vertical arrows indicate the years in which thinning and/or canopy disturbance was applied. In these scenarios all exotic plantation trees are killed and left standing 25 years after planting. Following canopy disturbance, mānuka and kānuka are planted at 1,100 sph with 550 stems of each species. Shaded areas indicate 95% confidence bounds (across sites) for total native (green) and exotic (blue) and native + exotic (grey) carbon stocks. Planting was assumed to occur in the same year as canopy disturbances. Native carbon values for each site represent the mean taken across PPA simulation runs, since the PPA is a stochastic model.**

### *Thinning with coupe and early canopy intervention*

For *P. radiata* the integral of native carbon stocks was significantly higher for the early intervention with native planting scenario than all other early intervention and coupe scenarios, and there were no significant differences between any of the other scenarios (Figure 6; Table 2). These results were repeated for carbon stocks at all of the stand ages examined (Table 4).

The integral (sum across years) of total carbon is significantly lower in the early intervention scenario than in the coupe scenario, and both are much lower than in the corresponding 'do nothing' scenarios (Figure 6; Table 3). The decline of exotic carbon stocks is slower over time for the coupe scenario (because exotic cover is removed more gradually) and native carbon stocks are greater at the time of final exotic overstorey removal, resulting in a somewhat smoother transition in terms of carbon stocks compared to the early intervention or whole-stand disturbance scenarios.

However, there is a trough in carbon stocks during the transition from exotic to native forest composition. There were no significant differences in total carbon stocks between any of the *P. radiata* early intervention and coupe scenarios until a stand age of 75 years, where the early intervention with native planting scenario was significantly higher than the other scenarios (Figure 6; Table 5). Notably, total carbon stocks do not recover to a pre-disturbance peak within 100 years in any scenario except early intervention with native planting (Figure 6).

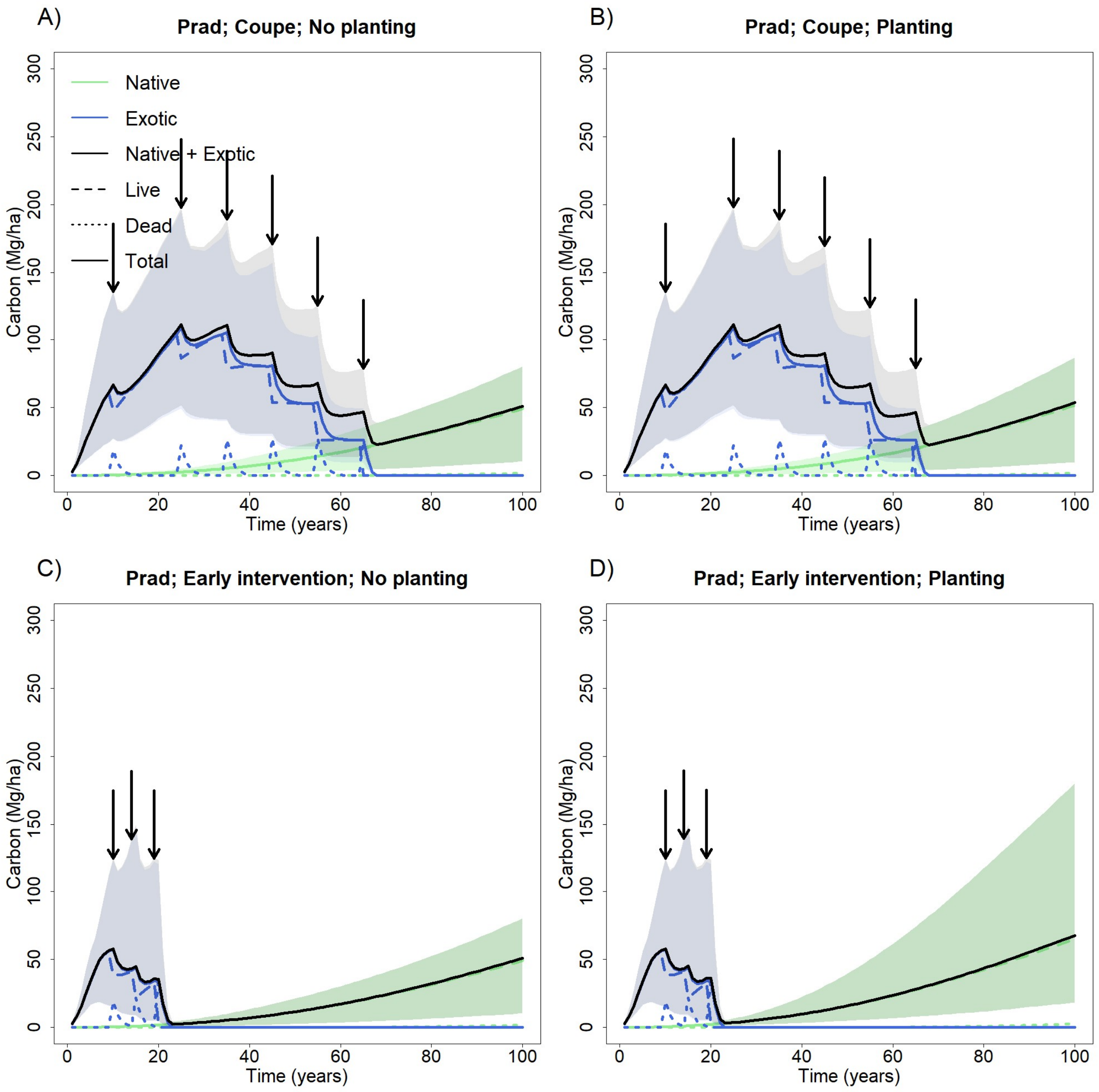

**Figure 6. Time series of live (dashed lines), dead (dotted lines), and total (live + dead, solid lines) native (green), exotic (blue), and native + exotic (black) carbon pools for the Pinus radiata (Prad) new forest disturbance scenarios, with and without supplementary planting of natives.**

**Notes: Vertical arrows indicate the years in which thinning and/or canopy disturbance was applied. Early intervention involved tree removals of one-third of stems, beginning 9 years after planting and separated by 5-year intervals. In the coupe scenarios, exotic stands are thinned to 600 sph 9 years after stand establishment, followed by five removals of 20% of the exotic stand area beginning 25 years after stand establishment and separated by 10-year intervals. The native species selected for planting at each site was the canopy dominant (drawn from forest canopy-dominant conifers, beech species and tawa), with the highest predicted occurrence probability (based on occurrences in LUCAS data). Native planting rate in both disturbance scenarios was one native planted for every two exotic stems removed at the year of removal. Shaded areas indicate 95% confidence bounds (across sites) for total native (green) and exotic (blue) and native + exotic (grey) carbon stocks. Planting was assumed to occur in the same year as canopy disturbances. Native carbon values for each site represent the mean taken across PPA simulation runs, since the PPA is a stochastic model.**

For *E. fastigata*, the integral of native carbon was significantly higher for the coupe with no native planting scenario than the coupe with native planting and the early intervention with no native planting scenarios; the early intervention and coupe with native planting scenarios were significantly greater than the early intervention with no planting scenario (Table 2). These results were repeated at each of the stand ages examined (Table 4).

The integral of total carbon was significantly lower in the early intervention scenarios compared to the coupe scenarios, and coupe scenarios for *E. fastigata* were significantly lower than those for *P. radiata* (Figures 6 & 7; Table 3). There was no significant difference for the integral of total carbon stocks between *E. fastigata* and *P. radiata* early intervention scenarios (Table 5). Total carbon stocks recover to a pre-disturbance peak, or close to it, within 100 years for all scenarios, although for early intervention with planting it appears to reach the target 10 years earlier.

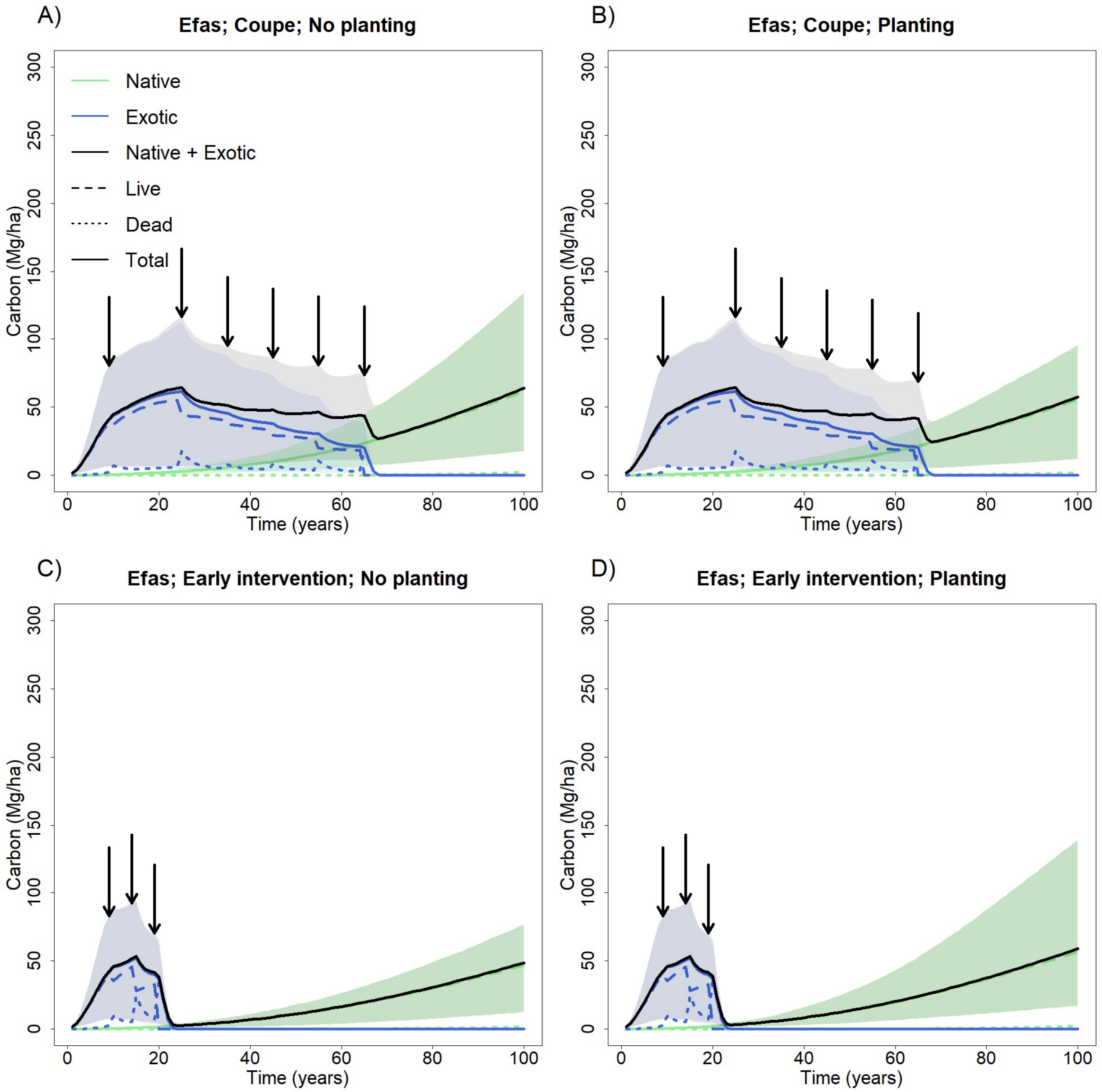

**Figure 7. Time series of live (dashed lines), dead (dotted lines), and total (live + dead, solid lines) native (green), exotic (blue), and native + exotic (black) carbon pools for the Eucalyptus fastigata (Efas) new forest disturbance scenarios, with and without supplementary planting of natives. Notes: Vertical arrows indicate the years in which thinning and/or canopy disturbance was applied. Early intervention involved tree removals of one-third of stems beginning 9 years after planting and separated by 5-year intervals. In the coupe scenarios exotic stands are thinned to 600 sph 9 years after stand establishment, followed by five removals of 20% of the exotic stand area beginning 25 years after stand establishment and separated by 10-year intervals. The native species selected for planting at each site was the canopy dominant (drawn from forest canopy-dominant conifers, beech species and tawa) with the highest predicted occurrence probability (based on occurrences in LUCAS data). Native planting rate in both disturbance scenarios was one native planted for every two exotic stems removed at the year of removal. Shaded areas indicate 95% confidence bounds (across sites) for total native (green) and exotic (blue), and native + exotic (grey) carbon stocks. Native carbon values for each site represent the mean taken across PPA simulation runs, since the PPA is a stochastic model.**

### 4.1.2 Comparison among scenarios

The highest values for the integral of native carbon stocks are observed in the *P. radiata* early intervention with planting scenario, as well as in the *P. radiata* and *E. fastigata* whole-stand disturbance scenarios with dense mānuka/kānuka planting. Conversely, the lowest values are found in the 'do nothing' scenarios for both *E. fastigata* and *P. radiata*. It may be useful to link these findings to the time required to reach these carbon values (Table 2).

The highest values for the integral of total carbon are observed in the *P. radiata* 'do nothing' scenarios, the *E. fastigata* 'do nothing' scenarios, and the *P. radiata* coupe scenario. Conversely, the lowest values for the integral of total carbon are found in the early intervention scenarios for both exotic species (Table 3).

### 4.1.3 Effect of management and site variables on the integral of carbon stocks

Mean annual temperature (nz_mat) is by far the most important predictor of the integral of native carbon stocks, followed by mean annual rainfall (nz_mar) and disturbance (0 = none, 1 = coupe, 2 = early intervention) (Figure 8). A cross-validated correlation of 0.792 indicates a good fit between the fitted and observed values. Native carbon increased with temperature and rainfall and was lower in the 'do nothing' scenarios compared to other disturbance scenarios (Figure 9). The largest interaction was between temperature and rainfall, with native carbon highest when both temperature and rainfall are high, particularly under high temperature with coupe and early intervention disturbances, and under *P. radiata* with early intervention disturbance, or *E. fastigata* with either coupe or early intervention disturbance (Figure 10).

