

RESEARCH ARTICLE

Quantifying the risk of non-native conifer establishment across heterogeneous landscapes

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Handling Editor: Anibal Pauchard**Abstract**

1. Pines (genus *Pinus*) are cultivated extensively for forestry purposes, particularly in regions that are outside the genus' native range. The most common forestry species are also typically those most likely to escape cultivation and spread rapidly, and thus pines constitute a substantial weed problem in many regions. However, there is limited knowledge of the factors underlying the spread of pines from plantations. Assessments across heterogeneous landscapes are required to provide rigorous data to support management tools and policies aiming to protect vulnerable ecosystems from pine invasions.
2. We examined the spread of *Pinus radiata* from forestry plantations over a ~9,000 km² landscape on Banks Peninsula, New Zealand. We used ground-based surveys from a set of viewpoints to determine tree locations, coupled with geographical information system (GIS) viewsheds to define the area surveyed. We used boosted regression trees to build a habitat model for *P. radiata* establishment on Banks Peninsula.
3. We surveyed an area approximately 107 km², recording 470 naturally established *P. radiata* individuals. Our habitat models suggested that proximity to the nearest plantation forest was the most important variable predicting *P. radiata* establishment, with individuals most likely to establish within 150 m of a plantation. Individuals were also most likely to establish in early successional shrub communities, proximate to roads, and on steeper topography. Highly grazed habitats were least vulnerable to *P. radiata* establishment.
4. The slope and aspect of the source plantation influenced the distances from the plantation at which *P. radiata* individuals were recorded, with individuals recorded furthest away likely to have originated from plantations that were south-facing or on steeper slopes, and therefore most exposed to strong winds.
5. *Synthesis and applications.* Our findings on distances from plantations at which individuals established, vulnerable habitats, and the interactions we detected among our predictor variables, can be extended to aid management of non-native conifer plantings elsewhere in the Southern Hemisphere. These data can be used to contribute to improvements of decision support systems that assess likely spread risk

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from non-native conifer plantings. Such tools can reduce the likelihood of future pine establishment, potentially preventing biological invasions.

KEYWORDS

alien, invasion, laser rangefinder, LiDAR, spatial ecology, species distribution modelling, viewshed analysis, wilding conifer

1 | INTRODUCTION

Pines (*Pinus* species) have long been cultivated for timber and other forest products, with the result that they have been planted extensively outside their native range, particularly in the Southern Hemisphere (Le Maitre, 1998; Richardson & Rundel, 1998). Unfortunately, pine species favoured by the forestry industry are generally those with the most rapid growth rates and greatest heights at maturity and, as a result, are also those most likely to escape cultivation and spread rapidly (McGregor et al., 2012; Wyse & Hulme, 2021). The spread of pines from plantations represents a substantial and intractable weed problem where non-native conifers form the bulk of commercial forestry plantings (Nuñez et al., 2017). Once established outside of cultivation, non-native pines can have negative effects on native biodiversity values and pastoral productivity, modify hydrology and nutrient cycling, and change fire regimes through increased fuel loads (Franzese et al., 2017; Nuñez et al., 2017; Peltzer, 2018; Taylor et al., 2017), resulting in direct and indirect economic costs. As a result, a conflict exists between environmental concerns and forestry benefits associated with non-native pine plantations. This conflict between commercial and environmental interests, alongside a loss of focus on control outcomes in areas where local job creation becomes a goal of pine management programmes, means that non-native pines often result in complex and contentious management issues (Woodford et al., 2016).

The threats posed by non-native pine plantation forestry can be minimised through measures such as careful species and site selection, and thorough invasion monitoring (Nuñez et al., 2017). To this end, afforestation policies are often designed to reduce the likelihood that future plantations will lead to severe pine invasions. For example, in South Africa, commercial forestry requires permits to plant pine species classified as 'invasive', and landowners are required to take steps to limit their spread (van Wilgen & Richardson, 2012), while in New Zealand forestry permits are only issued where a risk assessment has demonstrated a low risk of invasive spread from the proposed plantation based on species and landscape attributes (Ministry for Primary Industries, 2014). While considerable work has been undertaken to determine which pines are most likely to escape from plantations and become established (Grotkopp et al., 2002; Rejmánek & Richardson, 1996; Wyse & Hulme, 2021), there have been few attempts to quantify the factors underlying the establishment of pines from plantations at a landscape scale (although see McConnachie et al., 2015). Rigorous assessments across heterogeneous landscapes are required to assess

the relative vulnerability of habitats to non-native pine establishment, the roles of abiotic (e.g. climate, soil type) and biotic (e.g. grazing, native vegetation cover) variables of the source plantation and the receiving land, and to understand potential interactions among variables (Kaplan et al., 2014). For example, sufficient propagule pressure such as could occur immediately adjacent to a seed source may reduce the effectiveness of biotic barriers (browsing by herbivores, competition from certain vegetation types) on pine establishment (Richardson et al., 1994), while herbivore browsing pressure is likely to vary with topography due to herbivore behaviour and habitat use (Augustine & Derner, 2014; Long et al., 2014). Such data are fundamental for the robust assessment of the invasion risk arising from forestry plantations and to ensure policies designed to protect vulnerable ecosystems are fit for purpose.

