

RESEARCH ARTICLE

Differential seedling survival of early-planted, late-successional trees: Results from three forest restoration experiments

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Abstract

1. The recruitment of late-successional and canopy-dominant tree species into early-successional plantings is essential for long-term forest restoration. Introducing these species early enhances the stability of the emerging ecosystem and boosts its ecological functions and biodiversity. However, many genetic, ecological and environmental factors can alter the survival of late-successional trees in early-successional, open-field environments. Despite the critical role late-successional trees play in forming resilient and diverse forests, significant knowledge gaps remain regarding optimal planting strategies, including tree density and composition, and the impact of microhabitats on the establishment of these species.
2. To address this, we employed aster models to analyse the survival of 1840 late-successional trees planted between 2019 and 2022 across three afforested and restored past agroecosystem sites as part of the Auckland University of Technology Living Laboratories programme.
3. Our experiment revealed that four of the six late-successional tree species planted demonstrated high survival when planted simultaneously with early-successional trees, while the other two did not. We also showed that a spacing of 2 m between early-successional trees significantly improved the survival of late-successional trees compared to smaller or larger spacings. This 2-m spacing appeared to effectively balance the benefits of shelter provided by early-successional trees and the drawbacks of shading and competition. In addition, greater amounts of dead and live vegetation increased seedling survival, while soil chemical characteristics related to nutrient richness and solar radiation altered seedling survival in a site-specific way. These effects were likely driven by differences in species functional traits and ecological requirements and the environmental and ecological contexts of the experimental sites.
4. *Practical implication.* Our study demonstrates that simultaneously planting both late- and early-successional tree species is effective for the establishment of late-successional trees on agricultural lands designated for restoration. Furthermore, it indicates that a 2-m spacing between early-successional trees is

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an optimal strategy to enhance late-successional trees' survival when planting them simultaneously.

KEYWORDS

aster model, forest restoration, late-successional tree, soil characteristics, survival, tree density, vegetation cover

1 | INTRODUCTION

The recruitment of late-successional and canopy-dominant tree species into early-successional plantings is crucial for long-term forest restoration (Laughlin & Clarkson, 2018). Late-successional tree species are characterized by their late dominance in a forest's development trajectory, shade tolerance at the seedling stage (Gilbert et al., 2001; Pausas & Lavorel, 2003), large size, emergent canopy position, high biomass (Whitmore, 1989) and high root-to-shoot ratio (Shukla & Ramakrishnan, 1984). These species are recognized for their significant functional roles in forest ecosystems, often acting as 'foundation species' (Ellison, 2019). Enrichment planting—strategically introducing late-successional species—can accelerate the development of multi-tiered, resilient and complex mature forests (Aide et al., 2000; Griscom & Ashton, 2011; Laughlin & Clarkson, 2018; Martínez-Garza & Howe, 2003, but see Hilderbrand et al., 2005). Introducing these species early enhances ecological functions and biodiversity, especially in areas with distant seed sources (Schleicher et al., 2011), while also stabilizing the emerging ecosystem by shading out the ground, thereby limiting alternative successional trajectories and 'forcing' the ecosystem to transition (back) to a forest (Aide et al., 2000; Griscom & Ashton, 2011). Despite the importance of late-successional trees, gaps remain regarding optimal strategies for introducing late-successional species and how initial canopy composition affects their establishment (Buckley et al., 2023; Osorio-Salomón et al., 2021). Yet, understanding the conditions that promote seedling survival, particularly of future canopy trees in forest understories, is essential for improving forest-restoration outcomes.