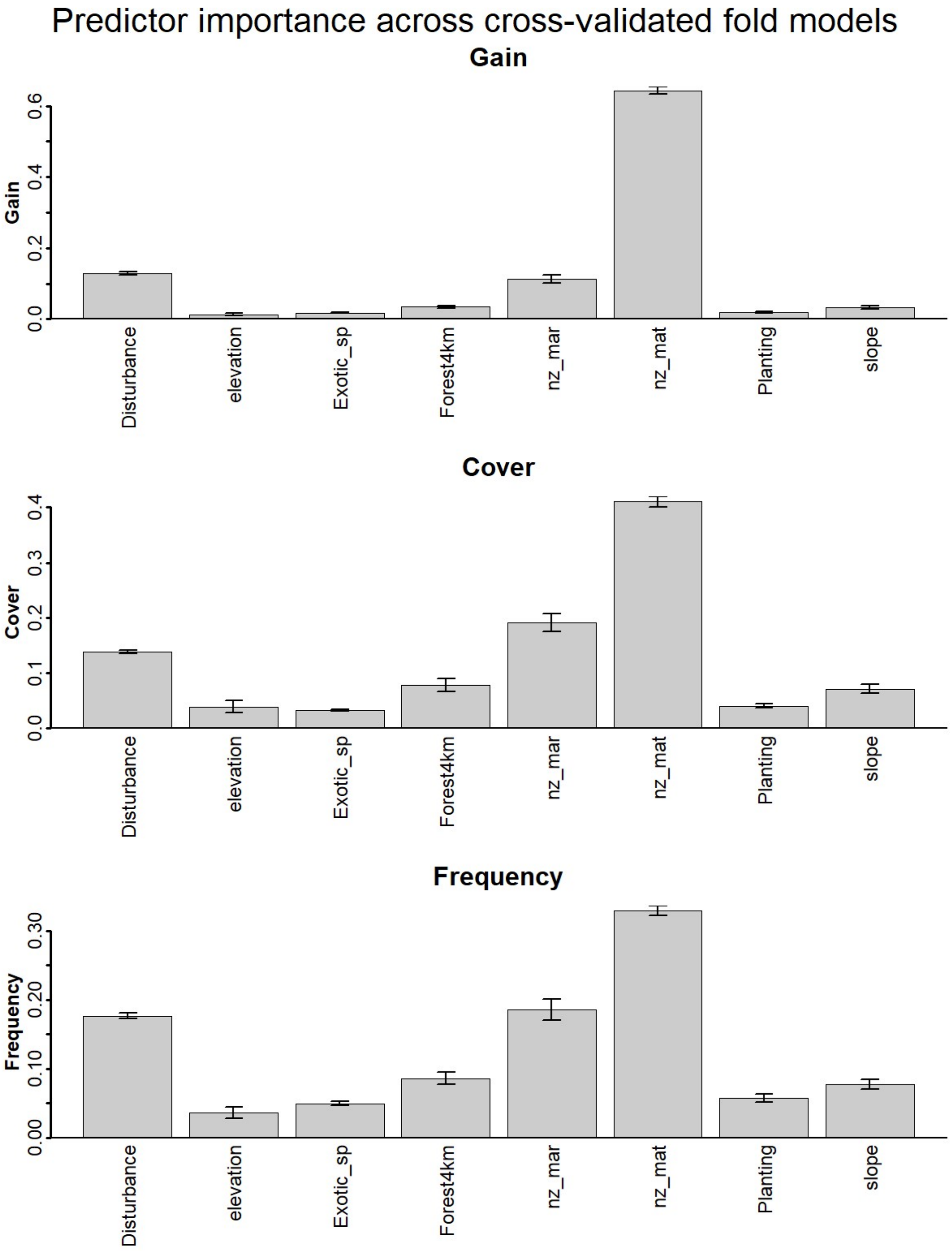

**Figure 8. Importance of predictors in xgboost regression tree models for the integral (summed across years) of native carbon.**

**Notes: Gain is the reduction in unexplained deviance when the variable is used to make a split in the data set. Cover is the proportion of observations covered by splits in the data set involving each predictor. Frequency is the proportion of splits involving each predictor. Disturbance = exotic canopy disturbance type (0 = none, 1 = coupe, 2 = early intervention); elevation = altitude; Exotic_sp = exotic canopy species (0 = Efas, 1 = Prad); Forest4km = the amount of native forest cover within a 4 km radius; nz_mar = mean annual rainfall; nz_mat = mean annual temperature; Planting = whether or not native planting was applied to supplement natural recruitment; slope = topographic slope, derived from 15 m digital elevation model.**

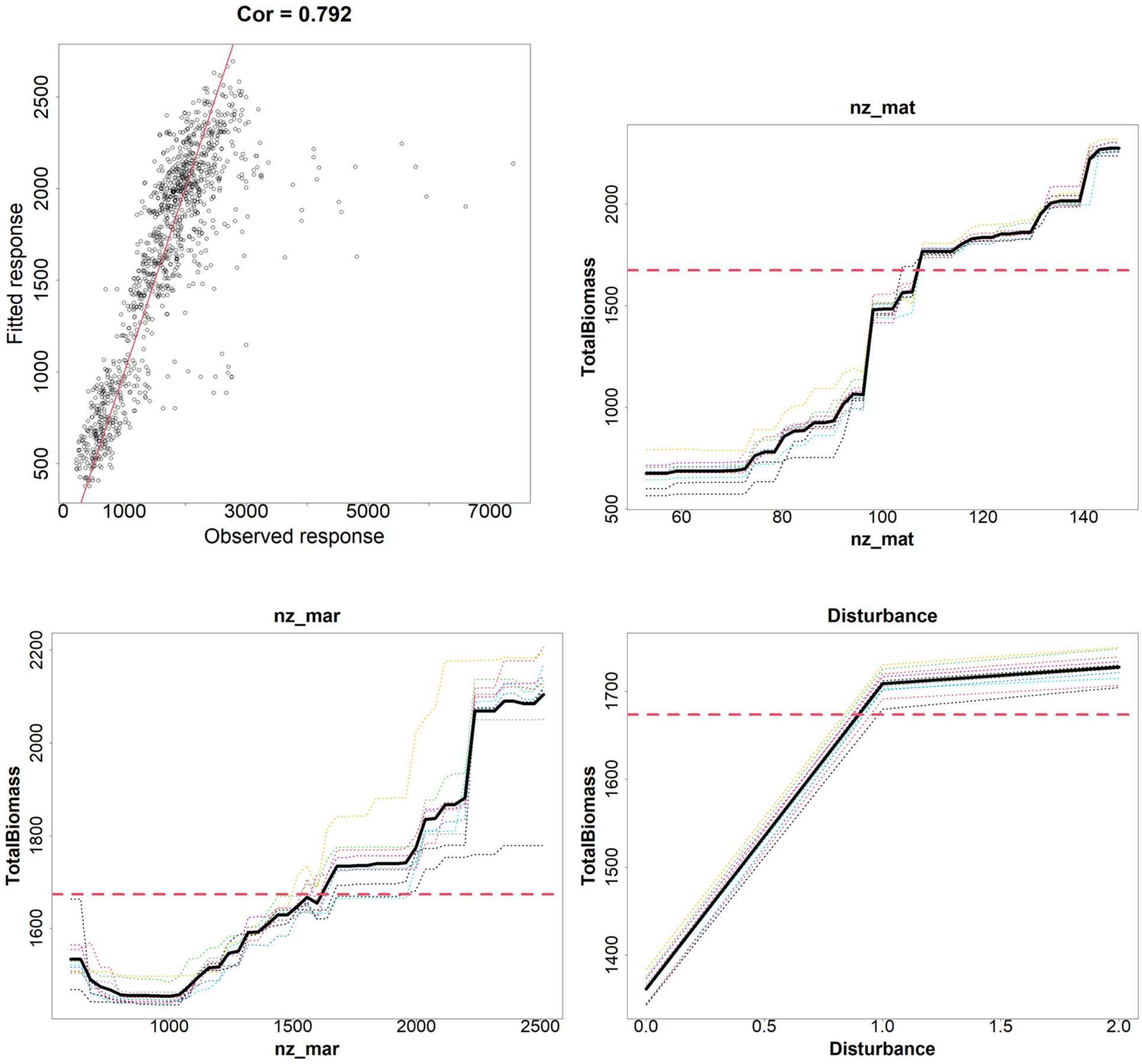

**Figure 9. Cross-validated fitted native carbon values from xgboost regression tree models against observed values, and partial dependence plots (effect independent of other predictors) for selected predictor variables: mean annual temperature (nz_mat), mean annual rainfall (nz_mar), and exotic canopy disturbance type (Disturbance).**

**Notes: Disturbance is expressed on an ordinal scale (0 = do nothing, 1 = coupe, and 2 = early intervention). Mean annual temperature is expressed as ˚C × 10.**

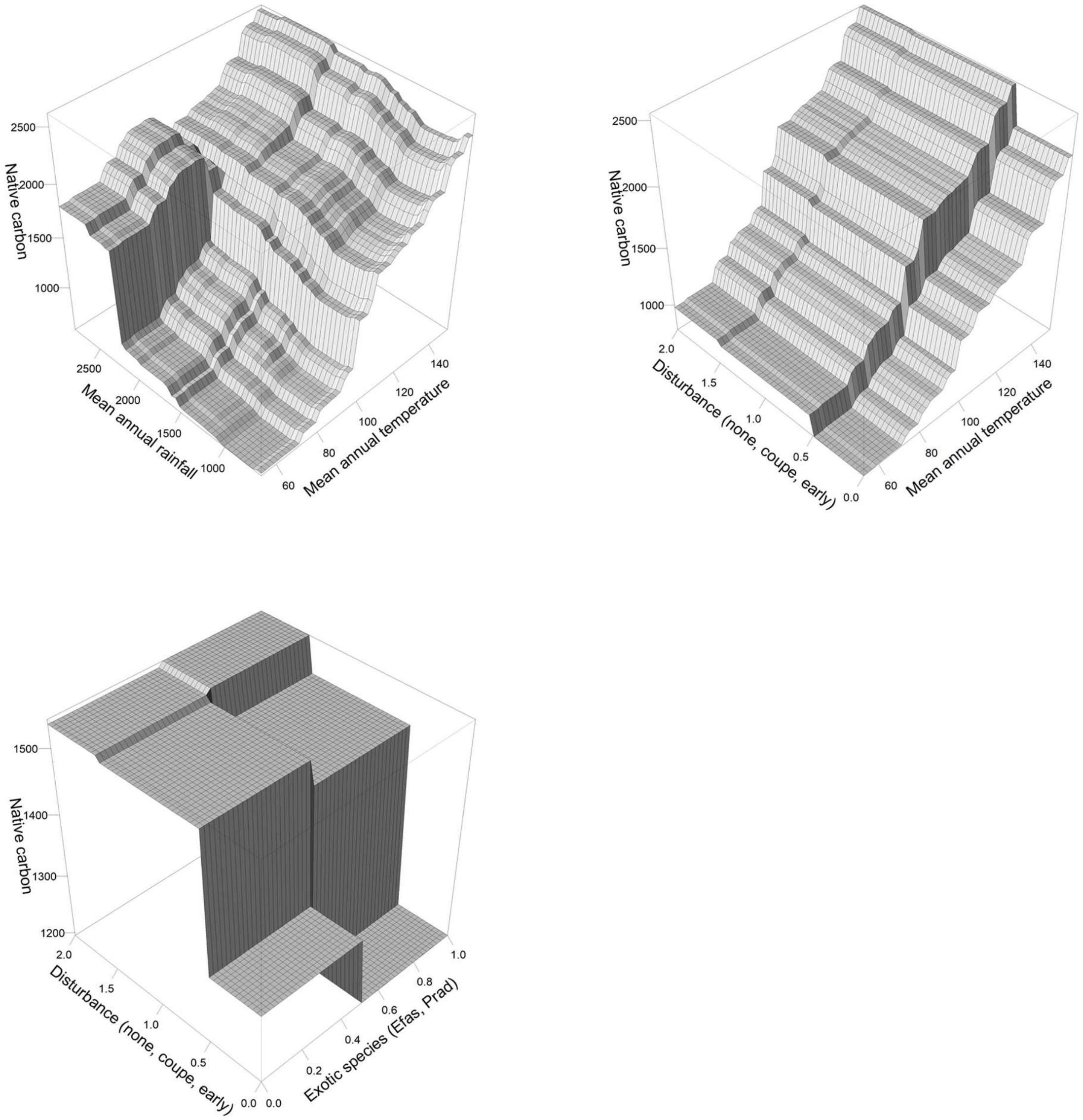

**Figure 10. Perspective plots of strongest interactions between predictors in xgboost regression tree models for native carbon.**
**Notes: Disturbance is expressed on an ordinal scale (0 = do nothing, 1 = coupe and 2 = early intervention). Mean annual temperature is expressed as ˚C × 10. Exotic species is expressed on an ordinal scale (0 = E. fastigata, 1 = Pinus radiata).**

Mean annual temperature (nz_mat) and disturbance (0 = none, 1 = coupe, 2 = early intervention) are the most important predictors of the integral of total (native plus exotic) carbon stocks, followed by exotic canopy species (Exotic_sp, 0 = *E. fastigata*, 1 = *P. radiata*) and rainfall (nz_mar) (Figure 11). A cross-validated correlation of 0.845 indicates a good fit between the fitted and observed values. Total carbon increased with temperature and was higher in the ‘do nothing’ scenarios compared to other disturbance scenarios, and higher for *P. radiata* than for *E. fastigata* (Figure 12). Total carbon is highest for the ‘do nothing’ disturbance scenario at high temperatures, for *P. radiata* at high temperatures, and for *P. radiata* with ‘do nothing’ disturbance at high rainfall (Figure 13).

