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RESEARCH

Patterns of seed rain into exotic plantation forests, Hawke's Bay, New Zealand

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Abstract: Ecological restoration to mitigate human impacts on the environment is increasingly widespread, particularly in forest ecosystems. Exotic plantation forests have been posited as beneficial for the restoration of forest ecosystems by creating a favourable microclimate in the understorey for native vegetation to establish. Native seed dispersal into plantation forests is a vital part of this process. We sampled seed rain across a 6-month period at three sites in mature (> 20 years) *Pinus radiata* plantation forest in the Hawke's Bay region of Aotearoa | New Zealand across a gradient from native forest edge into the plantation forest. Seed traps were exponentially spaced along three 620 m transects at each site. Vegetation sampling of the understorey was undertaken to compare vegetation composition with that of the seed rain. Over the sampling period, 2061 seeds of 19 different species were captured. Distance from native forest edge had a significant negative effect on the species richness and abundance of seed rain for both dry seeded and fleshy fruited seeds, with a similar pattern observed in woody species. However, this effect was significantly stronger at the Blowhard site, which was adjacent to a more species-rich, mature native forest. *Cirsium* sp. and *Coriaria arborea* var. *arborea* were present in the seed rain but not in the plantation understorey vegetation. Seed rain was most abundant and diverse in the first 20 m of the plantation forest from the native forest edge. The presence of understorey vegetation along the transects, including 18 woody species that were not captured in the seed rain, suggests seed rain is penetrating the plantation forest up to 620 m, albeit at a lesser frequency beyond 20 m from the native edge. Frequent islands of native forest within a plantation forest matrix are likely to act as nuclei to increase the richness and cover of regenerating native plants in the plantation understorey.

Keywords: forest succession; forest transition; restoration; seed dispersal

Introduction

Ecological restoration is an important tool to address the effects of anthropogenic changes, including climate change and habitat loss, with restoration efforts being particularly focused on forest ecosystems (Suding et al. 2015; Crouzeilles et al. 2016). Global movements such as the U.N. Decade on Ecosystem Restoration aim to reverse declining biodiversity, improve the wellbeing of local communities, and respond to a changing climate (United Nations 2021). However, effective widespread ecosystem restoration can be resource intensive. Passive restoration is a method of restoring terrestrial ecosystems that requires less labour and monetary input and allows regeneration of vegetation to occur through natural seed dispersal into a site. This contrasts with active restoration where a site is managed by way of clearing unwanted vegetation, planting of desired species, and/or direct seeding (Benayas et al. 2008). While passive restoration may appear to be a more cost-effective option for forest restoration, there are often less obvious and perhaps longer-term costs involved with passive restoration projects such as the establishment and maintenance of fencing and labour for site monitoring (Zahawi et al. 2014).

Another method of native forest restoration being explored is making use of exotic tree species, often in plantations, as a facilitator for the natural regeneration of native vegetation. Globally, research has found that exotic plantation forests often harbour understories of regenerating native vegetation (Ogden et al. 1997; Brockerhoff et al. 2008; Tárrega et al. 2011; Onaindia et al. 2013; Onyekwelu & Olabiwonnu 2016; Marshall et al. 2024). The coverage of plantations is expanding worldwide alongside an increasing focus on biodiversity restoration (Wang et al. 2022). Plantation forests create a favourable microclimate for the establishment of late-succession species by tempering exposure to the harsh elements of an open site and by reducing competition with herbaceous weed species that the plantation canopy shades out (Forbes et al. 2015). Over time, the plantation species will theoretically senesce and the native vegetation in the understorey will assume dominance, thus transitioning the forest from an exotic plantation to a native forest (Marshall et al. 2023). This scenario could occur where a plantation forest has been established for the purpose of carbon sequestration or where it has been established on land that is not economically viable or socially acceptable to harvest. Native species have been found in the seed rain and soil seed bank of a 30-year-old plantation *Pinus radiata* forest near Wellington, New Zealand (Moles & Drake 1999). While

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there was a greater richness of native species than of exotic species in the seed rain and the soil seed bank, there were also many exotic weed species, with the total abundance of seed in the soil seed bank dominated by exotic weed species (Moles & Drake 1999). Some research has also found that plantation forests do not support the regeneration of native forest when compared with other vegetation transition types, or when managed intensively for timber production (Wang et al. 2022; Zhu et al. 2023).

A critical element to forest restoration, especially via passive management, is the arrival of propagules. The regeneration of vegetation can be limited by either the availability of suitable sites or by insufficient seed supply (Duncan et al. 2009), both of which may be limiting factors in the context of exotic plantation to native forest transitions. Restoration sites that are isolated from native forest have a reduced abundance and richness of native species in the seed rain (Overdyck & Clarkson 2012) which may limit the rate at which native vegetation establishes, as well as the species composition (Clark et al. 1998; Overdyck & Clarkson 2012). The receiving environment of the seed rain has also been found to affect the composition of seed rain (Vespa et al. 2014). Dry seeds have greater dispersal into sites that have a contrasting structure to their source, e.g. from a native forest to an open site. In contrast, fleshy fruited seeds are dispersed more readily into a structurally similar site, e.g. from a native forest to an exotic plantation forest (Vespa et al. 2014). Soil seed banks may also contribute to regeneration of vegetation, though many seeds native to Aotearoa | New Zealand do not persist in the soil for long periods of time (Overdyck & Clarkson 2012).

In Aotearoa | New Zealand, approximately 33% of all native plant species are dispersed through endozoochory, where seeds are ingested by an animal (Thorsen et al. 2009), and 59% of tree species have fleshy fruits (Kelly et al. 2010). There are no native terrestrial mammals other than three species of bat (*Chalinolobus tuberculatus*, *Mystacina robusta* [considered extinct], and *Mystacina tuberculata*), meaning that the primary dispersal mechanism for the fleshy-fruited tree species is via birds (Clout & Hay 1989). Unfortunately, several frugivorous native bird species are either now extinct (four species) or threatened (eight species), resulting in an overall reduction in effective seed dispersal, especially for tree species with fruit larger than 1 cm diameter (Clout & Hay 1989; Kelly et al. 2010; Miskelly 2013). While frugivorous and nectivorous birds have been found to be less common in exotic plantation forest, their abundance in forestry areas within 5 km of an adjacent native forest is no different than in native forest (Clout & Gaze 1984).

Kererū (*Hemiphaga novaeseelandiae*) are an important seed disperser in Aotearoa | New Zealand due to their ability to consume large seeds and their long seed retention time which allows them to more effectively spread seed away from the parent tree (Wotton & Kelly 2012). Kererū can disperse seeds over long distances (> 1 km), however, 88% of seeds are dispersed within 100 m of the parent tree (Wotton & Kelly 2012). Populations of kererū have declined significantly in the 2000s compared with the 1980s (Carpenter et al. 2017), which has a negative impact on the dispersal and establishment of plant populations (Wotton & Kelly 2011). However, seed dispersal may not be entirely limited to birds. Invertebrates such as endemic wētā (Anostostomatidae and Rhaphidophoridae) can disperse small seeds in an intact state (Duthie et al. 2006). Native herpetofauna also contribute to the dispersal of fleshy fruited seeds (Alena et al. 2023). Exotic mammals such as brushtail possums (*Trichosurus vulpecula*) may also contribute to seed dispersal, although fewer seeds tend to be dispersed intact (Dungan 2002).