Here, we examined the relationship between the location of pine plantations and the attributes of locations of regenerating *Pinus radiata* on Banks Peninsula in Canterbury, New Zealand, and use these data to build a habitat model using machine learning techniques. We then use this habitat model to examine the filters acting on pine establishment linked to attributes of the most proximate source plantation, landscape and the recipient ecosystems, and the interactions among these variables. In particular, we ask the following: (a) do attributes of the plantation location such as aspect and exposure determine how far established individual trees are found from the plantation? (b) What are the important biotic and abiotic variables driving the establishment of *P. radiata* in this landscape? (c) Are there interactions among variables in recipient habitats that make areas more or less vulnerable to invasion? Finally, we used our habitat model to produce a risk map for *P. radiata* establishment on Banks Peninsula. The knowledge gained from this assessment of non-native pine establishment will provide important insights and guidance for invasion risk assessments associated with pine forestry in New Zealand and throughout the Southern Hemisphere, where these species are a fundamental component of forest industries.

2 | MATERIALS AND METHODS

2.1 | Study species

Pinus radiata (radiata pine, Monterey pine) is the most important non-native conifer in the global timber industry (Lavery & Mead, 1998), with over 4.5 million ha of plantations worldwide, 90% of which occur in the Southern Hemisphere (Mead, 2013). The species is light

demanding (Wyse & Hulme, 2022) and the density of naturally establishing seedlings in a fragmented forest in Chile was found to correlate negatively with canopy cover (Gómez et al., 2019). Roadsides and coastal habitats also provide suitable environments for *P. radiata* establishment (Williams & Wardle, 2007), while droughts, frost (Burdon & Miller, 1992) and strong browsing pressure from stock and other herbivores (Crozier & Ledgard, 1990) are thought to retard or inhibit establishment. In South Africa, naturalised *P. radiata* populations increase rapidly after fire, owing to the resultant availability of suitable habitat and the synchronous release of seed from serotinous cones (Richardson & Brown, 1986). Furthermore, while the majority of *P. radiata* seeds are deposited within a few hundred metres of a source plantation forest, long-distance dispersal over multiple kilometres is observed downwind of the prevailing wind direction (Williams & Wardle, 2007). While this evidence to date gathered throughout the introduced range of *P. radiata* provides some indication of the likely habitats vulnerable to its naturalised establishment, and the distances from a source plantation these individuals could be expected to occur, the data are compiled from few studies predominantly undertaken in single habitats of interest or under a limited range of abiotic and biotic conditions.

2.2 | Study area

Our research was conducted on Banks Peninsula in Canterbury, New Zealand; a once-forested heterogeneous landscape now heavily modified by human pastoral activities. Banks Peninsula is a highly heterogeneous landscape of volcanic origin with varied topography,

climate and land cover types, which both contains a large number of *P. radiata* plantations and is highly accessible by a road a walking track network. The study area ranges in elevation from sea level to 920m and soils derived from volcanic bedrock and loess are moderately to very fertile (Wilson, 2013a). The climate is temperate with annual mean temperature ranging from 9°C to 14°C and annual rainfall from 600 to 2,000mm, with greater rainfall at higher elevations (Wilson, 1999). The present-day landscape comprises a mosaic of approximately 10% original or regenerating native forest, 5% native scrub, 10% shrubland composed of non-native species (e.g. *Ulex europaeus* and *Cytisus scoparius*) and forest plantations, and 75% grassland that includes native tussocklands as well as highly modified pastures (Pouteau et al., 2015). The resulting study area was 87,934 ha (Figure 1), including 4,314 ha of non-native forestry plantations (Manaaki Whenua – Landcare Research, 2020), predominantly comprising *P. radiata*. Within the study area, *P. radiata* is the most common pine species established outside of cultivation, with other pines either rare or barely evident (Wilson, 1999).

2.3 | Survey technique

Pinus radiata is visually distinct from the other most common non-native conifers naturalised in the study area, *Pseudotsuga menziesii* and *Cupressus macrocarpa* (Wilson, 2013b), as well as indigenous conifer species such as *Podocarpus laetus* and *Podocarpus totara*. Due to this visual distinctiveness, we were able to use a ground-based technique to survey for all naturally established individuals (those that we were confident were not planted) visible from a set