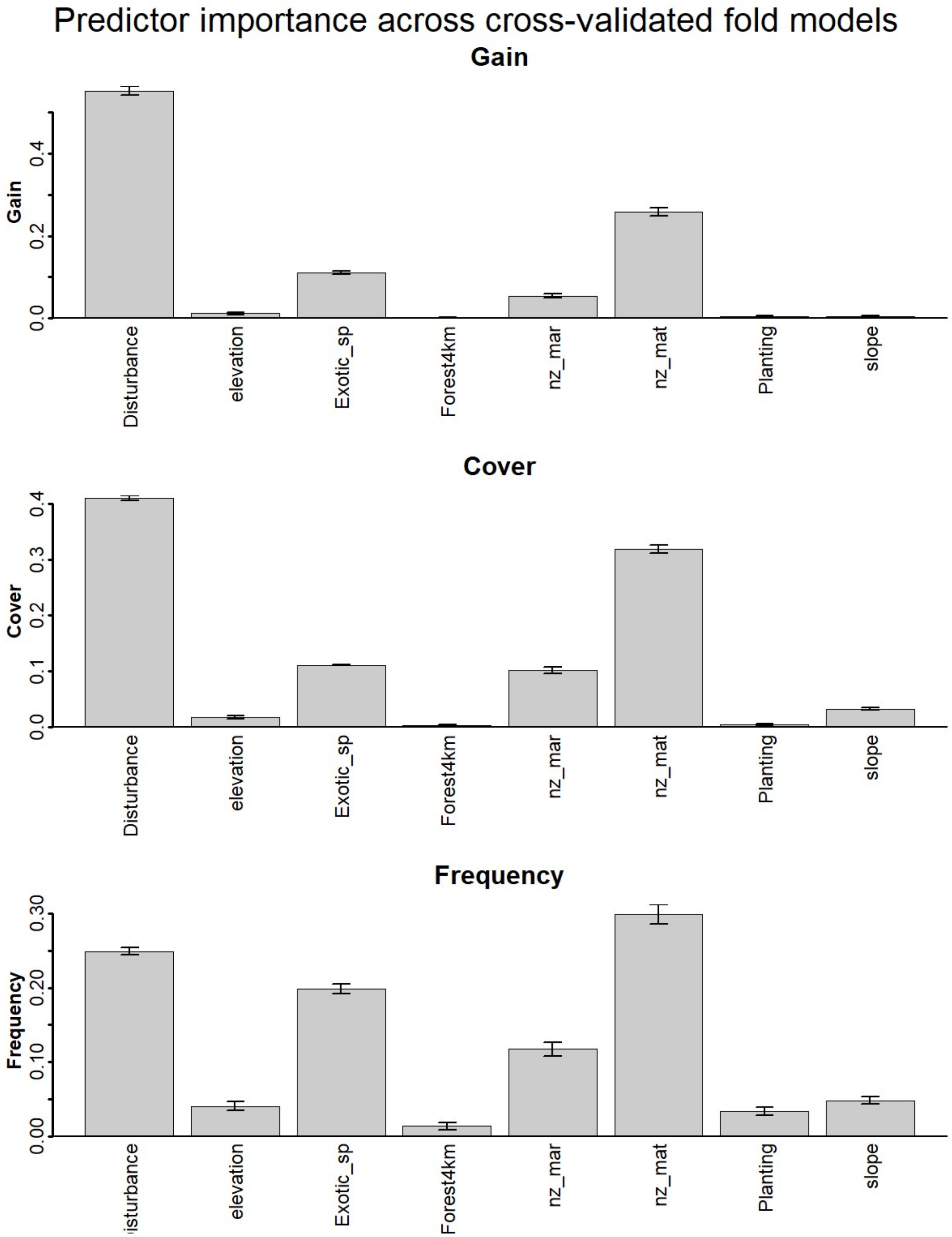

**Figure 11. Importance of predictors in xgboost regression tree models for the integral (sum across years) of total (native + exotic) carbon.**

**Notes: Gain is the reduction in unexplained deviance when the variable is used to make a split in the data set. Cover is the proportion of observations covered by splits in the data set involving each predictor. Frequency is the proportion of splits involving each predictor. Disturbance = exotic canopy disturbance type (0 = none, 1 = coupe, 2 = early intervention); elevation = altitude; Exotic_sp = exotic canopy species (0 = Efas, 1 = Prad); Forest4km = the amount of native forest cover within a 4 km radius; nz_mar = mean annual rainfall; nz_mat = mean annual temperature; Planting = whether or not native planting was applied to supplement natural recruitment; slope = topographic slope, derived from 15 m digital elevation model.**

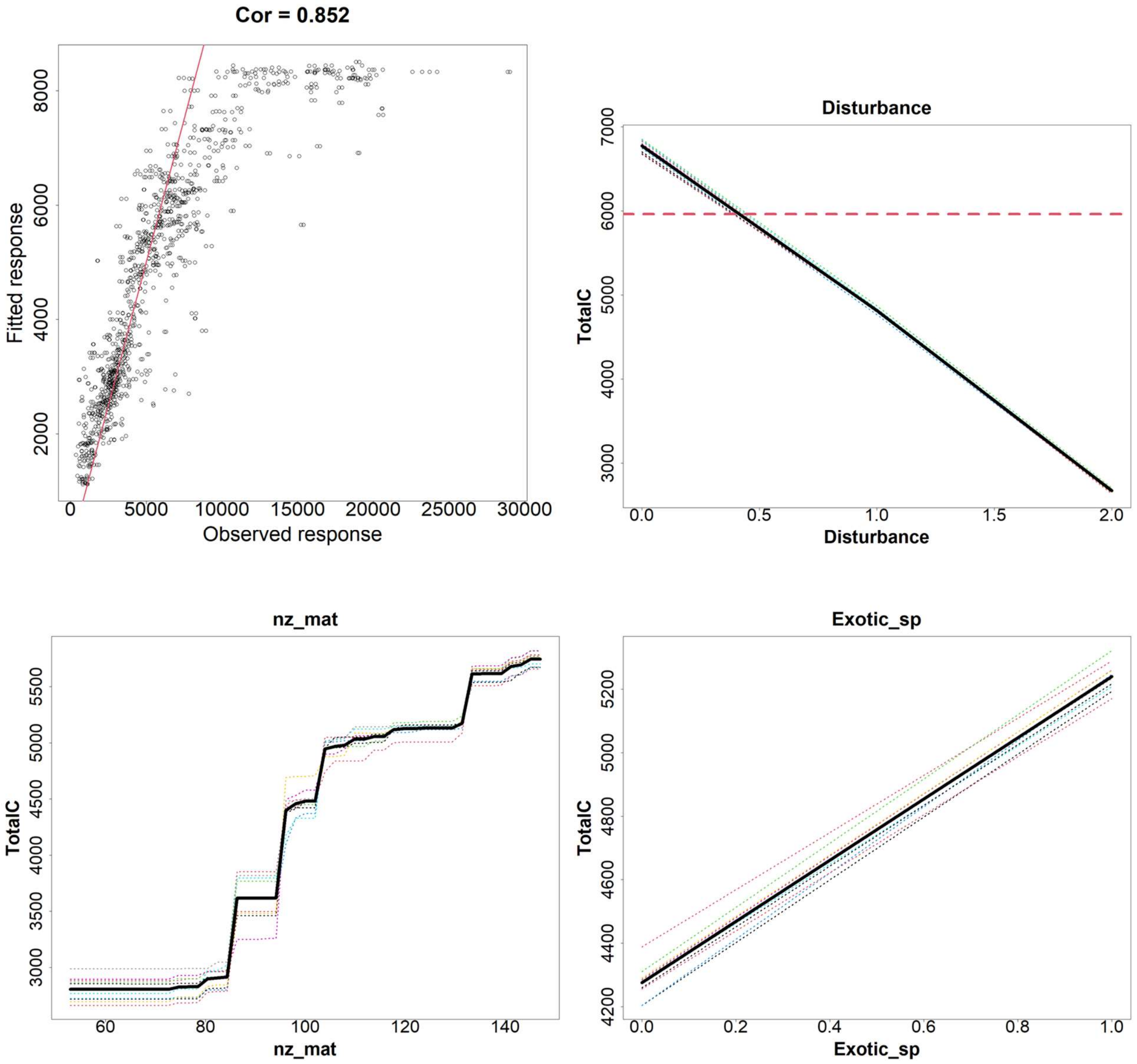

**Figure 12. Cross-validated fitted total carbon (native + exotic) values from xgboost regression tree models against observed values, and partial dependence plots (effect independent of other predictors) for selected predictors: mean annual temperature (nz_mat'), exotic canopy disturbance type (Disturbance), and exotic canopy species (Prad).**
**Notes: Disturbance is expressed on an ordinal scale (0 = do nothing, 1 = coupe and 2 = early intervention). Mean annual temperature is expressed as ˚C × 10. Prad is expressed on an ordinal scale (0 = E. fastigata, 1 = P. radiata).**

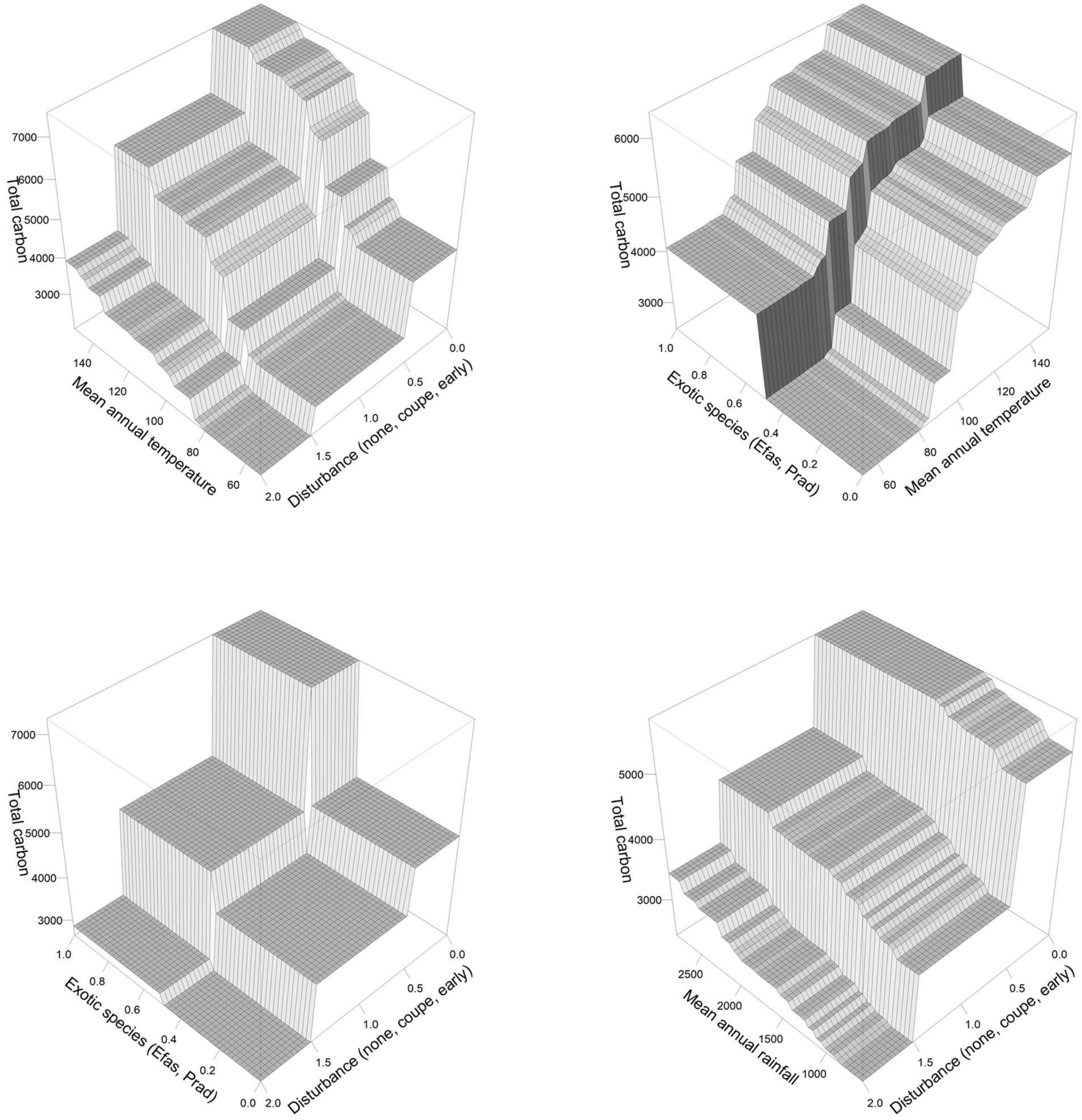

**Figure 13. Perspective plots of strongest interactions between predictors in xgboost regression tree models for total carbon (native + exotic).**

**Notes: Disturbance is expressed on an ordinal scale (0 = do nothing, 1 = coupe and 2 = early intervention). Mean annual temperature is expressed as ˚C × 10. Prad is expressed on an ordinal scale (0 = E. fastigata, 1 = P. radiata).**

### 4.1.4 Native species composition

Mānuka/kānuka was the most abundant group in the first 10 years of all scenarios (Appendix 4). After that, 'other' was the most abundant group. In the 'do nothing', whole-stand disturbance (with dense mānuka/kānuka planting), early intervention, and coupe disturbance scenarios without planting, canopy-dominant species were less abundant than mānuka/kānuka for the entire simulation period. Canopy dominant species become more abundant than mānuka/kānuka in all early intervention and coupe disturbance scenarios with native planting, except for coupe disturbance under *E. fastigata*.

The positive effects of planting on native and total carbon in early intervention scenarios is most likely due to the enhanced contribution of canopy dominant species. In the early intervention scenarios, earlier planting of canopy dominants allows them to make a larger contribution to carbon stocks within the 100-year simulation period (e.g. 15 Mg C/ha for early intervention with planting vs. 10 Mg C/ha for coupe scenario with planting under *P. radiata*). By contrast in the *E. fastigata* coupe disturbance scenario, planting did not noticeably increase the biomass of canopy dominant species (relative to the no planting scenario), and also resulted in lower biomass for the mānuka/kānuka and 'other' groups.

## 4.2 Pre-1990 forests

Among the pre-1990 scenarios, the integral of native carbon was significantly lower for the 'do nothing' scenario than for the coupe scenarios, and significantly higher for the coupe with native planting scenario than for all other pre-1990 scenarios (Figure 14; Table 6). The integral of total carbon stocks was significantly higher for the 'do nothing' scenario than for the pre-1990 coupe scenarios (Table 7). Total carbon achieved a similar peak value for coupe disturbance with or without planting, but was higher post disturbance with planting.