Whilst regenerating native vegetation is known to be common in the understorey of exotic plantation forests of *P. radiata* and *Pseudotsuga menziesii* in Aotearoa | New Zealand (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2008; Marshall et al. 2024) and in *P. radiata* plantations internationally (Onaindia et al. 2013; Kremer et al. 2021), little is known about the patterns of seed dispersal into the forest. Only one prior study exploring the seed rain in an exotic plantation in Aotearoa | New Zealand has been undertaken. While their research showed that seed rain of native plant species was entering the *P. radiata* plantation, including species not present in the understorey vegetation (Moles & Drake 1999), we do not know how the abundance and species richness of seed rain changes with distance from the plantation edge nor the influence of dispersal mechanism on seed dispersal into the plantation forest.

The dispersal of seeds into plantation forests is a critical element for the establishment of native vegetation in the understorey, and the potential for that understorey to persist and follow a succession towards canopy dominance. In this paper we explore the seed rain in an exotic *P. radiata* plantation forest along a gradient from a native forest edge into the plantation, with a particular emphasis on woody species due to their role in the transition of a plantation to a native forest. We do this by asking the following questions: (1) What is the abundance and species richness of seed rain in the plantation forest? (2) Do the abundance and species richness of seeds dispersed into the plantation forest change with distance from the native forest edge, and is this pattern consistent across sites? (3) Is fruit type (fleshy/dry) correlated with dispersal distance into the plantation? (4) What is the structure and composition of the understorey vegetation and how does this relate to the seed rain?

Methods

Study site

The study sites were in the foothills of the Kaweka ranges, inland in the Hawke's Bay region of Aotearoa | New Zealand (Fig. 1). The mean annual temperature is 11.5 (± 1.1 SE) °C, and the mean annual rainfall is 1600 (± 205 SE) mm (Etherington et al. 2022). The seed traps were deployed in *P. radiata* plantation forest which ranged in age from 21–26 years old. Three sites were chosen where the plantation forest bordered a large tract of native forest to quantify the dispersal of seeds into mature plantation forest from a native edge inward. The elevation range of the sites was 760–800 m above sea level. The sites share the same history of conversion to *P. radiata* plantation forest in the 1970s. Harvesting occurred in the late 1990s/early 2000s followed by re-establishment in 1998 (Blowhard), 2000 (Kuripapa), and 2003 (Castlerock). All three sites share a similar topography of flat and rolling terrain. The direction of the transects perpendicular to the native forest edge varied between the sites, with the Blowhard transects running west to east, the Kuripapa transects running north to south, and the Castlerock transects running northeast to southwest (Fig. 1). The sites where the seed traps were deployed exist in a landscape matrix of *P. radiata* plantation forest stands of various ages, patches of native forest within the plantation, and larger tracts of public conservation land consisting of native forest and

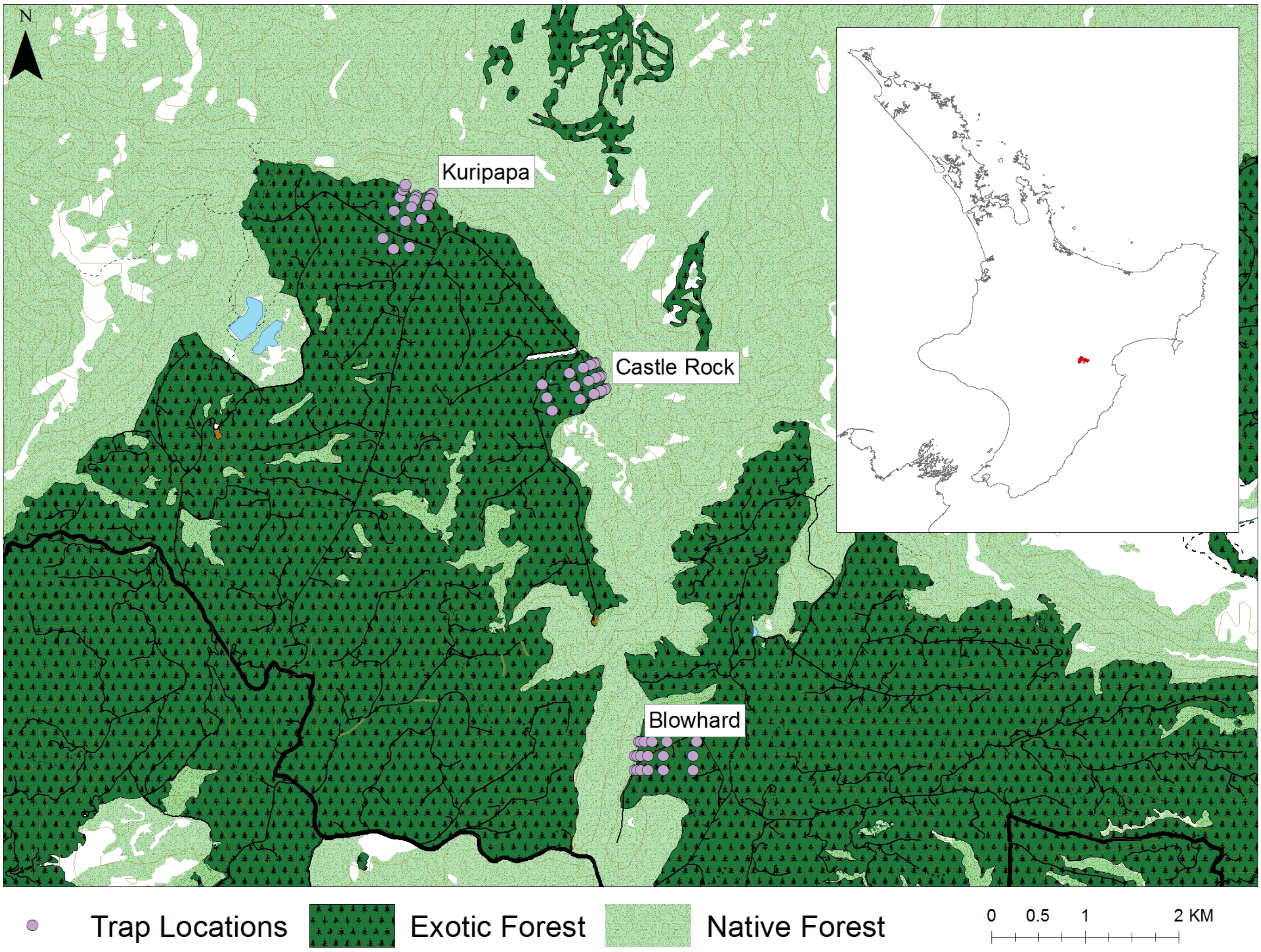

Figure 1. Map of trap locations in the Kaweka forest in the Hawke's Bay region. Areas in white are unmapped areas which are not native or exotic forest. Inset: North Island of Aotearoa | New Zealand and location of Kaweka forest.

scrub (defined as dense shrubland with an approximate height range of 0.2–3 m; Wardle 1991). Plant species lists recorded in the Blowhard reserve and in the adjacent publicly owned land show that the reserve is a mixed podocarp-beech-broadleaf forest (Druce 1960) and suggest that the publicly owned land is a mixed podocarp-broadleaf forest (Cunningham 1974).

Sampling methodology

Seeds were collected in seed traps which consisted of a 42 L circular tub with a surface area of 0.16 m^2 secured between three 0.9 m stakes. The tubs had eight 2.5 mm drainage holes drilled into their base and two layers of insect screen mesh with a hole size of 0.8 × 0.8 mm secured over the base to prevent material being lost through the drainage holes. Bird netting with a 16 mm diamond mesh was secured over the top of the trap to discourage vertebrates from entering the trap.