Late-successional tree survival in early-successional environments is determined largely by a combination of genetic, ecological and environmental influences. First, survival varies among species due to differences in fundamental niches and ecological traits (Löf et al., 2014; Martínez-Garza et al., 2005; Osorio-Salomón et al., 2021). Second, many late-successional species face challenges when planted in agricultural lands designated for restoration, as they rely on early-successional trees, known as 'nurse trees', to support their establishment, survival and growth (Bonanomi et al., 2021; Niering et al., 1963). Nurse trees create favourable microclimatic conditions (Gómez-Aparicio et al., 2008; Rose et al., 2020), such as optimal temperature and moisture levels, that benefit other trees, usually slower growing late-successional species by enhancing their fitness. They also provide shade, shelter from wind and suppress competitors, like grasses

(Hooper et al., 2002; Padilla & Pugnaire, 2006; Pozo Inofuentes & Säumel, 2022; Urretavizcaya & Defossé, 2013). Thus, the density, composition and stature of early-successional trees—such as their height and crown width—are expected to impact the establishment and survival of late-successional trees in both planted and natural forests. High densities of early-successional trees may increase competition for resources like light, water and nutrients and hinder late-successional species' growth (Pacala et al., 1994). Conversely, low densities may reduce competition but expose late-successional species to greater environmental stress and less favourable microclimatic conditions, including drought and high temperatures (Dupuy & Chazdon, 2008; Facelli & Pickett, 1991; Vázquez-Yanes & Orozco-Segovia, 1992).

In addition to woody vegetation, herbaceous plants play an important role in creating favourable microhabitats for late-successional tree seedlings. They enhance moisture retention, improve nutrient availability and reduce competition from invasive species (Martínez-Garza et al., 2005; Pozo Inofuentes & Säumel, 2022). However, overly dense herbaceous cover may hinder late-successional tree establishment (Holl et al., 2018). For instance, invasive grass species, such as kikuyu (*Cenchrus clandestinus* Morrone), reduce survival of young trees by outcompeting them (Forbes & Craig, 2013). Dead vegetation also influences early life stages of trees by enhancing humidity and nutrient availability, reducing solar radiation and modifying soil temperature (Dupuy & Chazdon, 2008; Facelli & Pickett, 1991; Martínez-Garza et al., 2005; Urretavizcaya & Defossé, 2013; Vázquez-Yanes & Orozco-Segovia, 1992). Furthermore, environmental factors like soil chemistry, land slope, solar radiation, soil moisture and compaction are known to influence the early establishment of late-successional trees (Grigal & Vance, 2000; Martínez-Garza et al., 2016).

To enhance our understanding of the conditions that facilitate the introduction of late-successional species into past-agroecosystem lands, we used data from the Auckland University of Technology (AUT) Living Laboratories programme, which comprises three forest restoration experiments (Buckley et al., 2023). This transdisciplinary research initiative aims to understand how to support holistic approaches to forest restoration that tackle multiple issues, including climate change and biodiversity loss, forming partnerships with landowners and engaging respectfully with Indigenous knowledge and rights. The programme also seeks to better understand the socio-cultural and economic contexts that influence successful restoration outcomes.

The present study focuses on three key questions: (1) Do late-successional tree species differ in early-life survival, and can high

survival be achieved by planting them simultaneously with early-successional trees? (2) How do the density, composition and stature of early-successional species affect early late-successional tree survival? (3) How do variations in seedling microhabitats, such as vegetation cover, soil chemistry and compaction, moisture, land slope and solar radiation, impact early late-successional tree survival? To answer these questions, we analysed early survival at the individual level of a total of 1840 late-successional trees planted between 2019 and 2022 across the three AUT Living Laboratories' restored past-agroecosystem and afforested sites (i.e. sites that were not forested in the past 50 years but have now been planted with trees to restore a forest; Hamilton et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Experimental design

The AUT Living Laboratories programme, detailed in Buckley et al. (2023), comprises three long-term restoration experiments within the greater Auckland City region of Aotearoa New Zealand's upper Te Ika-a-Māui North Island: Te Muri, Pūkoro and Te Pourewa (Figure S1). This region experiences subtropical to temperate conditions, with daily minimum and maximum temperatures of 7.5°C and 24°C, respectively, and a mean annual precipitation of approximately 1100 mm (World Meteorological Organization, 2025). Each site differs in environmental context, experimental treatments and species of late-successional and early-successional trees. Late-successional trees of various species (see below) were randomly planted on a regular 6-m grid across all sites (except four blocks at Te Muri, where an 8-m grid was used). Each site was then divided into blocks. Treatments were applied to multiple blocks randomly distributed across the site. As a result, all trees within a given block received the same treatment (see below). The number of blocks per treatment level is consistent across all treatment levels within each site. All tree seedlings were grown under uniform conditions in a nursery. Late-successional tree species' known ecological traits and habitat characteristics are summarized in Table 1.