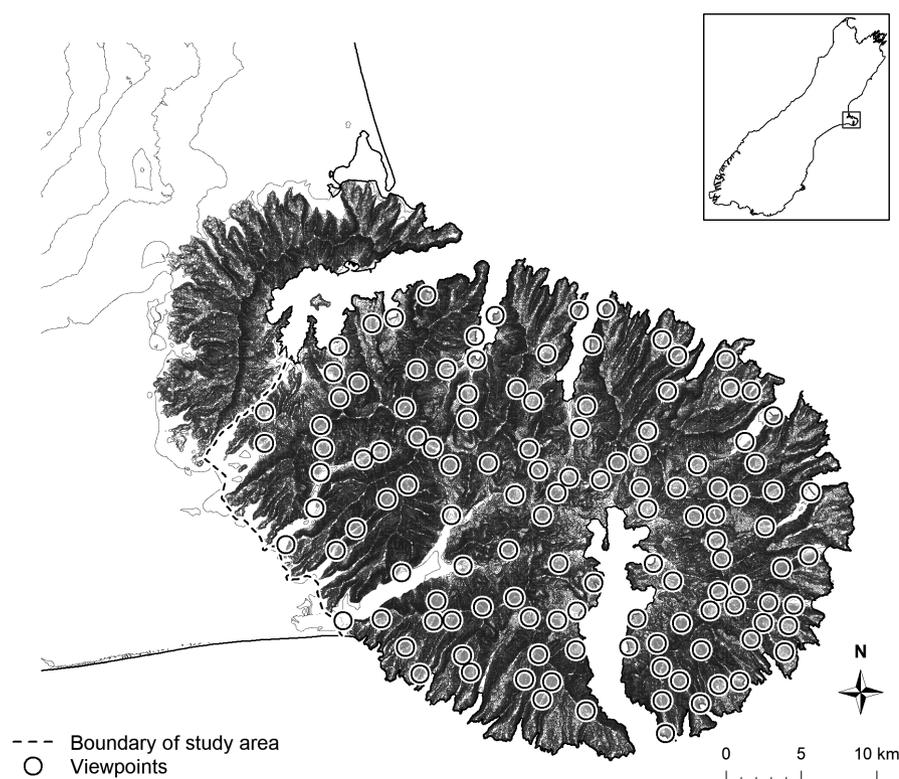


FIGURE 1 Map of Banks Peninsula, Canterbury, New Zealand, illustrating the locations of the viewpoints. Viewpoints are drawn to scale, with radii of 600m. Grey lines depict 10 m contours. Inset: the location of the mapped area on the South Island, New Zealand

of viewpoints, thereby efficiently surveying more land area than would be possible using a plot-based approach (Wyse, Hulme, & Etherington, 2022). We traversed the study area using the road and public walking track networks, in addition to access to private farm tracks, and performed surveys from 124 viewpoints that collectively ranged in elevation from sea level to 783 m (Figure 1). Permissions were obtained from private landowners where required. The mean distance between a viewpoint and its nearest neighbour was 1,785 m (range = 1,200–3,342 m). At each viewpoint, we used binoculars (20 × 50) to identify all naturally established *P. radiata* visible within a 600 m radius from the survey location. We used a Bushnell Prime 1300 laser rangefinder (ranging performance for trees = 731.5 m) and a Suunto KB-14/360R hand-bearing precision sighting compass (accuracy = 1/3°, precision = 0.5°) to measure the horizontal distance and bearing from the viewpoint to each tree. Locations of the viewpoints were determined using a Garmin GPSmap 60CSx. After accounting for magnetic declination (24°) and using the New Zealand Transverse Mercator 2000 (NZTM2000) projected coordinate system, we then used these data to calculate the locations of the observed *P. radiata*. Within 600 m, the location accuracy is within the resolution (25 m) of the environmental raster data used for our subsequent analyses, with a median location error of 4 m (Wyse, Hulme, & Etherington, 2022). To determine the area surveyed at each viewpoint, we calculated viewsheds from a 1 m resolution digital surface model (DSM) derived from LiDAR data (Land Information New Zealand, 2020), using the *ViewshedGenerate* function (Wang et al., 2000) from the *GDAL* package (version 3.1.0; GDAL/OGR contributors, 2021) in Python version 3.5.5 (Pérez et al., 2011), as described by Wyse, Hulme, and Etherington (2022). We specified a maximum viewing distance of 600 m matching our observation limit, observer eye height of 1.52 m and target height of 4 m.

2.4 | Environmental data

To facilitate our subsequent analyses of biotic and abiotic variables that explain the occurrence of *P. radiata*, we obtained openly available vector and raster data layers describing our site (Appendix S1). We collated, integrated and created raster layers for two sets of predictor variables, those variables describing characteristics of the nearest plantation forest to each cell that may limit seed arrival (forest height, mean slope, mean aspect, mean minimum temperature and mean water deficit), and those describing pertinent environmental characteristics of each cell that may limit seedling survival (land cover, minimum temperature, water deficit, slope, aspect, distance from the nearest road, and distance and bearing from the nearest plantation forest). Seed arrival is determined by the production of cones and seeds, the opening of cones and then the distances seeds are dispersed. Forest height, slope and aspect are likely to influence dispersal distance, while low temperature and water deficit may impact seed production, and potentially influence the opening of the

serotinous cones (Wyse et al., 2019). All raster layers were created at 25 m resolution.

2.5 | Data analysis

To assess the importance of different predictor variables and their relationships with the occurrence of *P. radiata*, as well as to generate a risk map for *P. radiata* establishment in the study area, we built a presence versus pseudo-absence habitat model using boosted regression trees (BRT), a machine learning technique that performs well at generating species distribution and habitat models (Barbet-Massin et al., 2012; Elith et al., 2008; McCarthy et al., 2021).

The BRT models were built using our 470 *P. radiata* presence observations with 470 pseudo-absence points, as simulation studies have found that BRT models perform best when a number of pseudo-absences is generated equal to the number of presences (Barbet-Massin et al., 2012). Models were constructed and evaluated within the *gbm.step* function from the *DISMO* package (Hijmans et al., 2020) in R (R Core Team, 2020) using 10-fold spatial block cross-validation (Roberts et al., 2017). The blocks were defined as a series of strips running north–south, positioned such that each block contained 47 presence points (Bahn & McGill, 2013). In all, 47 pseudo-absence points were randomly generated within each spatial block. Pseudo-absence points were randomly generated within visible cells in the viewsheds, which had been aggregated to 25 m resolution to match the environmental data, but were not permitted in any cells containing a presence point. Following testing as recommended by Elith et al. (2008), all models were conducted using a tree complexity (number of interactions) of 2, a learning rate of 0.01 (the contribution of each individual tree to the developing model) and a bag fraction (the proportion of observations used in each step) of 0.5. The number of trees was optimised for each individual model using the *gbm.step* function and ranged from 500 to 1,250. The *gbm.step* function was also used to calculate the relative contributions of each predictor variable, and the area under the receiver operating curve (AUC). This latter statistic was used to provide an assessment of model performance. To account for potential stochastic effects due to the random nature of the absence points, we generated 50 sets of pseudo-absence points and correspondingly computed 50 BRT models, with our final results representing the mean and variation of these 50 models.