At each study site, three 620 m transects were laid 150 m apart and perpendicular to the forest edge. The position of the first trap on the first transect was randomly located along the boundary between the native and plantation forests, with the next two transects placed to the east of the first for the Kuripapa and Castle Rocks sites, and to the north of the first at the Blowhard site. The seed traps were set out with exponential spacing along the transect from the boundary to capture the expected rapid decline in native seeds being dispersed further into the plantation forest. The first trap was located at the very edge of the plantation forest and traps were then placed along the transect at 20 m, 60 m, 140 m, 300 m, and 620 m from the native forest edge. There were three transects at each site, giving 18 seed traps per site and 54 seed traps in total. The total area sampled by the 54 seed traps was 8.6 m^2.

The seed traps were installed from the 18th–21st of December 2023 and were emptied every four weeks for the next six months until the 6th of June 2024, giving a total sampling period of 172 days. Samples from each trap were air dried upon return from the field before seeds were separated, identified, measured for length on the long-axis, and counted. Seeds were identified using the "Seeds of New Zealand" series (Webb & Simpson 2001; Webb 2019) and through comparison with collections held in the School of Biological Sciences, University of Canterbury. Seeds that were unable to be identified were germinated and grown until the plant could be identified. Unidentified seeds that did not germinate are referred to as unknown taxon.

Vegetation surrounding the seed traps was also measured at three points along the transects. Three vegetation plots were established along each transect at the first, fifth, and sixth seed traps, which captured the middle and each end of the transect. A 10 m × 10 m plot was established using the seed trap as the centre and data were collected on all seed plants following the RECCE (relevé) method (Hurst & Allen 2022) which allows for an understanding of understorey vegetation structure, cover, and composition. Ferns were excluded, as our focus here is on seed plant dispersal. Using the RECCE method, each plot was split into height tiers (0–30 cm; > 30 cm–2 m; > 2–5 m; > 5–12 m; > 12–25 m), and each species within each tier was assigned a cover abundance class (1 = < 1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; 6 = 76–100%). Nomenclature in text follows the Manaaki Whenua – Landcare Research online database "Ngā Tipu Aotearoa – New Zealand Plants" within the Biota of New Zealand portal (biotanz.landcareresearch.co.nz/).

The cover abundance scores for each species in each tier were converted to a single species importance value (IV) by multiplying the cover class score (COV) from each tier with a corresponding tier weight (TW) and then summing all tiers to produce the importance value (*i* = tiers 1–6; Eqn. 1) (Burns & Leathwick 1996). The cover class scores were produced by taking the mid-point of the cover abundance range (e.g. cover abundance class 3 (6–25%) = 15.5) and the tier multiplier was the maximum height of each tier (e.g. tier 2 (12–25m) = 25).

$$IV = \sum \log 10\left(\left(COV_i * TW_i\right) + 1\right) \qquad (1)$$

Data analysis

Seed rain from *P. radiata* was included in the description of the seed rain composition but was excluded from further analyses, as the purpose of this research was to explore the seed rain of species other than the existing exotic plantation to gain an understanding of the potential succession of the forest. To explore how distance from the native forest edge was affecting the seed rain entering the *P. radiata* plantation forest we calculated the mean and standard error for the number of seeds in each trap along the transect. All means presented are given as ± standard error. We then log transformed the seed count data and the seed trap distance from native edge to achieve linearity and improve model fit. Linear mixed-effects models were then used to test the relationship of distance from native forest edge with seed rain abundance and species richness. Site was used as the random factor in linear mixed-effects models in the data analysis. We then explored the interaction of site with seed rain abundance and species richness using linear models where the outcomes were compared using Tukey post-hoc pairwise comparison. The relationship between seed rain abundance, species richness, and distance from native edge was then explored at a site level to show how the linear relationships differed by site. We then considered the differences in seed rain abundance and species richness in relation to edge distance for fleshy fruited and dry seeded species. This was undertaken using linear mixed effects models where the response variable was (1) the proportion that fleshy fruited seeds contributed to the total seed rain or (2) the proportion that fleshy fruited species contributed to the total species richness. We then tested the differences in seed rain abundance and species richness in relation to distance from native edge for woody species only. Woody species were defined as all species with "significant lignification of above ground parts", as defined by McGlone and Richardson (2023).

Understorey vegetation composition was compared to the composition of the seed rain. A Mantel test was conducted using the function *mantel* in the "vegan" package (Oksanen et al. 2022) to assess the correlation between the species compositions of the vegetation plots and those of the corresponding seed traps. There was potential that vegetation above 2 m in height within the plantation understorey could have contributed to the seed rain collected in the seed traps. We examined the composition of vegetation recorded in tiers 1–4 (> 2m) to see whether there were species present in these taller height tiers in the understorey vegetation that were also present in the seed rain. We also examined the vegetation composition in height tiers 5 and 6 (< 2m) to see whether there were seedlings of tree species present in the understorey that were not present in the seed rain captured during our study. We then investigated the relationships of both seed rain abundance and species richness with understorey vegetation importance value using Spearman's ranked correlation tests. We investigated the relationship between distance from native edge, understorey vegetation importance value, and species richness using linear models fitted using the *lm* function in the "stats" package (R Core Team 2023). All data analysis was undertaken using R version 4.3.1 (R Core Team 2023).

Results

Seed rain species richness and abundance

Over the six-month sampling period a total of 2061 seeds were collected in the seed traps (Table 1). The seed rain was composed of 19 different species, 11 of which were native to Aotearoa | New Zealand (57.9%), two of which were exotic (10.5%), and six of which were unable to be identified (31.6%). Of the two identified exotic species, one was the canopy species *P. radiata*, and the other belonged to the exotic herb genus *Cirsium*. Of the identified species, five (38.5%) were fleshy fruited, and eight (61.5%) were dry seeded. Despite the distribution of the number of species recorded for each seed type, considerably more dry seeds were found in the seed traps, with 94.5% being dry seeded and 5.5% being fleshy fruited. Of the 19 species in the seed rain, nine were woody, four were herbs (including the seed that was only able to be identified to the family level of Asteraceae), and six were unknown taxa. Seed from woody species comprised most of the seed rain, with 92.7% of the total seed rain originating from plants with tree or shrub growth forms. There were approximately ten times more *Brachyglottis repanda* than the next most common species in the seed rain, *Kunzea ericoides*. The most common herb seed was that of *Austroderia fulvida* (2.9%) with 59 seeds recoded in the seed rain. The remaining 8.5% of the seed rain was comprised of seeds from ten species. One unknown taxon contributed 27 seeds to the seed rain. While this seed was not identified, eight of these seeds were found in brushtail possum (*T. vulpecula*) faeces, suggesting that it is likely to belong to a fleshy fruited species. The remaining five unknown taxa contributed 0.44% of the total seed rain.

The pattern of seed rain by month differed between dry seeded and fleshy fruited species. Most seed rain for dry seeded species was collected in February and March, with *Kunzea ericoides* peaking slightly later (Fig. 2a). The peak of seed rain for fleshy fruited seeds was in April and May, with *Melicytus ramiflorus* peaking earlier than the other fleshy fruited species (Fig. 2b).

Table 1: Description of seed rain found in all traps over the six-month sampling period. Growth form as per McGlone and Richardson (2023). Asterisk (*) defines known exotic species. # denotes canopy trees as per Wyse et al. (2023).