The significant differences in the integral of native carbon between scenarios were also observed for native carbon stocks at each of the stand ages examined (Table 8. Significant differences in total carbon stocks between the 'do-nothing' scenario and the two coupe disturbance scenarios were observed at all of the stand ages examined (Table 9). However, significant differences in total carbon between the coupe scenarios were only observed for stand ages ≥75 years.

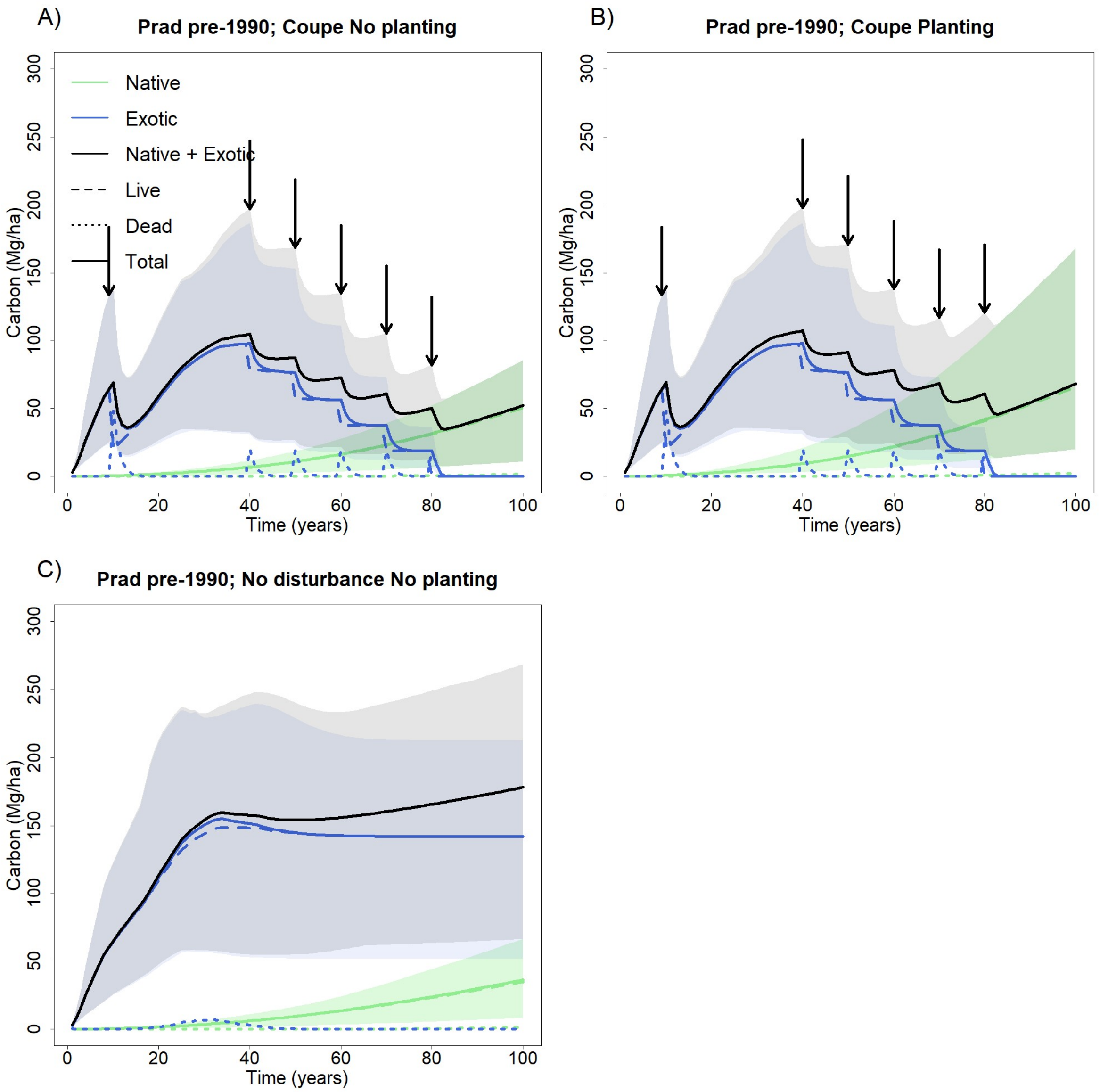

**Figure 14. Time series of native and exotic carbon pools for the Pinus radiata (Prad) pre-1990 forest coupe disturbance scenario with and without native planting, and for a 'do nothing' scenario. Notes: Vertical arrows indicate the years in which thinning and/or canopy disturbance was applied. In these scenarios exotic stands are thinned to 350 sph 9 years after stand establishment, followed by five removals of 20% of the exotic stand area beginning 40 years after stand establishment and separated by 10-year intervals. The native species selected for planting at each site was the canopy dominant (drawn from forest canopy-dominant conifers, beech species, and tawa) with the highest predicted occurrence probability (based on occurrences in LUCAS data). Native planting rate in both disturbance scenarios was one native planted for every two exotic stems removed at the year of removal.**

**Table 6. Post hoc analyses of a linear mixed-effects (LME) model predicting the integral of native carbon stocks (summed across years) from management scenario**

| Scenario | Mean | SE | df | 2.75% | 97.5% | Group |
|---|---|---|---|---|---|---|
| Prad pre-1990; coupe; no planting | 1,648 | 80.13 | 99 | 357 | 2,670 | b |
| Prad pre-1990; coupe; planting | 2,189 | 80.13 | 99 | 680 | 5,079 | c |
| Prad pre-1990; no disturbance; no planting | 1,283 | 80.13 | 99 | 308 | 2,266 | a |

Notes: 'Scenario' lists each pre-1990 forest scenario. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 005. SE and df are, respectively, standard error and degrees of freedom in the LME model. 2.75% and 97.5% are the 95% confidence bounds of carbon values for each scenario across sites.

**Table 7. Post hoc analyses of a linear mixed-effects (LME) model predicting the integral of total (native + exotic) carbon (summed across years) from management scenario**

| Scenario | Mean | SE | df | 2.75% | 97.5% | Group |
|---|---|---|---|---|---|---|
| Prad pre-1990; coupe; no planting | 6,168 | 331.93 | 99 | 2,059 | 10,313 | a |
| Prad pre-1990; coupe; planting | 6,709 | 331.93 | 99 | 2,314 | 11,149 | a |
| Prad pre-1990; no disturbance; no planting | 14,126 | 331.93 | 99 | 5,574 | 20,659 | b |

Notes: 'Scenario' lists each pre-1990 forest scenario. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 005. SE and df are, respectively, standard error and degrees of freedom in the LME model. 2.75% and 97.5% are the 95% confidence bounds of carbon values for each scenario across sites.

**Table 8. Post hoc analyses of linear mixed-effects (LME) models predicting native carbon stocks (Mg C/ha/year) from pre-1990 management scenarios for stand ages 25, 50, 75, and 100 years**

| Scenario | Mean (95 CI) 25 | | Mean (95 CI) 50 | | Mean (95 CI) 75 | | Mean (95 CI) 100 | |
|---|---|---|---|---|---|---|---|---|
| Prad pre-1990; coupe; no planting | 2.81<br>(0.685, 4.78) | b | 11<br>(2.41, 18.6) | b | 27.3<br>(5.81, 45.3) | b | 52.2<br>(11, 85.6) | b |
| Prad pre-1990; coupe; planting | 3.91<br>(1.58, 8) | c | 14.8<br>(4.9, 34) | c | 36.3<br>(11.2, 88.5) | c | 68.2<br>(20.2, 168) | c |
| Prad pre-1990; no disturbance; no planting | 2.55<br>(0.699, 4.58) | a | 9.6<br>(2.35, 16.8) | a | 21.2<br>(4.87, 38.9) | a | 36.5<br>(8.62, 66.5) | a |

Notes:' Scenario' lists each combination of exotic species, disturbance, and planting. Mean (95 CI) presents the mean and 95% confidence interval across sites for each scenario at each stand age. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 0.05.

**Table 9. Post hoc analyses of linear mixed-effects (LME) models predicting total (native + exotic) carbon stocks (Mg C/ha/year) from pre-1990 management scenarios for stand ages 25, 50, 75, and 100 years**

| Scenario | Mean (95 CI) 25 | | Mean (95 CI) 50 | | Mean (95 CI) 75 | | Mean (95 CI) 100 | |
|---|---|---|---|---|---|---|---|---|
| Prad pre-1990; coupe; no planting | 80<br>(34.8, 145) | a | 87.2<br>(26.7, 169) | a | 46.4<br>(11.8, 75.5) | a | 52.2<br>(11, 85.6) | a |
| Prad pre-1990; coupe; planting | 81.1<br>(35.5, 146) | a | 91.1<br>(28.9, 171) | a | 55.4<br>(17, 106) | b | 68.2<br>(20.2, 168) | b |
| Prad pre-1990; no disturbance; no planting | 140<br>(61.3, 237) | b | 155<br>(57.6, 241) | b | 163<br>(62.8, 244) | c | 178<br>(66.6, 268) | c |

Notes: 'Scenario' lists each combination of exotic species, disturbance, and planting. Mean (95 CI) presents the mean and 95% confidence interval across sites for each scenario at each stand age. Scenarios in different groups are significantly different from each other, based on a Tukey test with alpha = 0.05.

# 5 Discussion

Overall, the scenarios we have examined reveal a trade-off between total carbon sequestration and the transition to native-dominated forests. For both exotic plantation species the scenarios that did not disturb the exotic canopy ('do nothing' scenarios) gave the highest total carbon values but the lowest native carbon values. For both exotic plantation species the whole-stand disturbance scenario gave the highest native carbon values, indicating a faster transition to native forest composition, but comparatively low total carbon values.

The effect on native carbon of planting native canopy-dominant species to replace killed exotic trees varied according to the exotic species and disturbance scenario. Native planting increased native carbon for early intervention disturbance scenarios across both exotic species, had no effect in the *P. radiata* coupe disturbance scenario, and resulted in lower native carbon values for the *E. fastigata* coupe disturbance scenario. Planting native canopy-dominant species did not increase total carbon stocks for any of the early intervention and coupe disturbance scenarios.

Whether or not native carbon gain within the time frames we examined was sufficient to replace carbon lost due to exotic canopy disturbance depended on the exotic plantation species and scenario. For *P. radiata*, native carbon gain did not compensate for exotic carbon loss under the whole-stand and coupe disturbance scenarios, but did so under the early intervention scenarios. For *E. fastigata*, native carbon gain compensated for exotic carbon loss under all disturbance scenarios.

However, this difference between the two species is driven by the higher carbon stocks achieved by *P. radiata* compared to *E. fastigata*. This may be due to *E. fastigata*'s sensitivity to site conditions, particularly frost. Austin and Van Niel (2010) reported the strong influence of mean annual daily and July minimum temperature on the distribution of eucalypts in Australia, and on *E. fastigata* in particular . Furthermore, in general *Eucalyptus* species are more site sensitive than *P. radiata*, which is considered to be adapted to a wide range of climate conditions in New Zealand.

## 5.1 Effect of exotic plantation species

Differences among the modelled scenarios highlight the strong influence of the exotic species on both native and total carbon stocks, and the results suggest that the composition and structure of the initial exotic canopy will influence the carbon stocks of the forest as it transitions to native composition. The physiology and allometry of the exotic species and their stocking (both tree density and size) influence their use of resources such as light, soil water, and nutrients. Further, these factors influence the availability of resources for other vegetation, and ultimately the regeneration and growth rates of native species in the understorey. The synecology of *P. radiata* and *E. fastigata* strongly contrast. While both *P. radiata* and *E. fastigata* are fast-growing species, *P. radiata* tends to form a dense canopy and cast moderately deep shade (expressed as higher CAI values for *P. radiata*) compared to *E. fastigata*. Therefore, it is not surprising that the outcomes of management aiming to transition from these species to native forest differ.

Further, the carbon stocks of the 'do nothing' scenarios over time indicate that these exotic species continue to store large amounts of carbon long beyond the typical rotation age currently used in commercial forestry. There is a common misperception that these species will start to decline after approximately age 25 and start to transition to native species shortly thereafter. However, the results of our study suggest that the exotic overstorey will continue to dominate the forest for an extended period in the absence of an exogenous disturbance (e.g. harvesting, or catastrophic windthrow or wildfire). These modelling results are corroborated by 120-year-old stands of radiata pine in the Central North Island known to the authors, which have retained an intact pine canopy with well-developed under- and mid-storeys of native tree and shrub species. The canopies of these older radiata plantations have yet to transition to native composition and appear unlikely to do so until an external disturbance opens the canopy.

The forestry industry typically harvests radiata pine stands between ages 21 and 30 for financial and logistical reasons rather than due to ecological limitations, and radiata pine can continue to grow vigorously beyond this age. The patterns of growth exhibited by the models in our study are also corroborated by published literature and inventory data from older radiata pine stands in New Zealand and overseas. In its native range in North America, radiata pine is reported to reach full height by approximately 35–40 years and full size by 80–100 years, but can live to at least 150 years (Burns et al. 1990; Lindsay 1937; Roy 1966; Sudworth 1908). In New Zealand, radiata pine was first introduced approximately 160 years ago, but it was not widely planted until approximately 100 years ago. Permanent sample plot data held by Scion contain a good representation across the full age range of plantations in New Zealand conditions and a handful of stands up to 120 years old (as discussed above). Woollons and Manley (2012) summarised these data, demonstrating that radiata can live well beyond 100 years, with relatively stable stem densities and little mortality due to self-thinning after approximately age 30.