For each BRT model, we examined potential interactions between the distance from a plantation forest and forest variables likely to affect dispersal distance (mean forest aspect, slope and tree height), between the bearing and distance from a plantation forest, and between the land cover class and the distance to the nearest road. These analyses allowed us to investigate (a) which forest variables might affect the likelihood of seeds being dispersed over long distances, (b) the effects of wind direction on dispersal distance at our study site and (c) whether roadsides provided refugia from browsing on neighbouring grazing land, or a sufficient

canopy gap in forest habitats to allow seedling establishment. We assessed the relative strength of the interactions using the *gbm.interactions* function from the *DISMO* package (Hijmans et al., 2020). Interactions were averaged across all 50 BRT models, with the mean values computed.

3 | RESULTS

3.1 | Area surveyed

From our 124 viewpoints, our viewshed analysis determined that we surveyed 10,739 ha for *P. radiata* individuals, in which we recorded a total of 470 individuals between sea level and 735 m elevation. The area surveyed equated to 12.2% of Banks Peninsula (Table 1) and ranged in elevation from sea level to 858 m. When assessing the New Zealand Land Cover Database (LCDB; Manaaki Whenua – Landcare Research, 2020) land cover classes, Banks Peninsula was dominated by ‘high producing exotic grassland’ (66.6% of the land area), with ‘broadleaved indigenous hardwoods’, ‘mānuka or kānuka’, ‘low producing grassland’, ‘exotic forest’ and ‘gorse or broom’ each also present in over 3% of the area (Table 1). ‘High producing exotic grassland’ consists of pastures sown with non-native grasses and legumes of good pastoral quality with intensive grazing, while ‘low producing grassland’ is of poor pastoral quality with extensive grazing (i.e. low livestock densities) or non-agricultural use (Manaaki Whenua – Landcare Research, 2020). For the six dominant land cover types, the land area surveyed reflected the relative abundances of the land cover types within the study area (Table 1), with the percentage of a cover class surveyed ranging from 9.7% (‘exotic forest’) to 14.55% (‘broadleaved indigenous hardwoods’).

3.2 | Habitat modelling of *Pinus radiata* establishment on Banks Peninsula

Our 50 BRT models of the distribution of *P. radiata* performed well, with all models achieving AUC scores ≥ 0.8 (range = 0.800–0.865). When averaged across the 50 models, the distance from the nearest plantation forest was the most important variable predicting the occurrence of *P. radiata* (mean = 17.8%, standard error = 0.4; Figure 2a),

followed by proximity to a road (mean = 17.6%, standard error = 0.3; Figure 2b), the bearing from the nearest plantation forest to the location (mean = 12.8%, standard error = 0.2; Figure 2c), and the site land cover class (mean = 11.1%, standard error = 0.2; Figure 2d).

3.2.1 | Site abiotic variables

Sites within 150 m of a plantation forest were predicted to have the highest probability of *P. radiata* occurrence, with the lowest probabilities beyond 900 m (Figure 2a), while sites immediately adjacent to roads also had a high probability of *P. radiata* establishment (Figure 2b). The bearing of a site from the nearest plantation was also among the most important variables, with the highest probabilities of establishment occurring at sites to the north and east of the nearest plantation (Figure 2c). *Pinus radiata* were most likely to occur on slopes $>10^\circ$ (Figure 2f). The aspect of a site, site water deficit and minimum temperature of the coldest month were of little importance in the models (relative importance values <5.0).

3.2.2 | Site biotic variables

Of the dominant land cover classes, the models suggested that *P. radiata* was most likely to establish in ‘mānuka or kānuka’ or ‘broadleaved indigenous hardwoods’ habitats, with a low probability of *P. radiata* establishment in ‘high producing exotic grassland’ (Figure 2d). We observed an interaction between the land cover class and proximity to a road, which affected the probability of *P. radiata* establishment. Specifically, for some land cover types (‘exotic forest’, ‘low producing grassland’, and ‘high producing exotic grassland’), establishment was comparatively much more probable adjacent to a road (Figure 3e) (relative interaction strength = 1.85).