Species	Number recorded	Seed form	Seed length	Growth form
Brachyglottis repanda	1521	Dry seed	2.1–3.0 mm	Tree
Kunzea ericoides	151	Dry seed	0.8–2.1 mm	Tree #
*Pinus radiata**	146	Dry seed	4.5–9.1 mm	Tree #
Austroderia fulvida	59	Dry seed	2.3–5.5 mm	Herb
Cirsium sp.*	46	Dry seed	1.3–3.0 mm	Herb
Coprosma rhamnoides	34	Fleshy fruit	2.3–3.6 mm	Shrub
Unknown taxon 1	27		3.2–4.5 mm	
Coprosma robusta	20	Fleshy fruit	3.4–5.5 mm	Tree
Pseudopanax arboreus	17	Fleshy fruit	3.4–4.6 mm	Tree
Melicytus ramiflorus	11	Dry seed	2.0–3.7 mm	Tree #
Pittosporum tennuifolium	7	Fleshy fruit	2.7–4.2 mm	Tree
Coriaria arborea var. *arborea*	5	Fleshy fruit	1.6–2.0 mm	Tree
Unidentified Asteraceae	5	Dry seed	1.5–2.0 mm	
Carex sp.	3	Dry seed	3.7–5.1 mm	Herb
Unknown taxa 2–6 (1–4 seeds per taxon)	9			

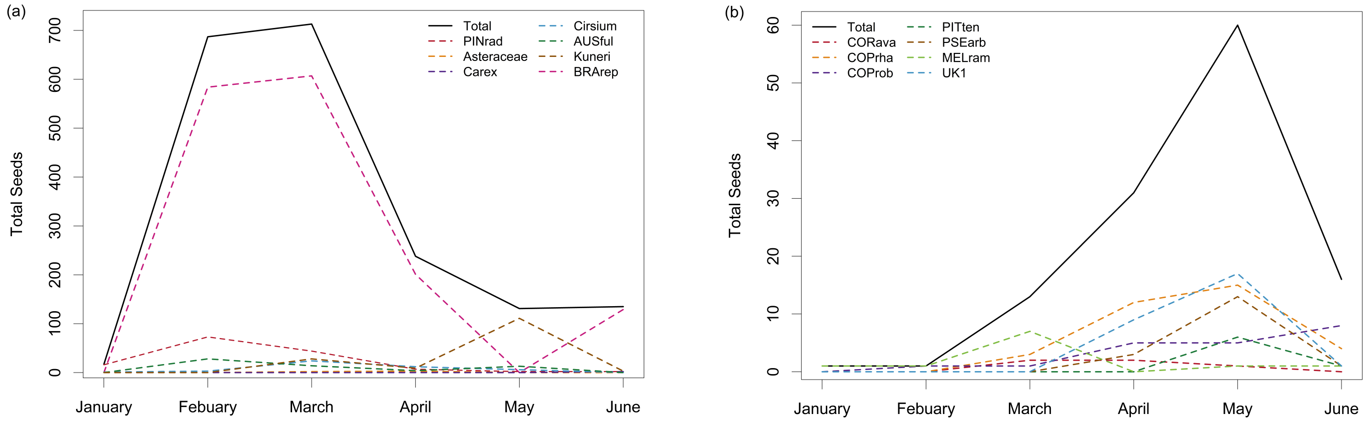

Figure 2. Time series of seed rain into all seed traps. Panel (a) shows dry seeded species. Panel (b) shows fleshy fruited species. UK1 denotes the most common unknown taxon from Table 1.

Effect of distance from native forest edge on seed rain

On average, the first trap in each transect captured 40.3% (± 5.9%) of the total seed rain for the transect, and the second trap at 20 m from the edge captured 24.8% (± 5.9%; Fig. 3a). For dry seeded species, 39.86% (± 5.7%) of the seed rain fell in the first trap, and 17.2% (± 5.7%) in the second trap (Fig. 3b). For fleshy fruited seeds, 42.4% (± 7.2%) of seed rain was captured in the first trap, and 34% (± 7.2%) in the second trap. A mean of 15 (± 5) fleshy fruited seeds per m^2 were collected from traps between 20 m and 300 m from the native forest edge, and there were no fleshy fruited seeds found in any traps at 620 m from the native forest edge (Fig. 3c). The number of dry seeds collected in traps beyond 20 m from the native forest edge was greater than the number of fleshy fruited seeds, with a mean of 68.1 (± 15.6) seeds per m^2 in traps 60 m or more from the forest edge. The proportion of dry seed also increased in traps at 620 m from the forest edge, comprising 25.1% (± 5.7%) of seed rain falling in these traps. This increase was driven by seed rain from *Austroderia fulvida* on two transects at Castlerock and one transect at Kuripapa.

Seeds from woody species followed a similar trend to the fleshy fruited seeds, with a sharp decline in the mean number of seeds per m^2 beyond the second trap at 20 m from the native forest edge. On average, the first trap contained 56.2% (± 9.1%) of woody seed rain, and the second trap 30.4% (± 9.1%) (Fig. 3d). *Pinus radiata* seeds were found throughout the transects, with their abundance in seed rain being significantly correlated with distance from native forest edge ($P < 0.001$, conditional $R^2 = 0.43$, marginal $R^2 = 0.23$; Fig 3e). Of the variation in abundance of *P. radiata* seed rain, 23% could be explained by distance from native forest edge, and a further 20% could be attributed to site.

A significant interaction between sites was found in the relationship between the species richness of seed rain and edge distance, and also in the relationship between seed rain abundance and edge distance. Pairwise comparison found that the Blowhard site had significantly greater seed rain abundance and species richness than the Castlerock or Kuripapa sites. The relationship between distance from native forest edge and seed rain abundance was highly significant at Blowhard