At Te Muri, located in Te Muri Regional Park north of Auckland, trees were planted in winter 2020 in an upland gully with ephemeral streams. Four late-successional tree species were planted: pūriri (*Vitex lucens* Kirk, Lamiaceae), rewarewa (*Knightia excelsa* Brown, Proteaceae), rimu (*Dacrydium cupressinum* Sol., Podocarpaceae) and tōtara (*Podocarpus totara* G. Benn., Podocarpaceae). The main experimental effects varying across treatment blocks were the density of early-successional trees planted 1, 2, 3 or 4 m apart using a mix of five species (*Kunzea robusta* Lange & Toelken, *Meliclytis ramiflorus* J. R. & G. Forster, *Coprosma robusta* Raoul, *Myrsine australis* A. Rich, *Aristotelia serrata* Oliv.; for details, see Buckley et al., 2023). This corresponded to an early-successional trees density of 10,000, 2500, 1111 and 625 trees/ha for 1-, 2-, 3- and 4-m spacing, respectively. The range of nearest-neighbour distances between late- and early-successional trees was 1–4.5 m depending on the block.

There were four blocks per treatment level, totalling 16 blocks of (mean \pm SD) 52.06 \pm 30.09 late-successional trees. The number of late-successional trees per treatment level (1-, 2-, 3- or 4-m spacing) was 193, 189, 292 and 159. Before human arrival, this site was covered by podocarp-broadleaved forest dominated by kauri (*Agathis australis* Steud., Araucariaceae; Singers et al., 2017). The forest was cleared for agriculture (Wardle, 1991), and the area was used for farming until 2019 (Buckley et al., 2023). Ngāti Manuhiri is mana whenua (first people) in this area.

At Pūkoro, trees were planted in winter 2022 on a steep, privately owned coastal site in the northeast Waikato region. Three late-successional tree species were planted: kahikatea (*Dacrycarpus dacrydioides* Laubenfels, Podocarpaceae), pūriri and tōtara. The main experimental effects varying across treatment blocks were the drought tolerance and stature of early-successional trees, with three levels: high stature (>6 m) and high drought tolerance, high stature (>6 m) and low drought tolerance and low stature (<6 m) with moderate drought tolerance. Each treatment included a mix of three early-successional species planted 1.5 m apart (for details, see Buckley et al., 2023). This corresponded to an early-successional trees density of 4444 trees/ha. The range of nearest-neighbour distances between late- and early-successional trees was 1.5–2.1 m. There were 15 blocks per treatment level, totalling 45 blocks of (mean \pm SD) 15.63 \pm 3.70 late-successional trees. The number of late-successional trees per treatment level (high stature & drought tolerance, high stature & low drought tolerance and short stature & moderate drought tolerance) was 250, 217 and 252. Prior to its settlement by humans and eventual conversion to a dairy farm, this area was likely covered by coastal broadleaved forests (Buckley et al., 2023).

At Te Pourewa, trees were initially planted in winter 2019 on a slope in Te Pourewa Valley, Auckland. Due to a severe summer drought that greatly affected the trees, new trees were planted in winter 2020. Four late-successional tree species were planted: pūriri, rimu, taraire (*Beilschmiedia tarairi* Kirk, Lauraceae) and tōtara. The main experimental effect varying across treatment blocks was the early-successional tree species composition, reflecting seed dispersal mode. This treatment had two levels: kānuka trees (*Kunzea robusta* Lange & Toelken, Myrtaceae), which are wind-dispersed, versus a mix of four bird-dispersed native tree species (for details, see Buckley et al., 2023). Early-successional trees were planted 1.5 m apart. This corresponded to an early-successional tree density of 4444 trees/ha. The range of nearest-neighbour distances between late- and early-successional trees was 1.5–2.1 m. There were six blocks per treatment level, totalling 12 blocks of (mean \pm SD) 48.00 \pm 7.72 late-successional trees. The number of late-successional trees per treatment level (kānuka or mixed trees) was 165 and 123. Similar to Te Muri, this site was historically covered by podocarp-broadleaved forest dominated by kauri (Singers et al., 2017). In the 1950s, the New Zealand government confiscated it from iwi (Māori tribe) ownership, converting it into farmland and later a horse-riding club. It has since been returned to iwi and is currently undergoing restoration (Buckley et al., 2023).