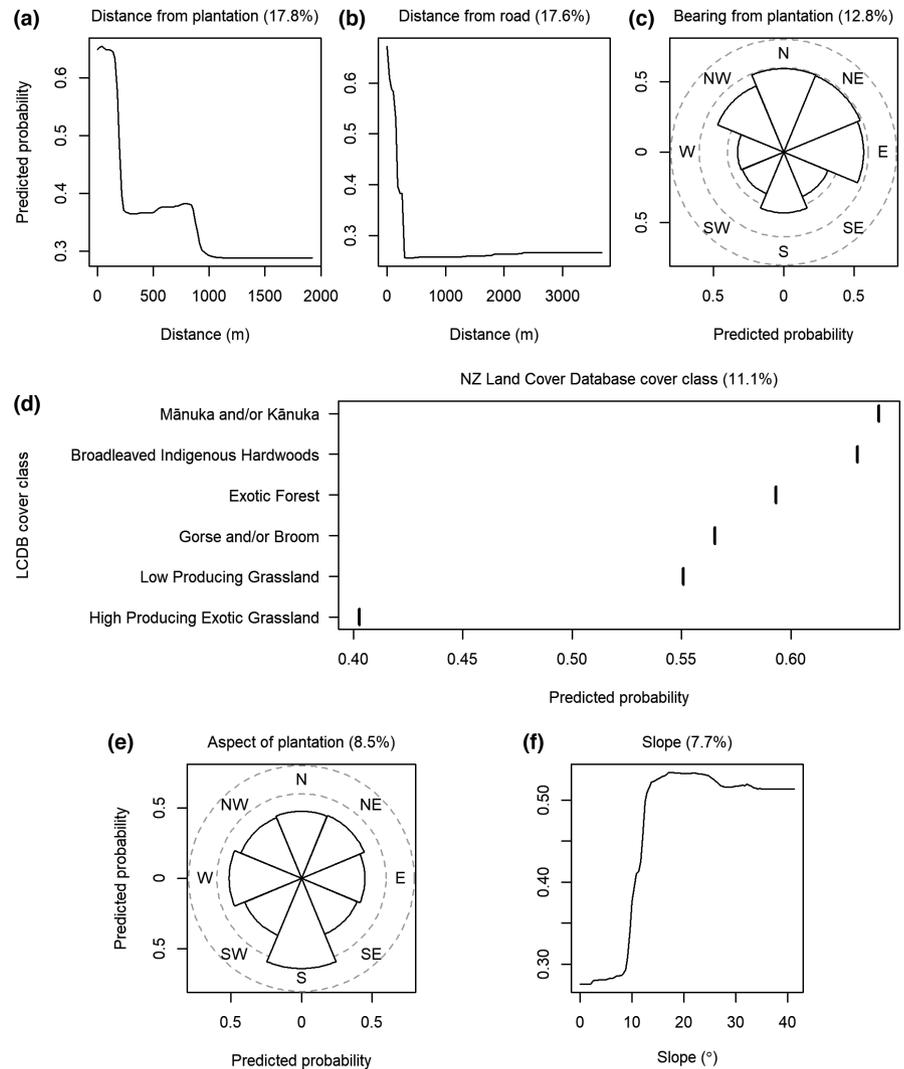
3.2.3 | Nearest plantation forest variables

Pinus radiata individuals were more likely to establish where the nearest plantation forest was south-facing (Figure 2e), while the mean slope on which the nearest plantation forest grew and the height of the nearest plantation forest were less important for predicting

LCDB class	Banks Peninsula (ha)	Area surveyed (ha)	Percentage surveyed
High Producing Exotic Grassland	58,529	7,165	12.24
Broadleaved Indigenous Hardwoods	7,879	1,146	14.55
Mānuka and/or Kānuka	5,601	627	11.20
Low Producing Grassland	5,556	742	13.35
Exotic Forest	4,314	419	9.70
Gorse and/or Broom	3,174	370	11.67
All LCDB classes	87,934	10,739	12.21

TABLE 1 The area of each of the dominant land cover classes on Banks Peninsula and the land surveyed during the study, as determined from viewshed analysis (remaining classes each represent $<1\%$ of the study area). Land cover classes from the New Zealand Land Cover Database (Manaaki Whenua – Landcare Research, 2020)

FIGURE 2 Mean partial response plots for the predictor variables (where relative importance >7%) across 50 Boosted Regression Trees models showing the marginal effects of the variables on the probability of *Pinus radiata* establishment. Land cover classes shown in (d) are the dominant cover classes in the study area. Dashed grey lines (c, e) indicate radii of 0.8, 0.6 and 0.4 (c) probability values to aid interpretation. Mean relative importance value for each variable, scaled from 0% to 100%, provided in brackets



establishment (relative importance = 4.5 and 4.6, respectively). Water deficit and minimum temperature of the coldest month for the nearest plantation forest were among the least important variables in the models (relative importance values <2.5).

We discerned few interactions in our BRTs between the distance from the nearest plantation forest and variables specific to those forests: mean aspect, slope and tree height (Figure 3a,c,d). The strongest interaction with distance from the nearest plantation was the bearing from the nearest plantation (relative interaction strength = 2.9; Figure 3b), as distances of more than 200m from the nearest plantation were comparatively more likely in north, north-east, north-west and easterly directions. Plantation aspect, plantation slope and plantation tree height had weak interactions with distance from plantation forest (mean relative strengths = 0.66, 0.37 and 0.05, respectively). Comparatively, *P. radiata* establishment was more likely at longer distances from the nearest forest plantations (i.e. >1,000m) where the nearest plantation faced south (Figure 3a), where the plantation was on a steeper slope (approximately 20°; Figure 3c), and from plantation forests with trees that were approximately 30m tall (Figure 3d). There was a low probability of establishment at long distances from taller plantation forests (40m), but this relationship with tree height reflects

the approximately normal distribution of plantation heights in the study area (mean = 27.4 m, standard deviation = 6.9 m), and may simply reflect that by chance more trees establish from plantations of the most common height, thus increasing the likelihood of observing establishment resulting from long-distance dispersal.