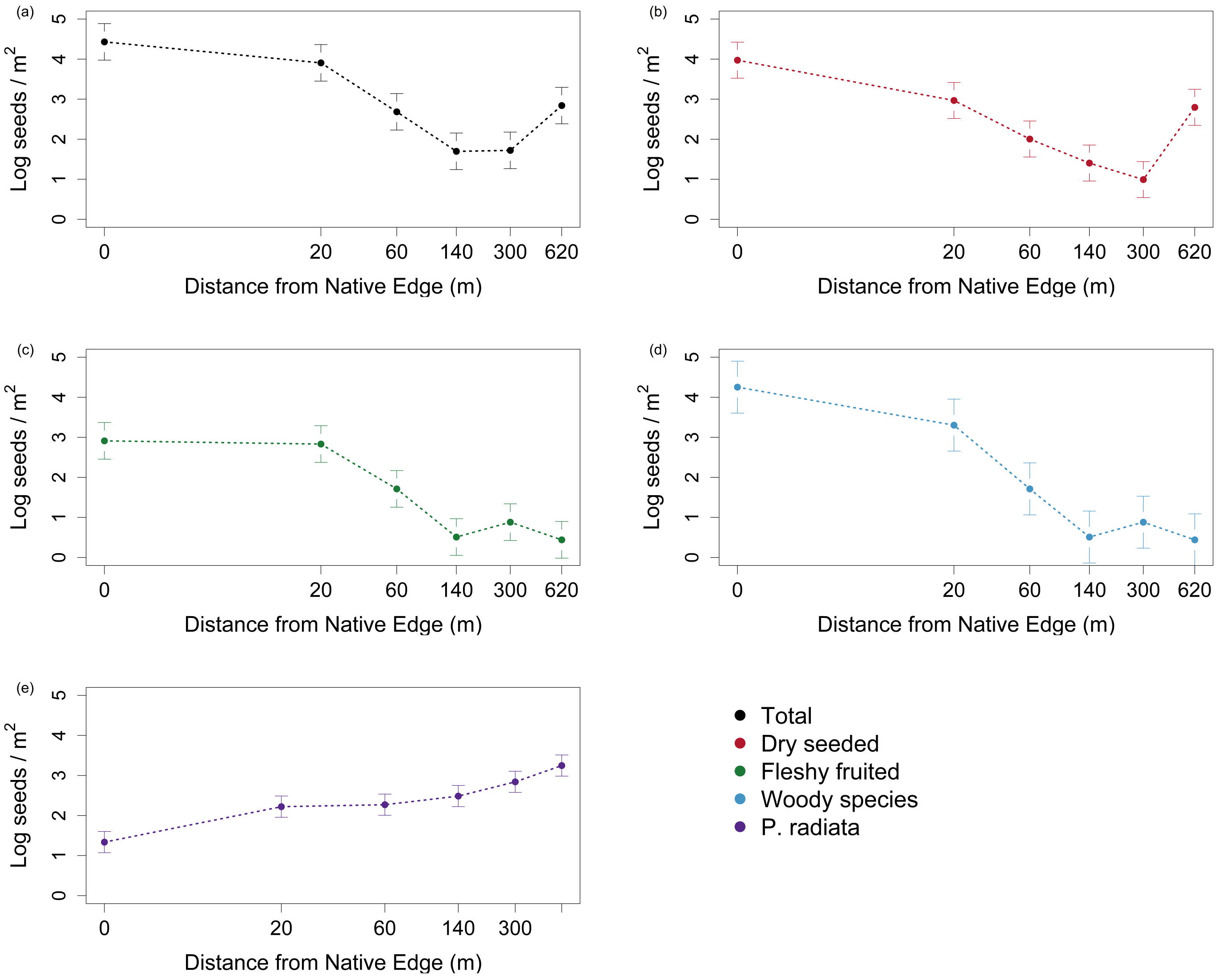

Figure 3. Panel (a) shows mean total seeds, excluding *P. radiata*, per m^2 at each trap distance from native edge. Panel (b) shows mean number of dry seeded seeds per m^2 at each trap distance, excluding *P. radiata*. Panel (c) shows mean number of fleshy fruited seeds per m^2 at each trap distance. Panel (d) shows mean number of seeds from woody species per m^2 at each trap distance. Panel (e) shows mean number of *P. radiata* seeds per m^2. Means were taken from log transformed seed counts. Error bars show standard error of the mean. The x-axis is presented on a log scale.

($P < 0.001$), with a moderately strong negative relationship ($R^2 = 0.58$; Fig. 4a). However, the effect of distance from native edge was not significant at Castlerock or Kuripapa, with no relationship between distance to native edge and seed rain abundance at the Castlerock site ($R^2 = -0.016$, $P = 0.41$; Fig. 4c) and no relationship at the Kuripapa site ($R^2 = 0.14$, $P = 0.072$; Fig. 4b). The relationship between distance from native forest edge and the species richness of the seed rain showed similar results, where the relationship was highly significant at Blowhard ($P < 0.001$), with a moderately strong negative relationship ($R^2 = 0.61$; Fig. 4d). Distance to native forest edge did not have a significant effect on seed rain species richness at Castlerock or Kuripapa, with no relationship at either site (Castlerock $R^2 = 0.05$, $P = 0.19$; Kuripapa $R^2 = 0.016$, $P = 0.27$; Figs. 4e & 4f).

Differences in dispersal by fruit type (fleshy/dry)

Distance from native forest edge had a highly significant negative effect on the proportion of fleshy fruited seed rain at the Blowhard and Castlerock sites ($P < 0.001$), and a significant negative effect at the Kuripapa site ($P < 0.05$). Distance from native forest edge did not have a significant effect on the proportion of species that were fleshy fruited at any of the three sites.

A significant interaction was found between woody seed rain abundance and site ($P < 0.001$), as well as between woody seed rain species richness and site ($P < 0.001$). Distance from native forest edge was a highly significant predictor of woody seed rain abundance at the Blowhard site ($P < 0.001$), as well as at Kuripapa ($P < 0.01$) and Castlerock ($P < 0.01$). Distance from native forest edge was a highly significant predictor of woody species richness at Blowhard ($P < 0.001$) and was also significant at Kuripapa ($P < 0.05$) and Castlerock ($P < 0.05$).