TABLE 1 Late-successional tree species' plantation sites, known ecological traits and habitat characteristics.

Species	Planted at	Seedlings' shade Tolerance	Seasonal drought Resistance	Habitat	Elevation	Miscellaneous
Kahikatea (<i>Dacrydium dacrydioides</i>)	Pūkoro	Moderate ^b	Moderate ^c	Moist (even swampy), nutrient-rich and reasonably well-aerated soils ^b	Lowland ^b	Conifer ^b , frost hardy seedlings ^c
Pūriri (<i>Vitex lucens</i>)	Te Muri, Pūkoro, Te Pourewa	High ^c	Moderate ^c	Nutrient-rich soils ^b	Coastal and lowland ^b	Colonizer ^b , frost tender seedlings ^c
Rewarewa (<i>Knightia excelsa</i>)	Te Muri	Low ^{a,b}	Moderate ^c	Nutrient-rich, slightly acidic to neutral soils ^c	Lowland ^b	Colonizer ^b , frost tender seedlings ^d
Rimu (<i>Dacrydium cupressinum</i>)	Te Muri, Te Pourewa	Low ^b	Low ^b	Acid ^d and rather nutrient-poor soils ^b	Lowland to mid-altitude ^b	Conifer ^b
Taraire (<i>Beilschmiedia tarairi</i>)	Te Pourewa	Low ^b	Low ^f	Basaltic soils ^g (i.e. rather nutrient-rich and slightly acidic to neutral soils)	Coastal and lowland ^b	Sensitive to soil compaction ^f
Tōtara (<i>Podocarpus totara</i>)	Te Muri, Pūkoro, Te Pourewa	Low ^b	High ^b	Dry, nutrient-rich soils ^b	Lowland ^b	Conifer, colonizer ^b

Note: All species are evergreen.

^aSpeculated shade intolerance of rewarewa seedlings, inferred from the species' tendency to be conspicuous early in forest regeneration.

^bDawson and Lucas (2016).

^cAuthors' observations.

^dNew Zealand Plant Conservation Network (2025a).

^eAdams and Norton (1991).

^fMyers and Court (2013).

^gNew Zealand Plant Conservation Network (2025b).

2.2 | Data collection

The survival of a total of 1840 late-successional trees was monitored annually; tree census sampling was conducted between 2021 and 2023 at Te Muri and Te Pourewa and between 2022 and 2024 at Pūkoro. Vegetation cover around each tree was assessed halfway through the 3-year monitoring period: in 2022 at Te Muri and Te Pourewa, and in 2023 at Pūkoro. Percent cover of non-planted woody vegetation, rushes, forbs, grasses and kikuyu grass (a highly competitive invasive species that forms dense tussocks in highly productive grasslands, originating from the highland East and Central African plateau; Marais, 2001) was assessed at two heights: between 0 and 20 cm above-ground level, referred hereafter to as the 'lower tier', and at 20 cm above-ground level, referred hereafter to as the 'upper tier'. These assessments were conducted within a 1-m² circular area surrounding each late-successional tree, where we visually estimated the proportion of the area covered by each vegetation type. At the lower tier, moss, bare soil and dead vegetation cover proportions were also assessed. We calculated the 'total live vegetation at lower & upper tiers' by summing all lower and upper tiers cover variables, except bare soil and dead vegetation cover. We then calculated the 'live vegetation at lower tier except kikuyu' by summing all lower-tier cover variables, except kikuyu, bare soil and dead vegetation, and the 'live vegetation at upper tier except kikuyu' by summing all upper tier cover variables, except kikuyu. This selection of vegetation cover variables had low correlations among them and helps to disentangle the effects of kikuyu from the rest of the vegetation. GPS coordinates were recorded for precise late-successional tree location tracking.