3.2.4 | Banks Peninsula risk map for *P. radiata* establishment

The predicted probabilities of *P. radiata* establishment across Banks Peninsula ranged from <0.01 to >0.95, with very similar results returned by the 50 model iterations (maximum standard error = 0.02). Approximately 3.4% of Banks Peninsula had a high probability of *P. radiata* establishment (predicted probability >0.7) (Figure 4). The areas with the highest predicted probabilities of *P. radiata* establishment (probability >0.9) were largely within 200m of the nearest plantation forest, with just 1.8% of this land further than 200m from the nearest plantation. Of these high probability areas, the land cover predominantly comprised 'mānuka and kānuka', 'broadleaved indigenous hardwoods', 'high producing exotic grassland' and 'exotic forest': all among

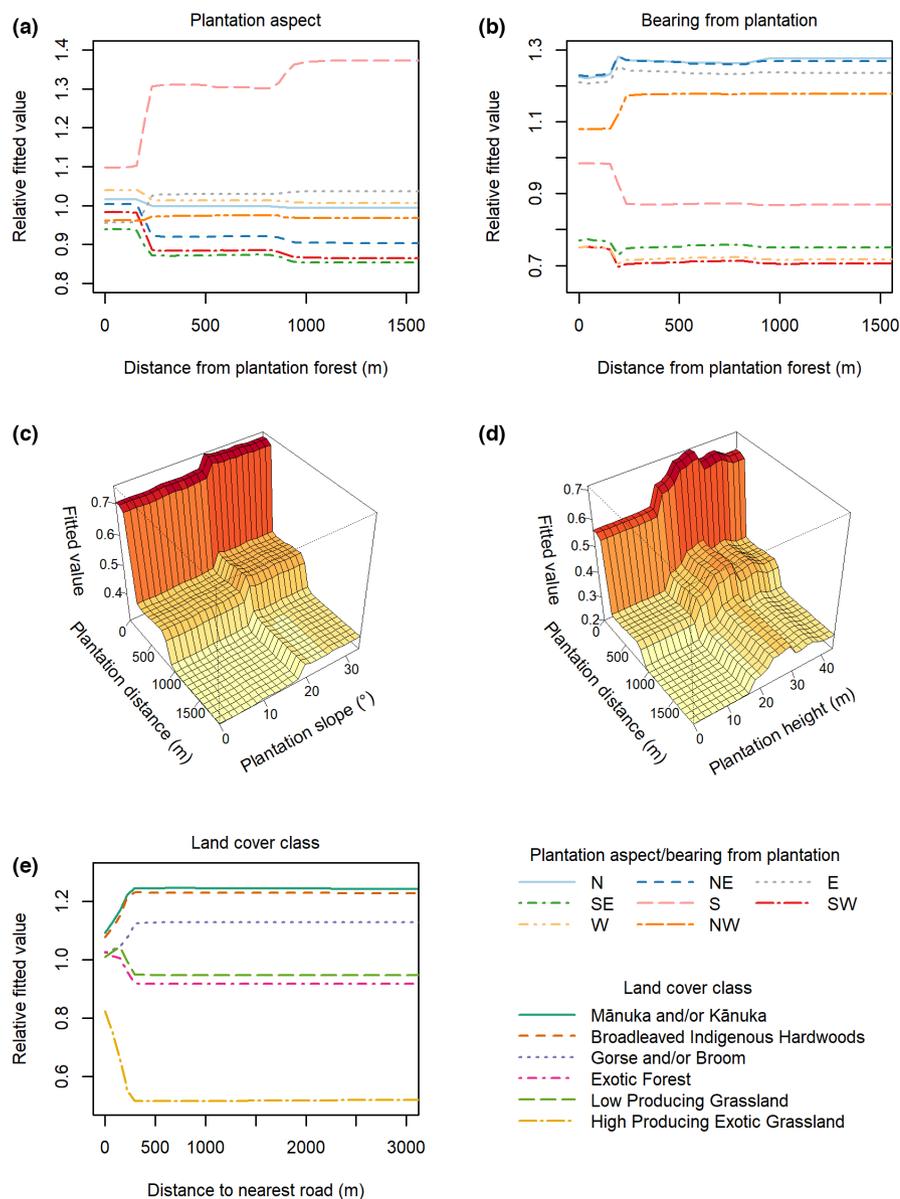


FIGURE 3 Interactions between important source plantation variables and the distance from the source plantation forest (a–d), and between the proximity to a road and the site land cover class (e), on the predicted likelihood of *Pinus radiata* establishment. (a) Interaction between source plantation forest aspect and distance from the source plantation forest, (b) interaction between the bearing and the distance from the source plantation, (c) interaction between source plantation forest slope and distance from the source plantation forest, (d) interaction between source plantation forest height and distance from the source plantation forest, and (e) interaction between distance from the nearest road and land cover class. Colour intensity in panels (c, d) indicates the intensity of the fitted values. Y-axis of panels (a, b, e) represents the fitted values per factor level relative to the mean, thus showing the comparative effects of the x variables on the fitted values for the different factor levels. Land cover classes displayed in panel (e) are the dominant land cover classes in the study area. Results are the mean of 50 Boosted Regression Trees models predicting the probability of *Pinus radiata* establishment on Banks Peninsula

dominant habitat types in the study area. While 'high producing exotic grassland' was a land cover type found to have a low probability for *P. radiata* establishment, the predictions of high probabilities of establishment in some areas of this land cover type were due to interactions among variables, particularly proximity to a road. For the 'high producing exotic grassland' with high probabilities of *P. radiata* establishment, most of the land was located in pixels within 30m of a road centre line. This was likewise the case for 'exotic forest', where the probability of *P. radiata* establishment was predicted to be comparatively high where a road cut through a forest. Approximately 29% of Banks Peninsula had a low probability of *P. radiata* establishment (probability <0.1), with areas of least concern typically high producing exotic grassland. Unlike the high producing exotic grassland most at risk of *P. radiata* establishment, this land was generally not adjacent to a roadside, with a median distance of 807 m from the nearest road compared with 35 m for the high-risk areas.