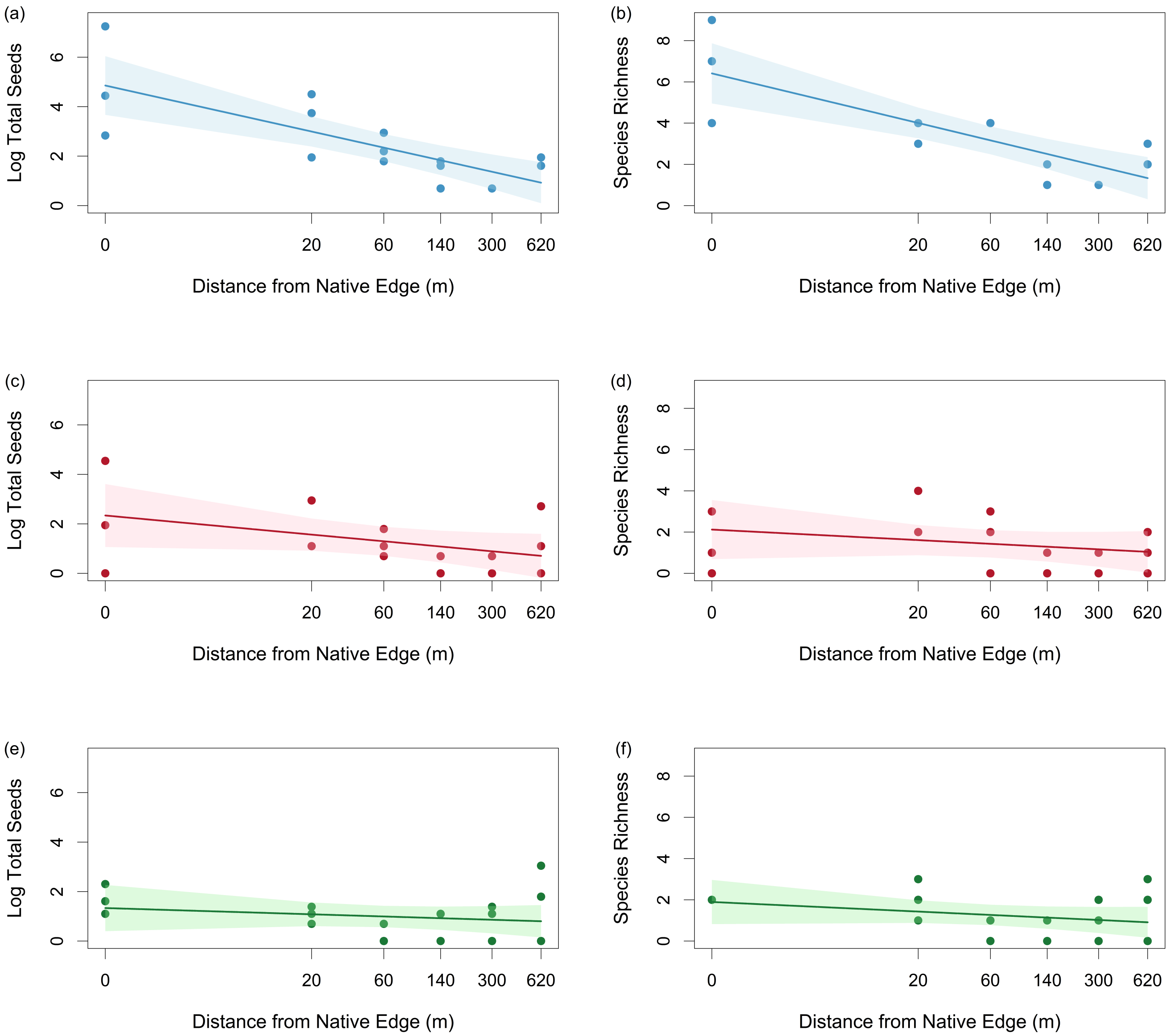

Figure 4. Relationships between logged total number of seeds and distance from native edge at (a) Blowhard, (c) Kuripapa, and (e) Castlerock. Relationships between species richness of seed rain and distance from native edge at (b) Blowhard, (d) Kuripapa, and (f) Castlerock. Shaded areas represent 95% confidence intervals. The x-axis is presented on a log scale.

Plantation understorey vegetation composition and relation to seed rain

Sampling of the understorey vegetation in the *P. radiata* plantation identified 28 species of vascular seed plants. Twenty (53%) of these were fleshy fruited and eight (21%) were dry seeded. *Cirsium* sp. and *Coriaria arborea* var. *arborea* were present in the seed rain but not in the plantation understorey. All vascular seed plants recorded were native, with no exotic species found within the vegetation plots. A Mantel test found a very weak, but non-significant, correlation between the species communities in the understorey vegetation and the seed rain (Mantel statistic R = 0.16, $P = 0.081$).

Of the 28 species of seed producing plants found, 19 (67.9%) were not present in the seed rain. Of the species not present in the seed rain, 15 (53.6%) were fleshy fruited and four (14.3%) were dry seeded. A total of 16 species were found to be over 2 m in height and therefore to have the potential to contribute to the seed rain collected from the seed traps (i.e. they were growing above the height of the seed traps). Five of these 16 species were present in the seed rain.

Kunzea ericoides was found in the height tiers above 2 m at all the sites and was the species with the highest importance value, both overall and per site. Few species were found in height tiers greater than 2 m at sites other than Blowhard. The Castlerock sites had two species present above 2 m in height, which were *K. ericoides* and *Pterophylla racemosa.* At the Kuripapa site, *K. ericoides*, *P. racemosa*, *Carpodetus serratus*, and *Rubus cissoides* were recorded in height tiers above 2 m. The Blowhard site had 11 species present in height tiers above 2 m. However, the canopy tree species *P. racemosa,* which was recorded above 2 m at both Castlerock and Kuripapa, was not present (Fig. 5a).

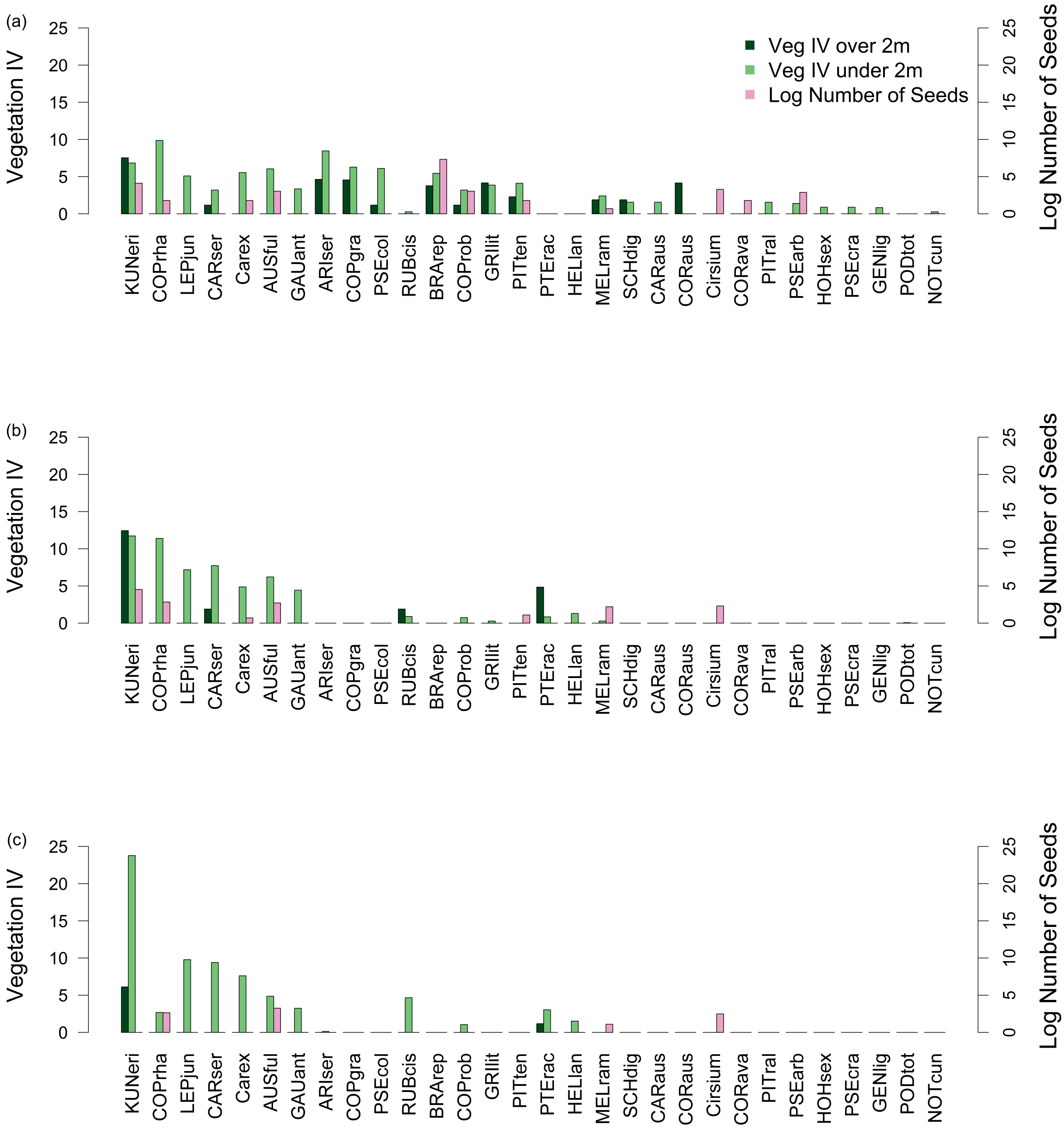

Figure 5. Importance values of understorey vegetation separated by site. Panel (a) shows the Blowhard site, panel (b) is the Kuripapa site, and panel (c) is the Castlerock site. Species codes are: KUNeri = *Kunzea ericoides*, COPrha = *Coprosma rhamnoides*, LEPjun = *Leptecophylla juniperina*, CARser = *Carpodetus serratus*, Carex = *Carex* spp., AUSful = *Austroderia fulvida*, GAUant = *Gaultheria antipoda*, ARIser = *Aristotelia serrata*, COPgra = *Coprosma grandifolia*, PSEcol = *Pseudowintera colorata*, RUBcis = *Rubus cissoides*, BRArep = *Brachyglottis repanda*, COProb = *Coprosma robusta*, GRIlit = *Griselinia littoralis*, PITten = *Pittosporum tennuifolium*, PTErac = *Pterophylla racemosa*, HELlan = *Helichrysum lanceolatum*, MELram = *Melicytus ramiflorus*, SCHdig = *Schefflera digitata*, CORaus = *Cordyline australis*, Cirsium = *Cirsium* spp., CORava = *Coriaria arborea* var. *arborea*, PITral = *Pittosporum ralphii*, PSEarb = *Pseudopanax arboreus*, HOHsex = *Hoheria sexstylosa*, PSEcra = *Pseudopanax crassifolius*, GENlig = *Genistoma ligustrifolium*, PODtot = *Podocarpus totara*, NOTcun = *Notelaea cunninghamii*.