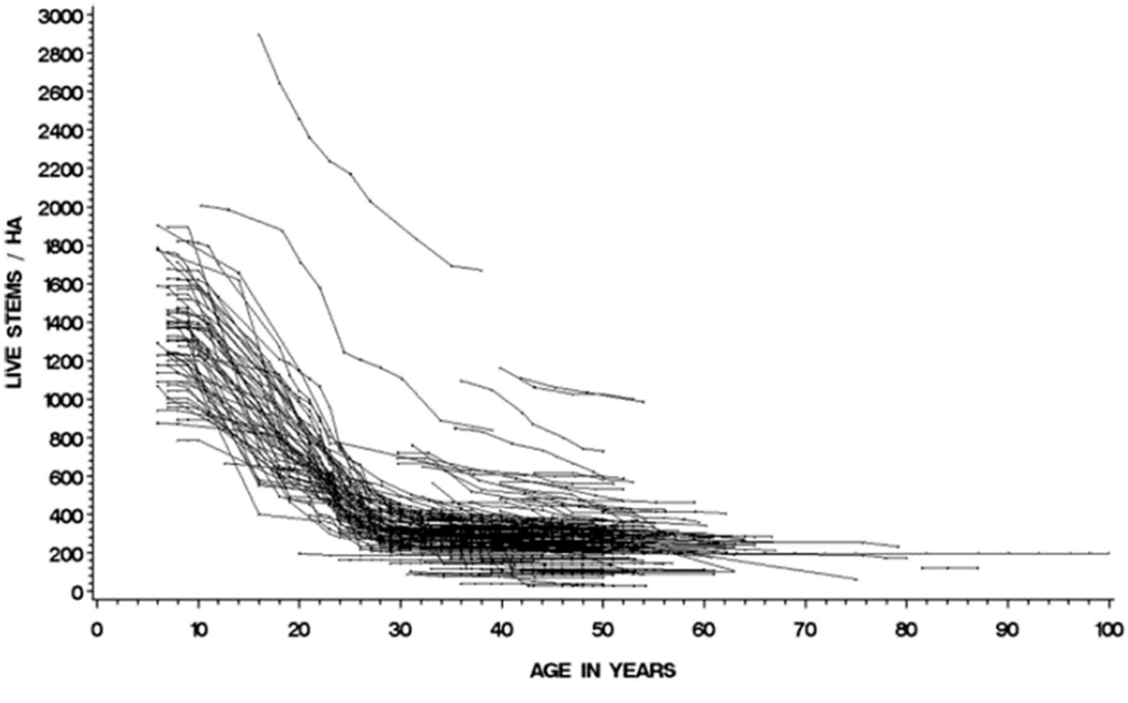

**Figure 15. Tree density (stems per hectare) over time for 140 radiata pine permanent sample plots. (Source: reproduced from Woollons & Manley 2012)**

In contrast with radiata pine, less is known about the development of *E. fastigata* plantations over long times within New Zealand. There are few known stands or permanent sample plots for stands over approximately 35 years for the three predominant species of *Eucalyptus* planted in New Zealand (including *E. fastigata*), probably due to the more recent history of commercial planting in contrast to *P. radiata* (only since the 1970s, Miller et al. 2000), and the typical industry practice of harvesting this species before age 20 to optimise financial returns over time. However, similar to radiata pine, it is likely that these plantations will continue to maintain a healthy canopy of *Eucalyptus* for an extended time beyond age 20, and there are published records of stands over 80 years old in New Zealand (Miller et al. 2000). While *E. fastigata* exhibited greater mortality due to low tolerance of cold temperatures, and self-thinning accompanied by declines in exotic carbon stocks over time compared to *P. radiata*, this decline was gradual over long time periods and the exotic canopy was still retained by year 100 (the end of the simulation).

## 5.2 Interaction between management, exotic species, and climate variables

Climate (mean annual rainfall and temperature) and exotic canopy disturbance were the main predictors of variation in native carbon. Temperature and rainfall are both included in functions modelling tree growth in the PPA, so it is not surprising that these variables emerged as strong predictors of native carbon stocks. The effect of disturbance was most positive at higher temperatures, perhaps reflecting greater potential for native species to increase growth rates in response to the removal of the exotic canopy at higher temperatures. The effect of *E. fasiculata* relative to *P. radiata* was most positive for the 'do nothing' and coupe disturbance scenarios. This most likely reflects the more intense suppression of native growth rates under the deeper shade (higher CAI values) of *P. radiata* canopies.

Mean annual temperature, disturbance, and exotic plantation species were the main predictors of variation in total carbon. Both mean annual rainfall and temperature are strong drivers of forest productivity within the 3-PG models for *P. radiata* and *E. fasiculata*, so it is not surprising that they were strong predictors of forest carbon stocks in this study.

On the other hand, the effect of disturbance on the integral of total carbon stocks was most negative at higher temperatures, while the difference between exotic species was greatest at lower temperatures and in the absence of disturbance. *E. fastigata* has a narrower ecological niche than *P. radiata* and is generally more suited to sites at moderate elevations in the North Island. Therefore, it is not surprising that the difference between the exotic species were greatest at the lower temperatures experienced in the South Island and at higher altitudes. *E. fastigata* is not widely planted in the South Island currently, with *E. nitens* historically more widely planted in the south. However, *E. nitens* is greatly affected by outbreaks of the insect *Paropsis charybdis* and widespread planting is now discouraged. Further, to achieve the objectives of this project we aimed to model the transition of forests across a wide range of sites, including unproductive sites not typically planted by industry.

## 5.3 Interaction between native planting, exotic species, disturbance, and carbon stocks

Our results show that the benefit of native planting for increasing native and total carbon stocks in transition forests will depend heavily on which exotic plantation species is used and what canopy disturbance is applied. As expected, the whole stand disturbance scenario followed by dense planting of mānuka/kānuka gave the highest native carbon stocks. This represents perhaps the most extreme intervention among the scenarios examined in this study, coupling drastic carbon loss from the killing of all exotic plantation trees with intensive (and costly) planting. It is unclear whether this will be a practicable scenario to apply at large scales.

The negative effect of planting on native carbon stocks in the *E. fasiculata* coupe scenario may be due to the lower CAI values of *E. fasiculata* relative to *P. radiata.* It is possible (as indicated by the lower biomass of the mānuka/kānuka and 'other' groups with native canopy-dominant planting) that the introduction of native canopy-dominant species suppressed fast-growing and light-demanding species that would otherwise have performed well under *E. fasiculata*. Such 'negative selection effects' have been noted in biodiversity–ecosystem function experiments (Hector et al. 2002).

The positive effect of native canopy-dominant planting in the early intervention scenarios suggests that planting such species earlier rather than later will enhance native contributions to carbon stocks. It is likely that the effects of planting would be greater at higher planting rates than the ratio of one native planted for every two exotic trees killed that we applied. It is also possible that the effects of planting might have been more apparent if we extended our simulations beyond the 100-year period used in this study.

## 5.4 Assumptions and limitations

Our results represent a first exploratory analysis of changes in carbon storage under various transition forest scenarios. There are many management interventions and scenarios we have not explored, and our models do not include some potentially important variables and processes. Below we discuss some of the main assumptions and limitations of our work and propose some future research directions. While our study used the best available science within the limitations of the scope of the study, this is a challenging area of science with a number of knowledge gaps. As highlighted above, this study represents a first exploratory analysis and as such provides an important leap forward in our understanding of transitioning forests; however, the results should be interpreted cautiously taking into consideration a number of caveats, discussed below.

Both the 3-PG and PPA forest models used in this study are not spatially explicit, and assume that the forest stands being simulated are spatially homogeneous. While this is a reasonable assumption when modelling typical plantation forests and many natural forests, the assumption of homogeneity is violated when attempting to simulate heterogeneous silvicultural treatments such as coupe felling. Coupe felling creates canopy gaps within a matrix of intact forest canopy, creating spatial variation in the forest structure and available growing resources and environmental conditions (e.g. light, water, nutrients, temperatures) between the matrix and the gaps. Furthermore, there is variation in the competition experienced by individual trees depending on their location (e.g. whether they are regenerating trees in the centre or on the edge of the canopy gap, or mature trees close to or far away from the edge of the canopy). This variation in biotic and abiotic factors strongly influences the growth and composition of the vegetation and therefore carbon sequestration over time.

While spatially explicit growth models do exist globally (e.g. HeteroFor and SORTIE), there is currently no spatially explicit alternative model adequately parameterised for New Zealand conditions. Although this assumption of homogeneity is problematic when simulating heterogenous forest structures, we mitigated its impact by restricting the simulated coupe size to just 20 m diameter canopy gaps. Given the likely height of the canopy, the environmental conditions inside these small openings is still likely to be strongly influenced by the surrounding canopy. The centre of smaller openings is likely to experience partial shading and moderate temperatures more similar to the forest understorey beneath the canopy than sites in the centre of larger gaps that could receive full sun and more extreme temperatures. Therefore, we have assumed that the environment and growth of regeneration inside these small canopy gaps will be most similar to a relatively homogeneously thinned forest. The simulation of larger gaps will require the development of a spatially explicit model for New Zealand conditions.

Similarly, a major limitation of all process-based models in New Zealand, including 3-PG and PPA, is the lack of appropriately detailed soil data. Soil conditions (e.g. soil texture and nutrients, and water availability) are accepted as major determinants of forest productivity, so the lack of robust soil data limits how this factor can be incorporated into forest models. Leaf litter layer is also highly influential on regeneration dynamics, and there are likely to be differences in the amount and quality of leaf litter layer among canopy species, but neither 3-PG nor PPA account for this variation.

The paucity of data sets from exotic plantation understoreys for parameterising and validating model results means that our results are hypothetical and should be interpreted with caution. Although there are published studies, there is still a lack of data on the exotic plantation forest understorey for calibration purposes (Allen et al. 1995; Brockerhoff et al. 2003; Marshall et al. 2024). This has implications for each of the demographic processes modelled within the PPA (recruitment, growth and mortality) as well as definition of the native species pool available for natural colonisation of transition forests at a given location.

In this study we were obliged to rely on permanent plot data primarily drawn from large contiguous areas of indigenous forest in parameterising demographic rates and defining local species pools available for natural colonisation. Consequently, it is possible that interspecific differences (arising from differences between modelled and actual species pools in transition forests) and intraspecific differences (i.e. within-species differences in demographic rates in native forests and transition forests) may cause our native carbon stock predictions to differ from actual values in transition forests.

The best way to remedy these issues would be to establish a representative network of permanent forest survey plots tracking native species composition and demographic rates in exotic plantation forests. This would provide baseline data for parameterising and validating demographic rates and species pools in intact forest and, over time, in response to exotic forest harvest or natural and intentional exotic canopy disturbance. Such a representative plot network could be complemented by targeted plots aligned to experimentally applied transition forest scenarios.

# 6 Conclusions

- Achieving native tree dominance in transition forests comes at the cost of reducing total carbon stocks, because native carbon stocks are enhanced by disturbance of the exotic canopy, while reducing total carbon stocks.
- Replacement of exotic trees killed during deliberate canopy disturbance by planting native canopy-dominant species enhances native carbon stocks when disturbance and planting occur earlier rather than later.
- The positive effect of deliberate exotic canopy disturbance on native tree carbon is moderated by the identity of the exotic plantation species (with the effect being larger under *P. radiata* than under *E. fasiculata*) and climate (with the effect being larger at warmer temperatures).
- The difference in total carbon stocks between exotic plantation species (higher for *P. radiata* than for *E. fastigata*) was moderated by climate (with the difference being greater at cooler temperatures). The negative effect of disturbance on total carbon stocks was also moderated by climate (with the effect being stronger at higher temperatures).

# 7 Recommendations

- Policies for incentivising transition forests within the Emissions Trading Scheme should consider how to assist landowners with the potential liability of surrendering carbon credits due to the deliberate exotic canopy disturbance required to promote native dominance.
- A representative network of permanent forest survey plots tracking native species composition and demographic rates in exotic plantation forests should be established.
- This should be complemented by targeted plots aligned to experimentally applied transition forest scenarios.

# 8 References

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## Appendix 1 – Focal site selection

We created raster layers with areas available for *P. radiata* and *E. fastigata* transition forests (Figures A1.1 and A1.2). To create these rasters, we excluded national parks and water bodies, native forests, areas with LUC ≤ 4, and areas higher than 1,210 metres and 800 metres in altitude for *P. radiata* and *E. fastigata*, respectively. We built a 100 × 100 m points grid using the available areas identified in the rasters and extracted the coordinates for each point. Then we extracted the environmental data from each of them from a data stack of mean annual rainfall, mean annual temperature, altitude, slope, and the amount of native forest in the surrounding landscape.

From these environmental data we selected all as predictors except altitude. We then standardised the data by subtracting the mean and dividing by the standard deviation for each column (except coordinates). Finally, we proceeded to select 100 points using a balanced sampling method with the package *BalancedSampling* (Grafström et al. 2024) in R. These points were used to estimate the occurrence probabilities for native species and for weighting distance to determine the probability of colonisation in transition forest, as described in Appendix 2.