Although tussock grasslands and sand dunes comprise only a small fraction of our study area (0.03% and 0.7%, respectively), it

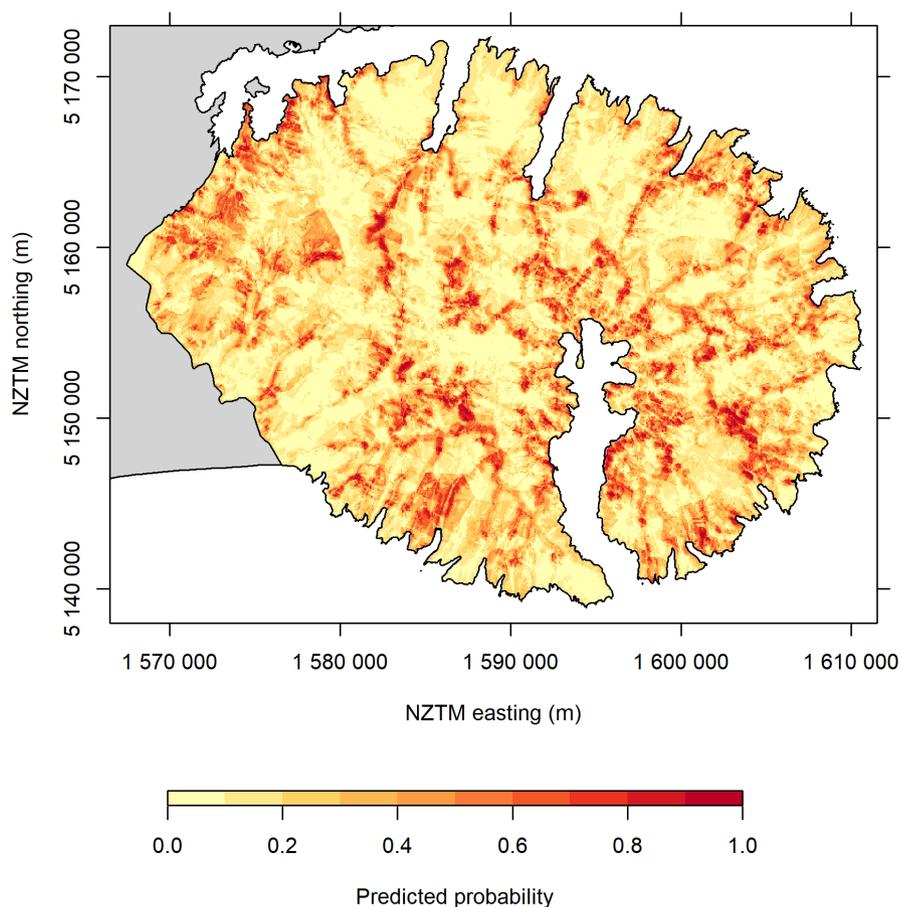
is evident that they are also vulnerable to *P. radiata* establishment on Banks Peninsula. Where these habitats occur within 200m of a plantation forest, the median probability for *P. radiata* establishment was 0.7 and 0.6, respectively. This is in contrast to indigenous forest (comprising 0.6% of Banks Peninsula), which had a mean probability value of 0.45 within 200m of a plantation forest, or managed habitats such as short rotation cropland (0.3% of Banks Peninsula; median probability proximate to a plantation = 0.35).

4 | DISCUSSION

4.1 | Drivers of *P. radiata* establishment outside of plantations

This study represents the most comprehensive examination to date of pine establishment across a heterogeneous landscape with varied vegetation communities, environmental conditions, and

FIGURE 4 Map of the Banks Peninsula study area (South Island, New Zealand) showing the mean predicted probability of *Pinus radiata* establishment from 50 Boosted Regression Trees models. Grey indicates land outside the area of the study. Some apparent sharp lines in the predicted probabilities pertain to boundaries in the identity of the nearest source plantation forest



topography. The patterns of *P. radiata* establishment determined on Banks Peninsula were largely as could be expected for a light-demanding wind-dispersed tree. Variables relating to dispersal ability and habitat suitability were key in predicting establishment success, and high-light environments with low browsing pressure from livestock were the most conducive to establishment. As expected, the proximity of a site to a plantation forest was the most important variable predicting *P. radiata* establishment, while strong southerly winds were clearly important for disseminating seeds. This latter finding was unexpected, given that cones of this serotinous pine are most likely open in hot conditions (Wyse et al., 2019). As such, we expected the hot, dry föhn winds from the north-west (Wilson, 2013b) to be a predominant driver of seed dispersal. However, it is evident that it is plantation forests on south-facing slopes that are responsible for the majority of, and the furthest dispersed, *P. radiata* at our site. Likewise, our findings provide some evidence that forests planted on steeper slopes will be more exposed to strong winds, and thus more likely to disperse seeds long distances.

With respect to the land cover types, high-light habitats were important for *P. radiata* establishment on Banks Peninsula. Pine seedlings are light demanding, and so are unable to establish beneath dense canopies and are easily suppressed by more vigorous species (Langdon et al., 2010; Ledgard, 2001; Richardson et al., 1994). Key habitats for *P. radiata* establishment on Banks Peninsula included those that represent the early stages of forest

succession, such as 'broadleaved indigenous hardwoods' and 'mānuka or kānuka', with individual pines observed emergent above the developing native early successional canopy. If *P. radiata* established alongside these native plant communities following a disturbance or grazing land being retired, pines may therefore affect forest succession. They are considered one of the most problematic non-native species affecting native forest regeneration on the south-east of Banks Peninsula (Peart & Woodhouse, 2021). However, once dense native vegetation becomes established, further regeneration will be unlikely except following disturbances such as fire (Gómez et al., 2019).