Of the 28 species of seed plants found in the understorey vegetation, 14 were not present in height tiers above 2 m. Of the vegetation found only below 2 m in height, *Coprosma rhamnoides* had the highest importance value. Other common species below 2 m in height were *Leptecophylla juniperina*, *Carex* spp., *Austroderia fulvida*, and *Gaultheria antipoda*, all of which have shrub or herb growth forms. Plants with tree growth forms that were only present in the understorey vegetation below 2 m in height were *Pittosporum ralphii*, *Pseudopanax arboreus*, *Pseudopanax crassifolius*, *Hoheria sextylosa*, *Geniostoma ligustrifolium*, *Notelaea cunninghamii*, and *Podocarpus totara*, although the combined importance values of these species made up just 3.1% of the total importance value of vegetation under 2 m in height (Fig. 5b).

The importance value of the understorey vegetation had a moderately strong positive correlation with the total number of seeds (log-transformed) recorded in the seed rain of each trap where a vegetation plot was placed (rho = 0.63; Fig. 6a). The correlation between the understorey vegetation species richness and the species richness of the seed rain was also positive, however the correlation was weak (rho = 0.27; Fig. 6b). However, both correlations were strongly influenced by

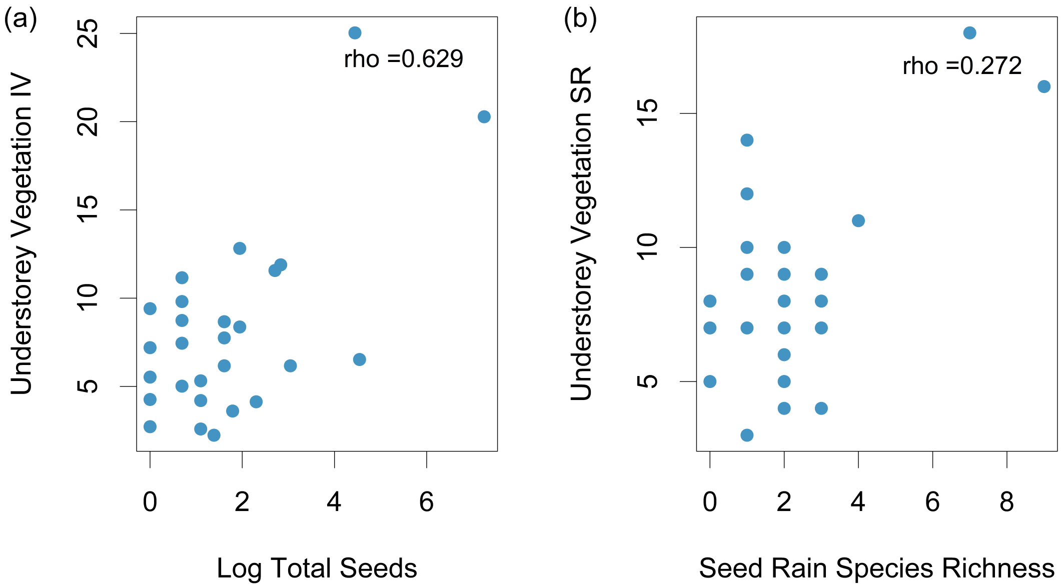

Figure 6. Correlations between (a) understorey vegetation importance value and logged total number of seeds, and (b) understorey species richness and the species richness of seed rain. Spearman's ranked correlation method was used to determine rho. Each point represents a seed trap where there was also a vegetation plot.

two points with high native vegetation importance values, seed rain abundance, and species richness. These points were from the first trap on two transects at the Blowhard site. When removed from the data, both the correlation of log total seeds (rho = 0.20) with native vegetation importance value and the correlation of seed rain species richness (0.11) with native vegetation species richness became weak. The distance from the native forest edge had a significant effect on understorey native vegetation importance value at Blowhard ($P < 0.01$) but was not significant at Kuripapa ($P = 0.16$) or Castlerock ($P = 0.37$). Species richness of the native understorey vegetation had a significant effect on the overall understorey vegetation species richness at Blowhard ($P < 0.05$), however, there was no effect at Kuripapa or Castlerock.

Discussion

The patterns of seed rain into exotic plantation forests are highly variable, with inputs being very localised in regard to the distance from the native forest edge, but also in regard to the nature of the native forest itself, including its age, composition, and structure. While seed rain was collected in all traps along the transect, most of the seed rain fell in the first two traps of each transect, at 0 m and 20 m from the native forest edge. This suggests that regeneration of native vegetation within the exotic plantation forest may be most prolific and diverse in the first 20 m from a native forest edge. However, the extant understorey vegetation did not entirely reflect this pattern. This may be due to many species in the seed rain, such as *Coriaria arborea* var. *arborea,* being light-demanding. The light conditions in the understorey of the plantation forest may be unsuitable for growth or establishment of such species, however, they could exploit gaps in the plantation canopy.

When the overall trend in abundance of seed rain was examined across the transects, there was an uptick of seed rain in the furthest traps, at 620 m from the native forest edge. When the seed rain was split into dry seeded and fleshy fruited seeds, the increase in seeds at the furthest trap was only present in dry seeded seed rain, whereas the fleshy fruited seed rain plateaued after 60 m from the native forest edge. The increase in dry seeded seed rain in the furthest traps was caused by one species, *Austroderia fulvida*. This species is often observed growing around the edges of plantation forest infrastructure such as secondary roads and landings. The density of these roads and landings increases further from the plantation edge. The seed traps placed at 620 m from the native forest edge were therefore in closer proximity to landings and roads than traps close to the native forest edge. Plantation forest infrastructure could be a source of seeds due to its open microclimate supporting different species than the plantation or native forest interior. Infrastructure could also be a source of propagules of exotic weed species, as plant material can be moved within and between forests on machinery and equipment, although we did not find an increase in exotic weed species near forest infrastructure in this study. However, the invasive grass species, *Cortaderia selloana*, occupies a similar habitat to *A. fulvida* and is often associated with infrastructure in *P. radiata* plantations (Gadgil et al. 1990).

The relationships between seed rain species richness, abundance, and distance from native forest edge were different across the three sites included in this study. While seed rain abundance and species richness were always greater closer to the native forest edge, the relationships were significantly stronger at the Blowhard site than at Kuripapa or Castlerock. The understorey vegetation of seed plants at the Blowhard site had an overall greater importance value and species richness than at the other two sites. While all sites were within the same plantation forest matrix and were proximate in location, the presence of a protected remnant of old growth native forest near the Blowhard site may have influenced the increased cover and species richness of understorey vegetation, seed rain abundance, and seed rain species richness. This remnant has been owned by the Royal Forest and Bird Protection Society since 1962 and regular pest and weed control is carried out in the reserve. While all sites are within flight distance of avian dispersers such as kererū (Wotton & Kelly 2012), they may be functionally isolated due to poorer utilisation of the plantation forest when compared with native forest (Clout & Gaze 1984).