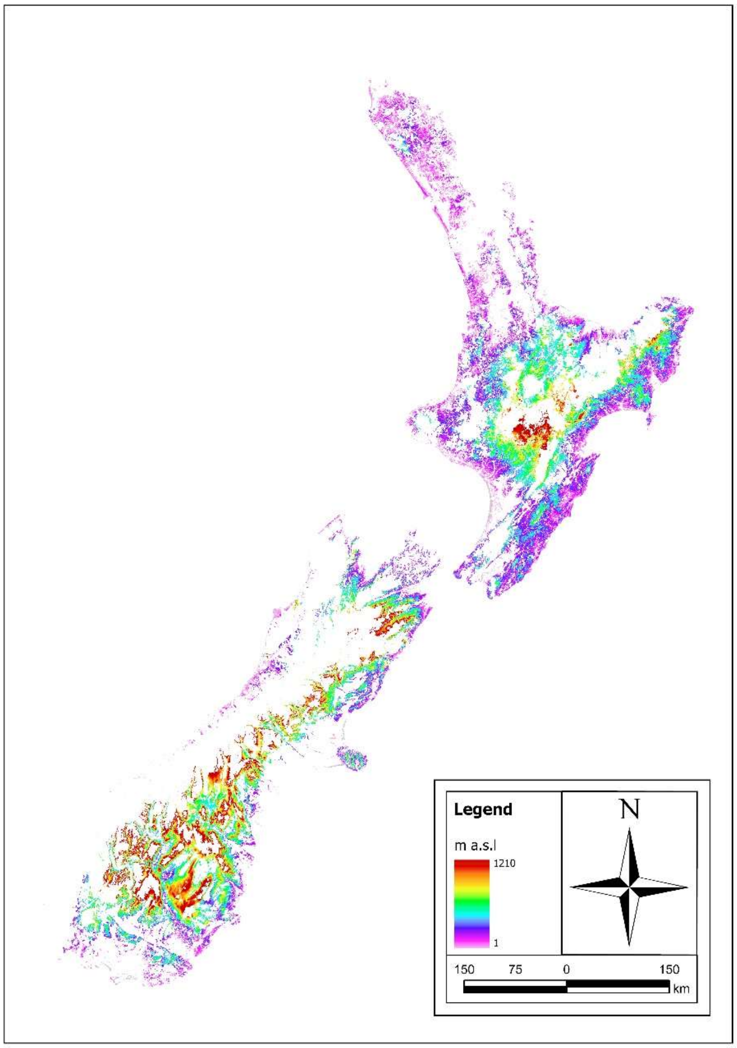

**Figure A1.1. Available areas to plant *P. radiata.* Colours indicate altitude (metres above sea level).**

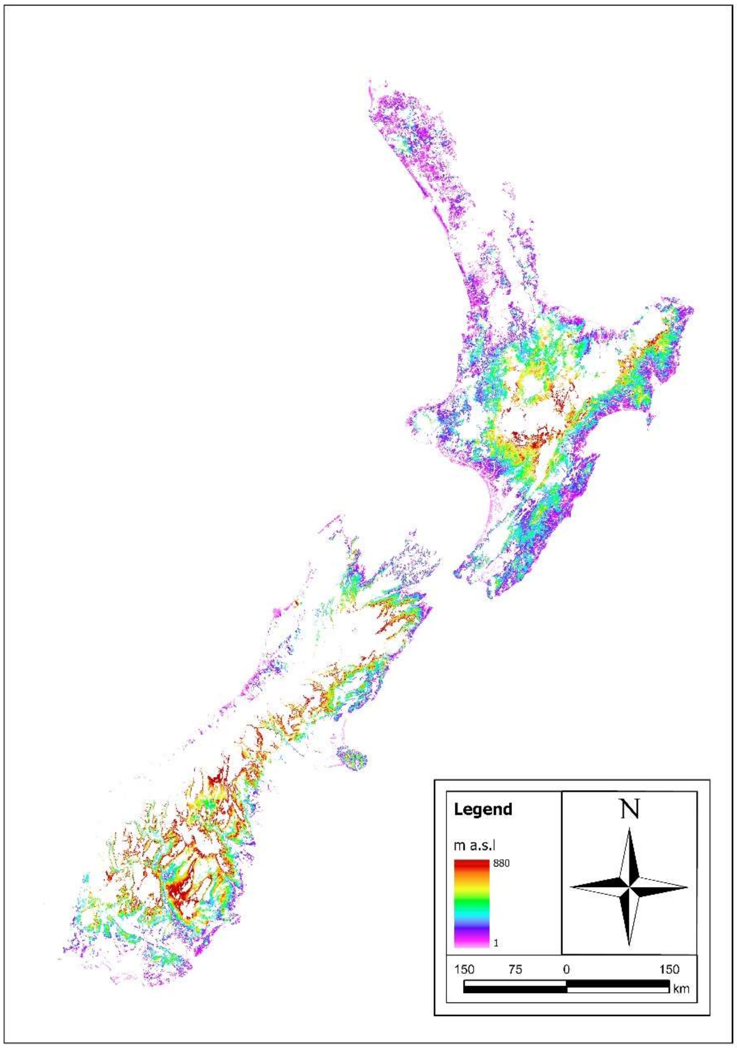

**Figure A1.2. Available areas to plant *E. fastigata.* Colours indicate altitude (metres above sea level).**

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## Appendix 2 – Calculating species occurrence probability and dispersal distance

We extracted species occurrence data for 109 species from LUCAS plots. In addition, we extracted environmental data for each LUCAS plot from a data stack. The data stack included mean annual temperature, mean annual rainfall, slope, acid-soluble phosphorus, water deficit, land cover (Leathwick et al. 2002), and the proportion of native forest (as mapped in Land Cover Database v5). We used these data to predict the probability of occurrence for each species using extreme gradient-boosted regression trees (xgb, Chen % Guestrin 2016), with cross-validation implemented in a custom package (https://github.com/manaakiwhenua/xgb.cv). The code used to fit species occurrence models is available in supplementary file LUCASPlotSpecies_xgb_OccurrenceForest4km.r.

For all the selected modelling locations (*P. radiata* and *E. fastigata* plantations), we built a 4 km buffer around each selected location. Using QGIS 3.36 we generated a grid of points, spaced 100 m apart. The buffers and the grid were intersected to produce a layer containing only the points within the 4 km buffers. These points were later used to extract information from the data stack described in Appendix 1. This information was then used to predict the species probability of occurrence at each point within the buffer. The distance from each point to the selected modelling location was calculated to estimate the probability of colonisation by this species after the interventions proposed in each scenario. The occurrence probabilities were weighted using the inverse of the distance to the centroid.

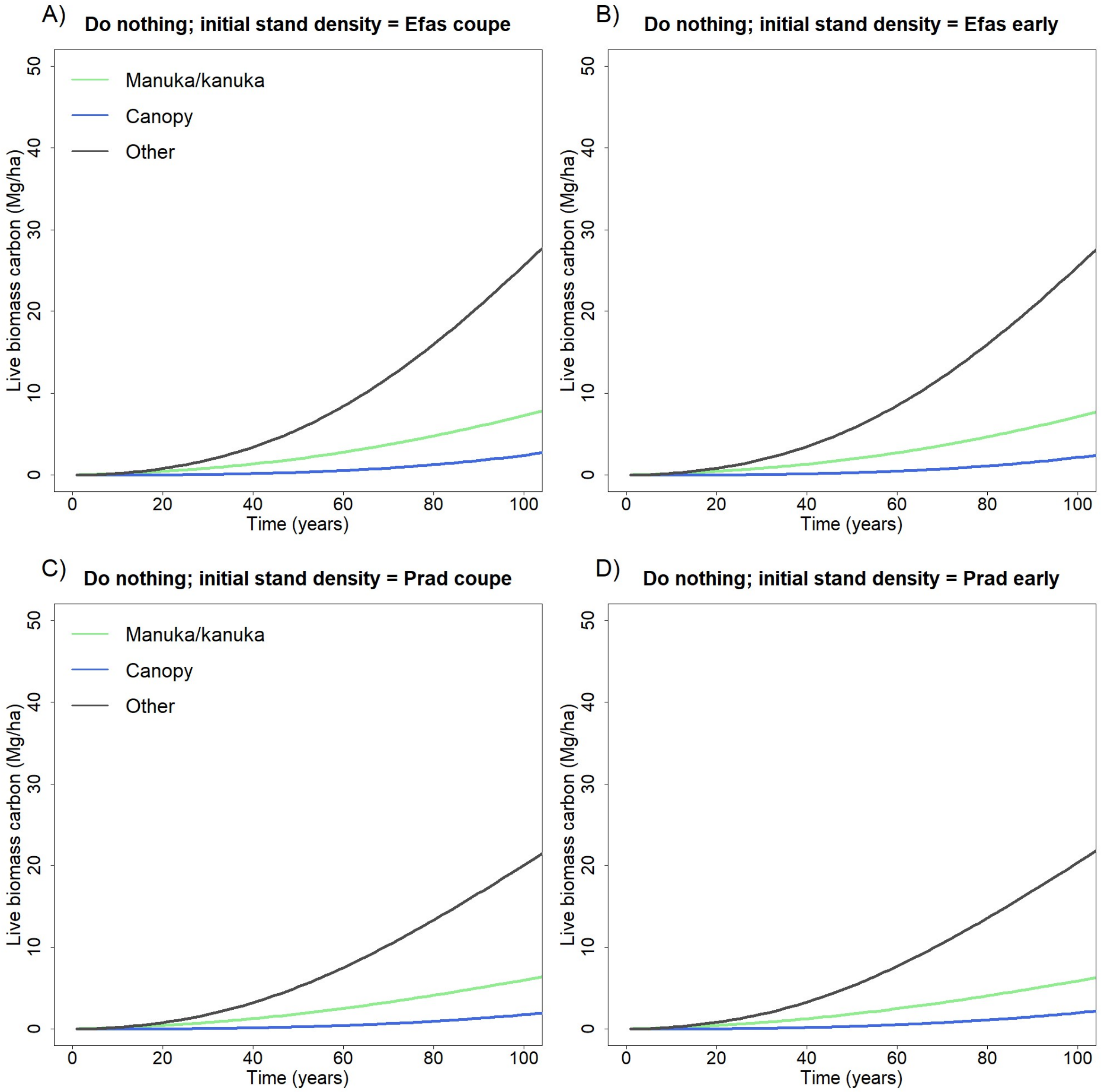
# Appendix 3 – Modelling scenarios

## Table A3.1. Modelled scenarios detailing the simulated management activities, by species and model used

| | | | | | | 3PG (Exotic species) | | | | | | | | | | PPA (Native species) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Simulation Number | Approach | | | | | 3PG simulation ID | Species | | Exotic planting density | | | Age of first harvest | Severity of thinning | Frequency of thinning | Harvesting | Natural regeneration | Natural with supplemental planted native | Native planting density |
| | Do nothing | Clearcut and restoration | Newly planted transition forests w/ early canopy intervention | Thinning with coupe ring-barking/poisioning | Pre-1990 forests | | *Eucalyptus fastigata* | *Pinus radiata* | 1250 | 1000 | 833 | | | | | | | |
| 1 | | X | | | | a | X | | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Clearcut to 0 sph at age 28 years | X | Mānuka/kānuka | 1100 sph |
| 2 | | X | | | | b | | X | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Clearcut to 0 sph at age 28 years | X | Mānuka/kānuka | 1100 sph |
| 3 | X | | | | | c | X | | | X | | N/A | N/A | N/A | N/A | X | | |
| 4 | X | | | | | d | | X | | X | | N/A | N/A | N/A | N/A | X | | |
| 5 | | | X | | | e | X | | | X | | ~9 (average age of canopy closure) | Homogenous thinning removing 33% sph of planted density | Every 5 years until 0 sph (i.e. age 9 harvest to 666 sph, at age 14 harvest to 333 sph, at age 19 harvest to 0sph) | N/A | X | | |
| 6 | | | X | | | e | X | | | X | | ~9 (average age of canopy closure) | Homogenous thinning removing 33% sph of planted density | Every 5 years until 0 sph (i.e. age 9 harvest to 666 sph, at age 14 harvest to 333 sph, at age 19 harvest to 0sph) | N/A | | X | |
| 7 | | | X | | | f | | X | | X | | ~9 (average age of canopy closure) | Homogenous thinning removing 33% sph of planted density | Every 5 years until 0 sph (i.e. age 9 harvest to 666 sph, at age 14 harvest to 333 sph, at age 19 harvest to 0sph) | N/A | X | | |
| 8 | | | X | | | f | | X | | X | | ~9 (average age of canopy closure) | Homogenous thinning removing 33% sph of planted density | Every 5 years until 0 sph (i.e. age 9 harvest to 666 sph, at age 14 harvest to 333 sph, at age 19 harvest to 0sph) | N/A | | X | |
| 9 | X | | | | | g | X | | | | X | N/A | N/A | N/A | N/A | X | | |
| 10 | X | | | | | h | | X | | | X | N/A | N/A | N/A | N/A | X | | |
| 11 | | | | X | | i | X | | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 25. 2% per year until all harvested (50 years). | X | | |
| 12 | | | | X | | i | X | | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 25. 2% per year until all harvested (50 years). | | X | |
| 13 | | | | X | | j | | X | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 25. 2% per year until all harvested (50 years). | X | | |
| 14 | | | | X | | j | | X | | | X | ~9 (average age of canopy closure) | Homogenous thinning down to 600 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 25. 2% per year until all harvested (50 years). | | X | |
| 15 | X | | | | | k | | X | X | | | N/A | N/A | N/A | N/A | X | | |
| 16 | | | | | X | l | | X | X | | | ~9 (average age of canopy closure) | Homogenous thinning down to 370 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 30. 2% per year until all harvested (50 years). | X | | |
| 17 | | | | | X | l | | X | X | | | ~9 (average age of canopy closure) | Homogenous thinning down to 370 sph | One thinning only | Coupe harvesting (ring-barking) starting at age 30. 2% per year until all harvested (50 years). | | X | |

# Appendix 4 – Temporal changes in species composition for modelling scenarios

The figures below plot changes in abundance (live stem biomass carbon) and relative abundance (percentage of total native biomass) in each modelling scenario for three groups of native tree species: mānuka/kānuka (all *Leptospermum* and *Kunzea* taxa), canopy dominants (miro, *Pectinopitys ferruginea*; mataī, *Prumnopitys taxifolia*; rimu, *Dacrydium cupressinum*; tōtara, *Podocarpus totara*; kahikatea, *Dacrycarpus dacrydioides*; beech species; and tawa, *Beilschmiedia tawa*).