Estimates of *P. radiata* palatability to grazing ungulates have ranged from being the most (Crozier & Ledgard, 1990) to the least preferred of common non-native conifers introduced throughout the Southern Hemisphere (Zamora-Nasca et al., 2020). However, it is evident in New Zealand and elsewhere that browsing by stock and other herbivores is likely to reduce the spread of pines such as *P. radiata* (Ledgard & Norton, 2008; Williams & Wardle, 2007). While we observed this pattern here, with high producing grassland having one of the lowest probabilities of *P. radiata* establishment, individual trees were still apparent in this land cover type. Our model results suggest that this may be due to individuals within high producing grassland predominantly occurring proximate to roads. Many of the roads within our study area passed through high producing grassland regularly stocked with sheep, with the rank grassland of the road margin fenced off from the

pasture and therefore protected from stock browsing. Road margins also provided suitable habitat for *P. radiata* establishment within other land cover types that otherwise offered relatively poor habitat for the establishment of these individuals, such as within areas of plantation forest itself. In addition to protection from grazing, roadsides provide a light gap within what otherwise may be dense vegetation. Our finding of a high proportion of *P. radiata* individuals along roadsides was in comparison with the pseudo-absence points randomly distributed within the viewed area, suggesting that it did not arise from bias in the locations of the viewpoints.

Within our study area, the abiotic variables soil moisture deficit and minimum temperature of the coldest month were not found to be important for determining *P. radiata* establishment, despite frost and drought being described as key causes of mortality in *P. radiata* seedlings elsewhere (Burdon & Miller, 1992). Minimum annual rainfall on Banks Peninsula is approximately 500–600 mm (Wilson, 2013a; Wilson, 2013b), and *P. radiata* has been found naturalising in heathlands, shrublands and woodlands in areas with <600 mm annual rainfall in Australia (Richardson & Higgins, 1998). Thus, the rainfall in the study area may not reach levels low enough to impact *P. radiata* establishment. Likewise, 99% of the Banks Peninsula study area is below 750 m, and so it is unsurprising that low temperature was not found to prevent *P. radiata* establishment anywhere within the study area. Species distribution modelling suggests that the entire Banks Peninsula is climatically suitable for *P. radiata* establishment and growth, both currently and under future climate scenarios (Etherington et al., 2022). However, our modelling demonstrates that within our study area microsite characteristics were the most important for determining the likelihood of *P. radiata* establishment. This finding illustrates that while broad-scale species distribution models based on climatic variables are useful for global- to regional-scale invasive species risk assessments, models required for finer scale invasive species management actions will need to include microsite characteristics to provide relevant predictions.

4.2 | Recommendations and implications for management

On Banks Peninsula, we have demonstrated that establishment of *P. radiata* from plantations is occurring in vulnerable habitats, up to 1.4 km from source trees. Given the large number of *P. radiata* plantations, we suggest that continued establishment of these species will represent an ongoing management concern. Furthermore, projections suggest the region may be targeted for further expansion of plantation forestry using *P. radiata* (Watt et al., 2011). Currently, approximately 3.4% of the peninsula is at high risk of *P. radiata* establishment. However, we estimate that 22% of the peninsula is within 200 m of a potential seed source and therefore highly likely to be receiving seed rain, with 91% within 1.4 km of a seed source and therefore potentially receiving low numbers of

seeds via long-distance seed transport. Therefore, should land use change in the future with reductions to the currently high grazing pressure, the risk of *P. radiata* spread could become much higher. In addition, it is evident that some plantations, specifically those that are south-facing and on steep slopes, pose a greater threat and should not be replanted in a non-native conifer species upon harvesting.

Within New Zealand, *P. radiata* is generally considered to be less likely to spread from plantations than many other non-native conifer species (Froude, 2011; Ledgard, 2001). However, as seen in other regions (McConnachie et al., 2015), we have demonstrated here that establishment of *P. radiata* is occurring from planted forests in New Zealand, including at relatively high densities at some sites. Based on our findings, we recommend that New Zealand forest managers must draw on global guidelines of the management of plantation forests (Brundu et al., 2020) and consider the ability of this species to spread from plantation forests, particularly if warming climates see this species planted at higher elevations where surrounding landscapes comprise more vulnerable habitats. Our methods and results should be used to contribute towards planning and risk assessments for future plantations, facilitating the design and location of plantations to minimise the risks to vulnerable habitats of the naturalised spread of this species, as well as to aid management of plantation forests in other parts of the world (Brundu et al., 2020). Furthermore, our findings can also be used to guide management programmes, particularly for conifer invasions in the Southern Hemisphere (Essl et al., 2010), thereby aiding a rapid response to any naturalised spread and thus reducing both control costs and environmental impacts.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

S.V.W. and P.E.H. conceived the ideas; P.E.H. obtained the funding; S.V.W. undertook the field work; S.V.W. and T.R.E. designed the methodology and undertook the analyses. All authors contributed to writing the manuscript.

DATA AVAILABILITY STATEMENT

R and Python code used in the manuscript are archived and made publicly available on Figshare (<https://doi.org/10.6084/m9.figsh>)

are.19492100.v1; Wyse, Etherington, & Hulme, 2022a). Data associated with this manuscript are also archived and made publicly available on Figshare (<https://doi.org/10.6084/m9.figshare.19492088.v1>; Wyse, Etherington, & Hulme, 2022b).

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