Examination of the understorey vegetation found that all woody species present in the seed rain, except for *C. arborea* var. *arborea*, were also present as understorey plants. These findings contrast with the research by Moles & Drake (1999), who found 12 of the 34 species comprising the seed rain were not present in the understorey vegetation. In our research, *C. robusta* and *M. ramiflorus* were both found in seed traps at sites where these species were not recorded in height tiers of over 2 m, giving evidence of seed dispersal into the plantation from the adjacent native forest. We also found 18 woody species in the understorey vegetation that were not captured in the seed rain. It is important to note that the plantation forest stands in this study are of second rotation and have undergone land preparation between rotations. While the density of soil seed banks beneath native forest is maintained over a long period of time due to continual inputs from the native canopy (Sem et al. 1995), in this study it is unlikely that the soil seed bank contributed to the extant understorey vegetation, as many native seeds do not remain viable in the soil seed bank for more than one year (Overdyck & Clarkson 2012). This suggests that any native understorey vegetation would have dispersed in from adjacent native forest. Some understorey species may not have been found in the seed rain due to the size of their seeds, which may have been small enough to be lost through the drainage holes of the seed traps. Examples of such species include *Gaultheria antipoda*, *Helichrysum lanceolatum*, and *Pterophylla racemosa.* There may have also been seed lost from the seed traps during the 4-week sampling interval due to consumption by invertebrates. Wētā are known to consume small seeds (Duthie et al. 2006) and were frequently observed in the seed traps. Some species fruit outside the window of seed collection from this study, such as *Coprosma grandifolia*, or have a very short fruiting window, such as *Schefflera digitata* and *Cordyline australis*, while others (e.g. Nothofagaceae and some Podocarpaceae) mast seed. There were also small shrubby species found in the understorey, such as *G. antipoda*, *H. lanceolatum*, and *Carmichaelia australis*, where the mature height may have been a barrier to seeds entering the seed traps, which were 0.9 m above the ground.

Most woody species present in the seed rain were fleshy fruited, with *B. repanda* and *K. ericoides* being the only two dry seeded woody species. Lack of seeds from dry seeded woody native species could be due to these seeds having difficulty penetrating the exotic plantation forest, as dry seeds have been shown to disperse more readily into receiving environments that are structurally different from their origin (Vespa et al. 2014). Dry seeded native plants also often have very small seeds that are inconspicuous and may be difficult to collect in seed traps. It has been suggested that certain seed trap designs, such as the one used in this experiment, may be less effective at capturing seed rain of dry seeds than ground-based seed traps (Page et al. 2002), which may also explain the dominance of fleshy fruited species in the seed rain collected.

Seed rain from *P. radiata* was found at all sites, at similar amounts in all traps along the transects. *Pinus radiata* is a serotinous pine that holds its seeds until high temperatures occur, which triggers seed release. Serotinous pines are adapted for fire-prone environments. Aotearoa | New Zealand is a non-fire prone environment, which may be a barrier to seed dispersal and spread of *P. radiata* (Froude 2011). However, ambient air temperatures in Canterbury can break *P. radiata* cone serotiny and trigger seed release (Wyse et al. 2019). The frequency of *P. radiata* seed rain in this experiment gives additional evidence for the capacity of late summer ambient air temperatures in Aotearoa | New Zealand to break cone serotiny and trigger seed release. While *P. radiata* was the third most common species in the seed rain, vegetation sampling did not find any regenerating *P. radiata* at any of the sites. This suggests that while there is plentiful seed rain from the *P. radiata* plantation canopy, the conditions in the understorey are not currently suitable for the establishment of this species. While the regeneration of the exotic plantation trees is not presently occurring, there is the potential that as the stands mature and the canopies become more open, the microclimate may become suitable for the establishment of *P. radiata*, as it has been shown to regenerate widely under its own canopy in older stands in Aotearoa | New Zealand (Marshall et al. 2024).

Vegetation sampling found native vegetation throughout the plantation stands, indicating that long distance seed dispersal is occurring, but may be less frequent than dispersal close to native forest boundaries. This has important implications for the potential transition of exotic plantation forest to native forest, as it shows that frequency and species richness of seed rain into the plantation is strongly influenced by distance from native forest. However, the overall effect of distance from native forest edge was mainly driven by the results at the Blowhard site. The results at the Blowhard site suggests that the composition of the adjacent native forest may be influencing the strength of the relationship between seed rain species richness, seed rain abundance, and distance from the native forest edge. The structure and fragmentation of the surrounding landscape influences the composition and abundance of seed rain (Murphy & Lovett-Doust 2004; Jesus et al. 2012). The Blowhard site results indicate that a more diverse, later-successional native forest is likely to produce seed rain that is more abundant and species rich in the first 20 m of the plantation forest than seed rain derived from an earlier successional and/or less diverse native forest. It is also important to note that the stands in this study exist within a matrix of forest types; therefore, it is difficult to entirely isolate the gradient from native forest edge from the surrounding matrix that may have some confounding effects on this study.

The movement of birds within an exotic plantation forest should be considered when implementing a managed transition to a native forest. Whilst birds are capable of moving seed significant distances (Wotton & Kelly 2012), they may not necessarily be dispersing this seed into exotic plantations. Exotic plantation forests tend to support more native insectivorous birds than frugivorous or nectar-feeding birds (Clout & Gaze 1984; Seaton et al. 2010), which may lessen the potential for fleshy fruited seed to be dispersed into plantation forest. Higher densities of native birds have been found on the edges of plantation forest stands than within the stands (Seaton et al. 2010), providing additional evidence that the dispersal of fleshy-fruited seeds by birds may be limited within the exotic plantation forest. Moderately large exotic birds that use plantation forests as habitat such as blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*) are capable of dispersing fleshy fruited native seed, although they have been found to be more effective at dispersing fleshy fruited invasive weed species (Macfarlane et al. 2016). We found that fleshy-fruited seed rain decreased sharply in abundance at distances greater than 20 m from the plantation edge. This suggests that while birds may be moving through the plantation, most seeds are dropped close to the edge of the native forest. A plantation could be managed to encourage bird movements, and therefore dispersal of seed, by creating and preserving islands of native forest within the plantation to increase suitable habitat area. This has the additional benefit of increasing sources of native seed and decreasing dispersal distances throughout the plantation.

When managing an exotic plantation forest towards a transition to a native forest, the distance to a patch of native forest is likely to have a strong influence on the species richness and speed of regeneration. This could be taken into consideration when managing a larger plantation estate, as a mosaic of native forest patches may increase both the species richness and frequency of seed rain, as well as benefiting native birds by increasing habitat area and encouraging movement throughout the plantation. This may aid in the transition of plantation stands that are not economically viable or socially acceptable to harvest. Plantation forests established for the purpose of carbon sequestration with no intention to harvest could be planned around existing native vegetation on a site to promote seed dispersal. The composition and successional stage of the native patches will also have a strong influence on the abundance and species richness of seed rain entering the plantation forest. The large amount of seed rain from the *P. radiata* canopy throughout the sites sampled implicates the likelihood that *P. radiata* will regenerate within the stand when microclimate conditions become favourable as the stand ages. If a stand is being managed for transition to a native forest, ongoing control of the self-seeded exotic species may be required.

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Additional Information and Declarations

Conflicts of interest: The authors declare that they have no competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability: The data and code used in this paper can be accessed at https://doi.org/10.6084/m9.figshare.28952981.v3

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