A) Do nothing; initial stand density = Efas coupe

B) Do nothing; initial stand density = Efas early

C) Do nothing; initial stand density = Prad coupe

D) Do nothing; initial stand density = Prad early

**Figure A4.1. Changes in live stem biomass carbon of native tree species groups in the 'do nothing' new forest scenarios throughout the simulation period.**

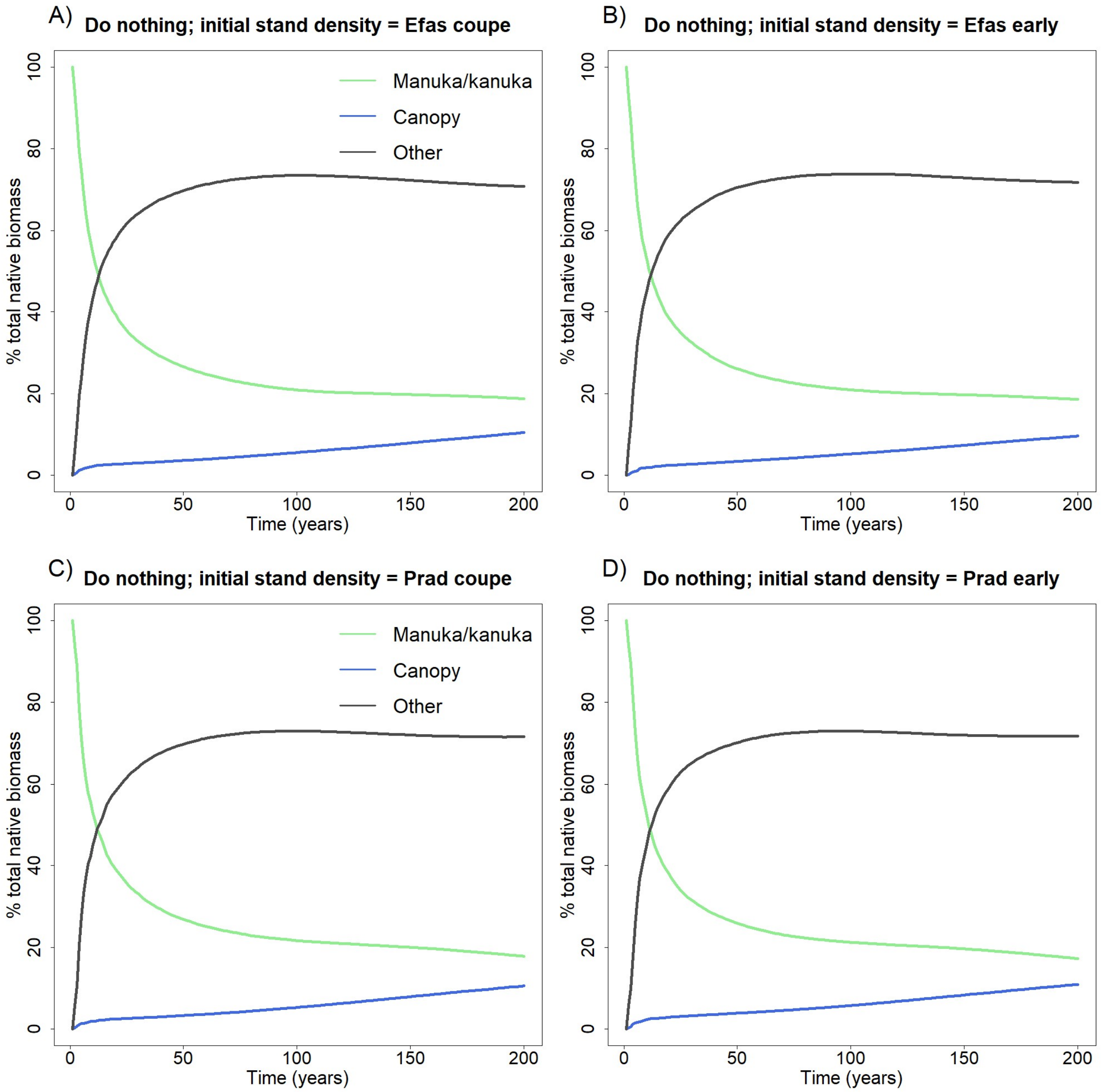


**Figure A4.2. Changes in relative abundance (weighted by live stem biomass carbon) of native tree species groups in the 'do nothing' new forest scenarios throughout the simulation period.**

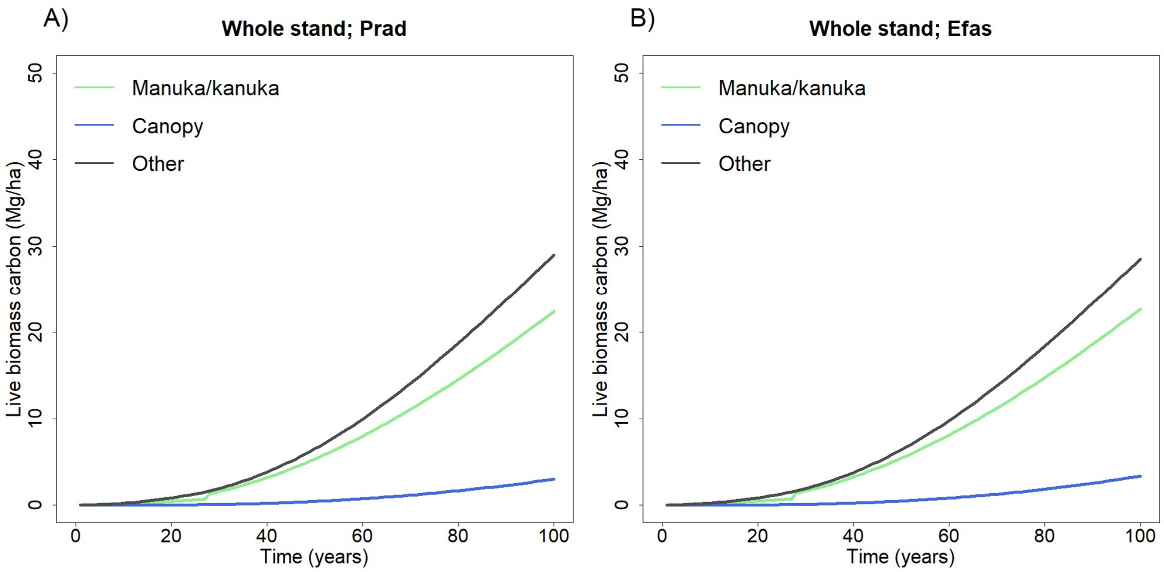


**Figure A4.3. Changes in live stem biomass carbon of native tree species groups in the whole stand disturbance new forest scenarios throughout the simulation period.**

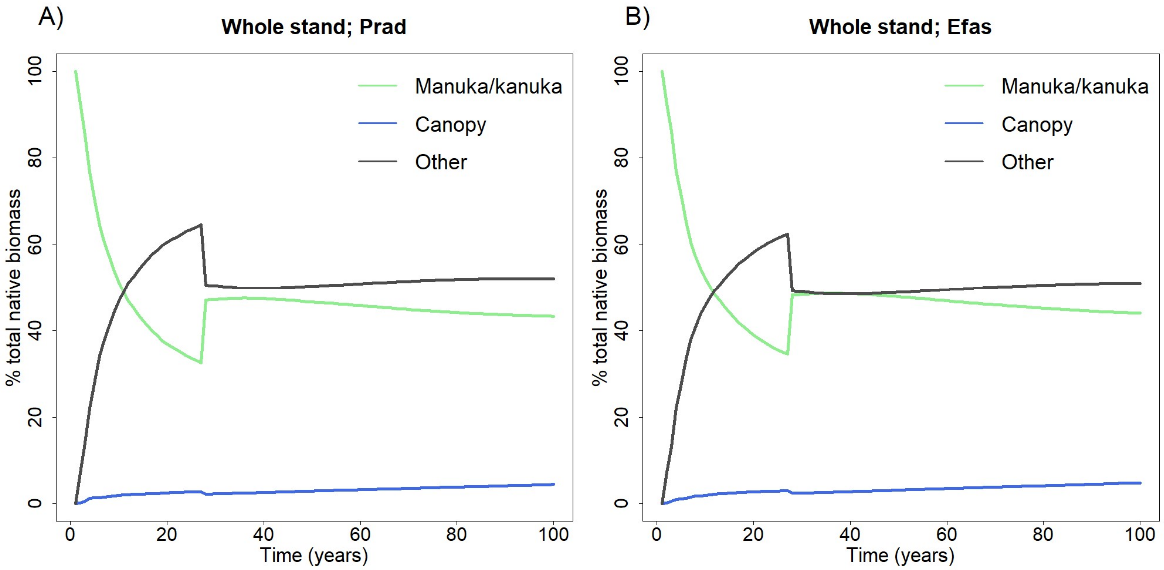


**Figure A4.4. Changes in relative abundance (weighted by live stem biomass carbon) of native tree species groups in the whole stand disturbance new forest scenarios throughout the simulation period.**

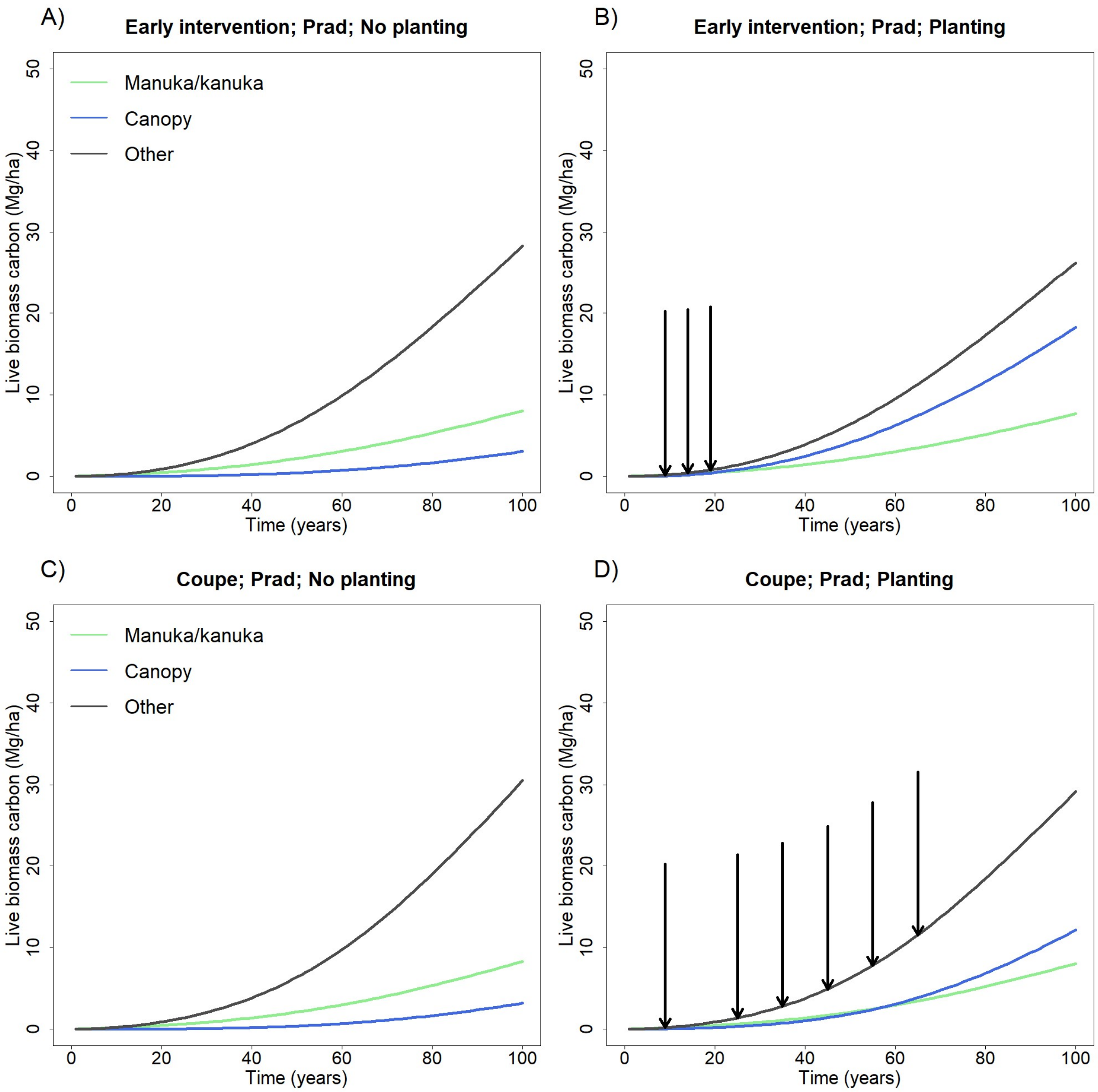


**Figure A4.5. Changes in live stem biomass carbon of native tree species groups in the early intervention and coupe disturbance new forest scenarios for *P. radiata* (Prad) throughout the simulation period.**

**Notes: Vertical arrows indicate years where canopy-dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**

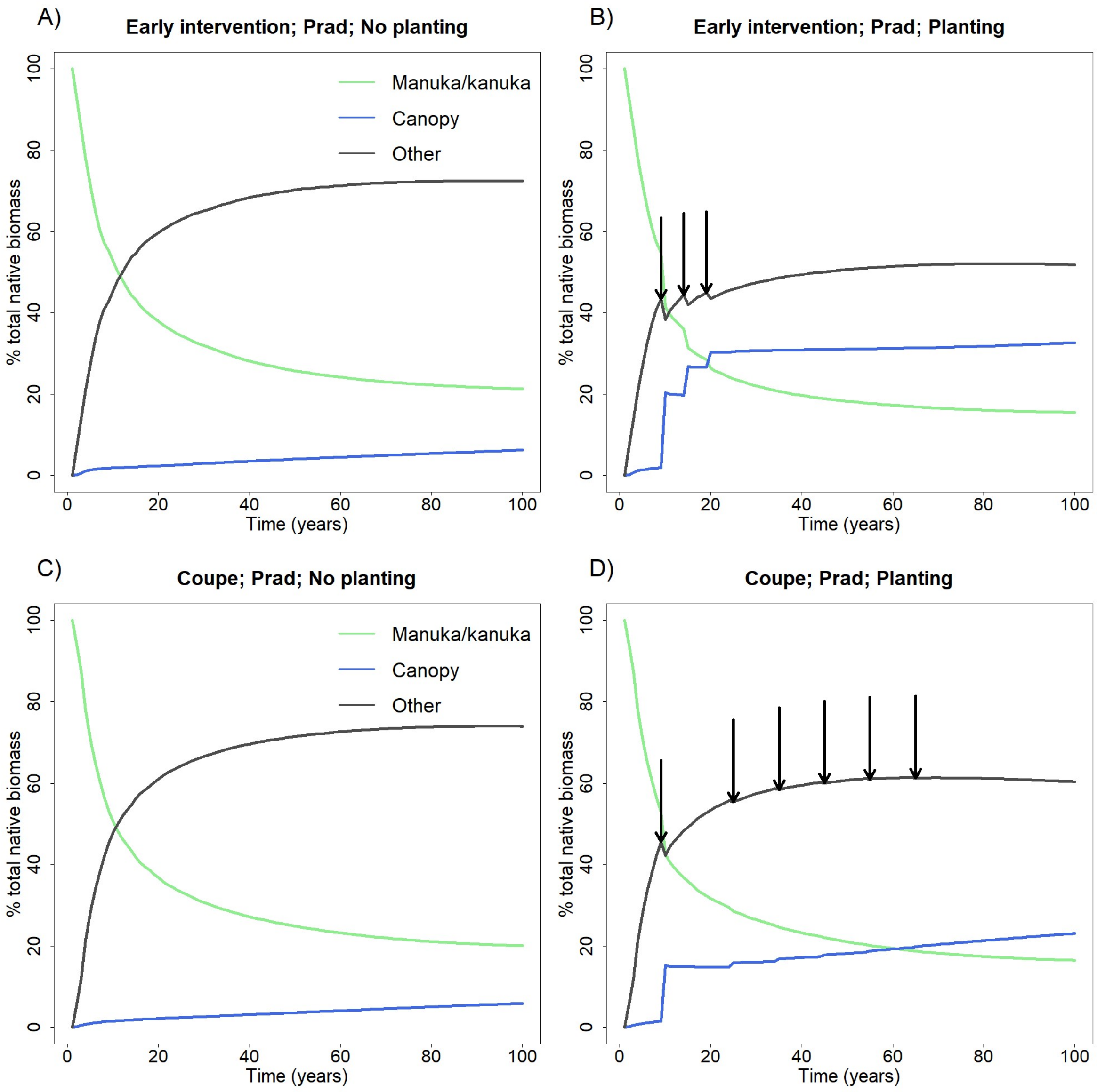


**Figure A4.6. Changes in relative abundance (weighted by live stem biomass carbon) of native tree species groups in the early intervention and coupe disturbance new forest scenarios for *P. radiata* (Prad) throughout the simulation period.**

**Notes: Vertical arrows indicate years where canopy-dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**

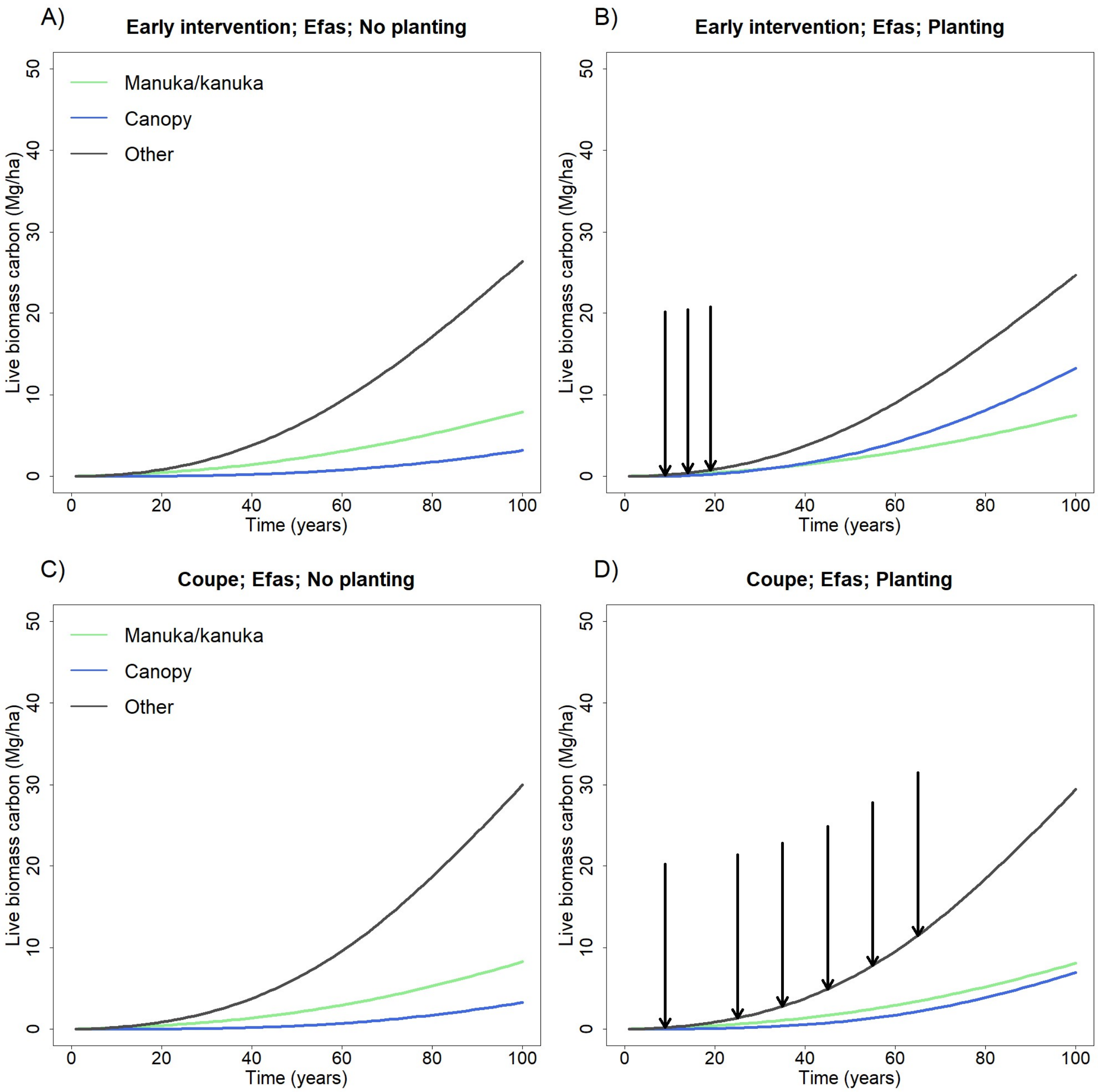


**Figure A4.7. Changes in live stem biomass carbon of native tree species groups in the early intervention and coupe disturbance new forest scenarios for *E. fastigata* (Efas) throughout the simulation period.**

**Notes: Vertical arrows indicate years where canopy-dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**

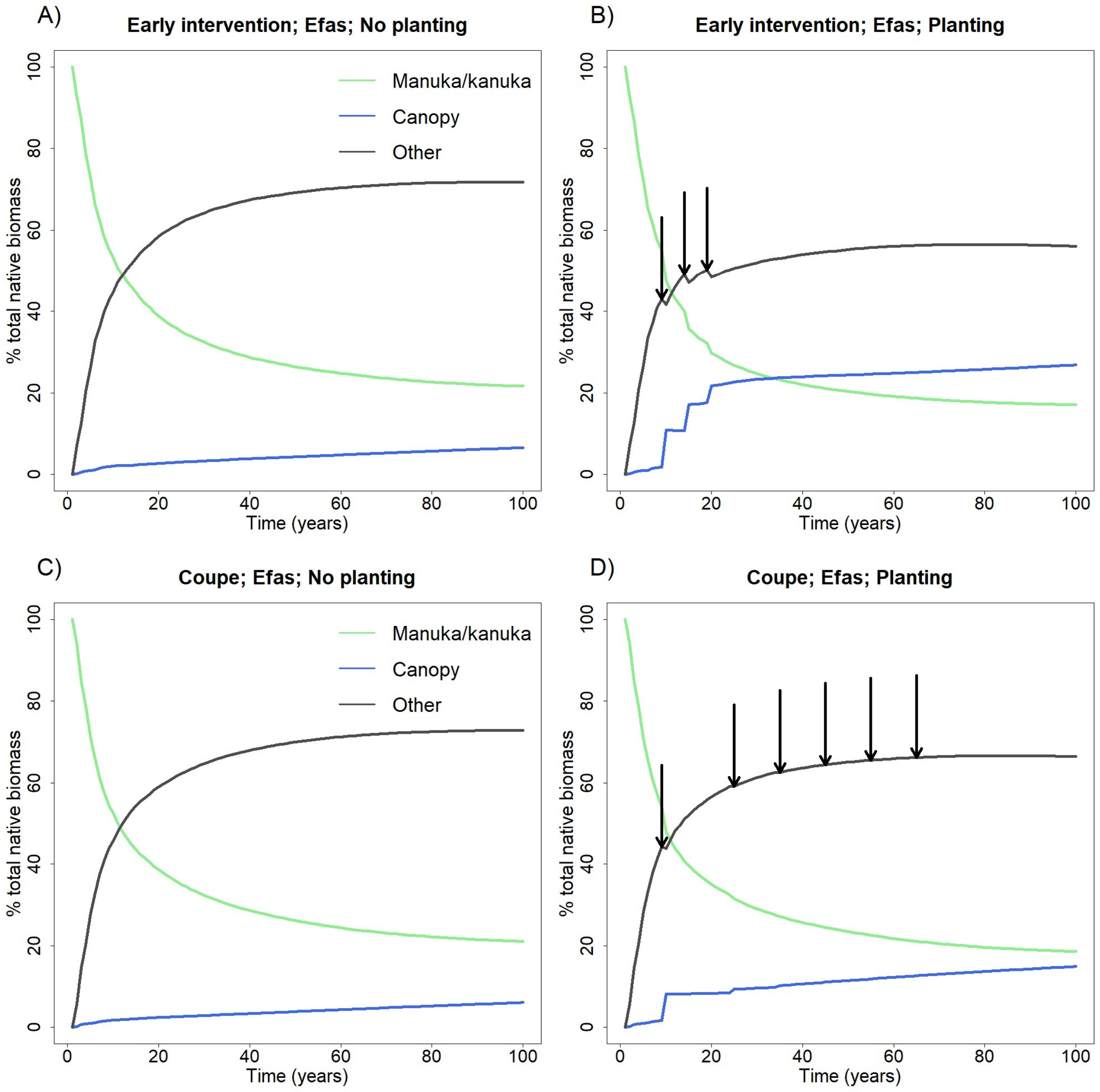


**Figure A4.8. Changes in relative abundance (weighted by live stem biomass carbon) of native tree species groups in the early intervention and coupe disturbance new forest scenarios for *E. fastigata* (Efas) throughout the simulation period.**

**Notes: Vertical arrows indicate years where canopy-dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**

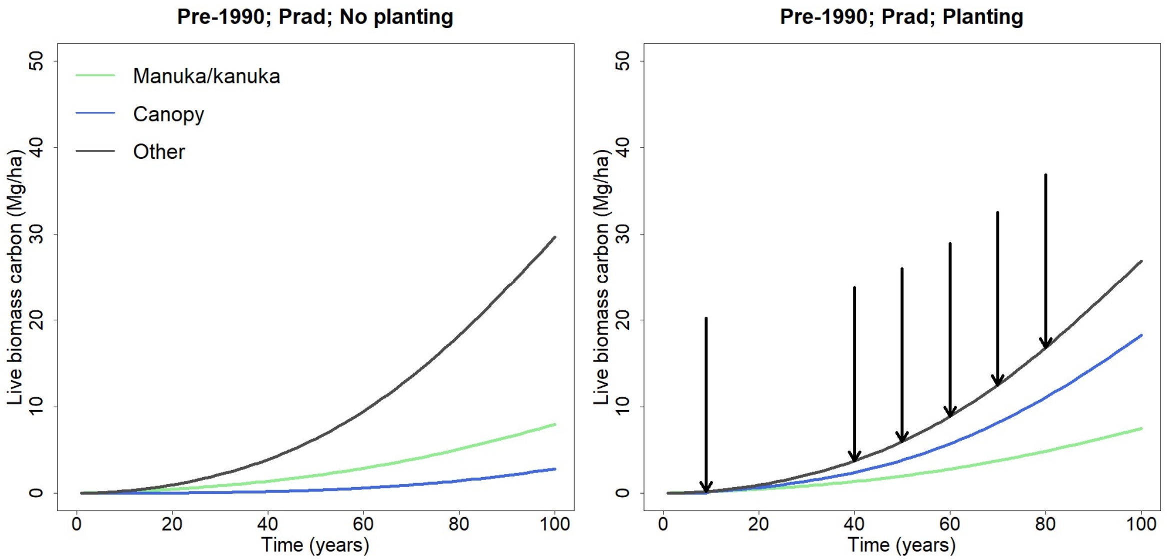


**Figure A4.9. Changes in live stem biomass carbon of native tree species groups in the coupe disturbance pre-1990 scenarios for *P. radiata* (Prad) throughout the simulation period.**
**Notes: Vertical arrows indicate years where canopy-dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**

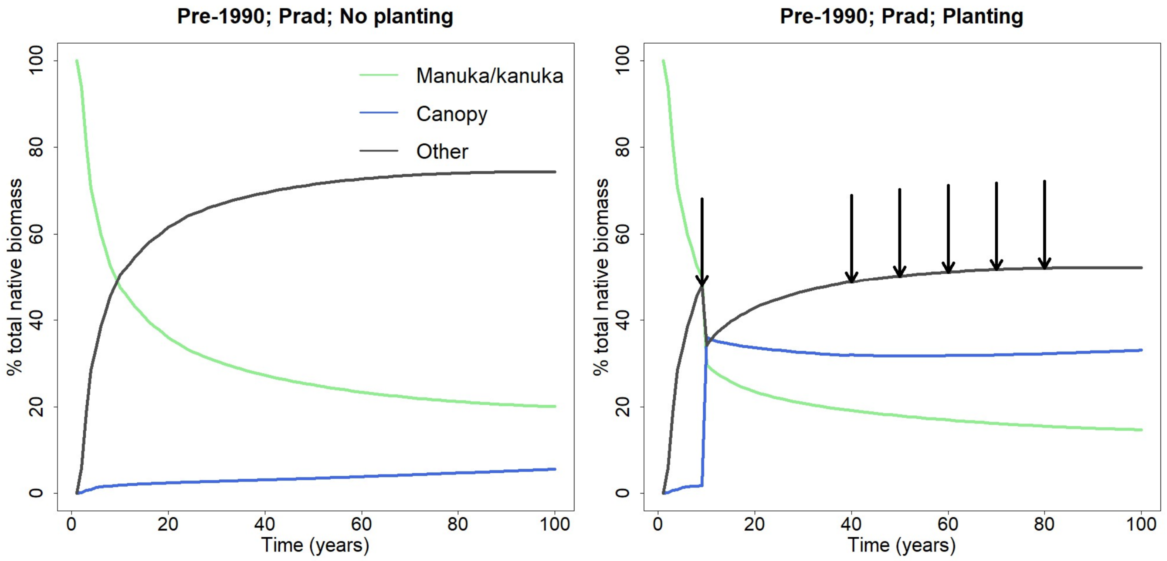


**Figure A4.10. Changes in relative abundance (weighted by live stem biomass carbon) of native tree species groups in the coupe disturbance pre-1990 scenarios for *P. radiata* (Prad) throughout the simulation period.**
**Notes: Vertical arrows indicate years where canopy dominant native species are planted to replace exotic canopy species killed at a rate of one native tree planted to two exotic trees killed.**