Soil chemistry was assessed in July 2019 at Te Pourewa and in July 2021 at Te Muri and Pūkoro, with soil samples taken on a 25-m GPS-positioned grid. At each sampling point, mineral soil was sampled from the top 10 cm using a coring device. The physico-chemical properties were analysed (Hill & Sparling, 2009), providing pH; Olsen phosphorus [mg/L]; anaerobically mineralizable nitrogen [μg/g]; organic matter (%); carbon/nitrogen ratio; total carbon (%); total nitrogen (%); potassium [me/100 g]; calcium [me/100 g]; magnesium [me/100 g]; sodium [me/100 g]; cation exchange capacity [me/100 g] (soil ability to hold and exchange positively charged ions, such as potassium, calcium and magnesium ions); total base saturation (%; proportion of soil's cation exchange capacity (CEC) that is occupied by basic cations). The above soil data were then spatially interpolated into continuous raster surfaces for each site in ArcGIS Pro v. 3.1.3 software (ESRI Inc., 2023), using a radial basis function interpolation method (i.e. a regularized spline surface is fit to the grid of points and their values to enable estimate to locations between points). Soil compaction [N/cm²] was measured with an Eijkelkamp hand penetrometer (Royal Eijkelkamp, 2025) in April 2022 at Te Muri, November 2022 at Te Pourewa and February 2024 at Pūkoro at depths of 15, 25, 35 and 45 cm around each late-successional tree, with average compaction calculated across all depths. Additionally, solar radiation [Wh/m²], percent slope gradient and topographical wetness index (unitless) were derived from freely available 1-m

LiDAR (Light Detection and Ranging) digital elevation model (DEM) data (available from <https://opentopography.org/>) in ArcGIS Pro. Slope gradient and solar radiation were computed using the Slope and Area Solar Radiation functions and reflect the topography effect on variation in light and heat (it thus did not account for neighbourhood shading). The Topographic Wetness Index (TWI), based on Beven and Kirkby's (1979) algorithm, was computed using a derived slope gradient and flow accumulation layer. This index essentially models the locations of likely water ponding based on terrain morphology. Values for these three GIS-derived variables were subsequently extracted at late-successional tree locations using basic GIS overlay procedures.

2.3 | Statistical analyses

We conducted fixed effects aster analyses (Geyer et al., 2007; Shaw et al., 2008) using the 'aster' package in R (Geyer, 2014; R Core Team, 2021) to assess how the survival of late-successional trees depended on early-successional tree density and composition, vegetation covers, solar radiation, land slope, soil chemistry, wetness and compaction. Separate aster models were run for each of the three AUT Living Laboratories sites, referred to as Te Muri, Pūkoro and Te Pourewa aster models. We selected aster models for our study because they are specifically designed to jointly analyse life-history components, such as survival, over multiple years. They use graphical models to account for dependencies between life-history components and thus allow the assessment of the effects of predictive factors on the mean individual fitness throughout the available monitoring period (Geyer et al., 2007; Shaw et al., 2008). Because the trees in our study were still young, survival was the only life-history component that was assessed and included in the aster models at this stage.

The graphical model for Te Muri, Pūkoro and Te Pourewa included the survival of late-successional trees over 3 years, comprising 833, 719 and 288 individuals, respectively. Because aster models consider the whole recorded life history of an individual when estimating the response variable, they yield the estimates of unconditional mean individual survival through the entire monitoring period. In other words, the unconditional mean individual survival incorporates all survival probabilities, including the possibility of dying early, up to the final monitoring. For each site, the operational measure of fitness was the unconditional expected survival per individual at the last monitoring, that is, 2023 for Te Muri and Te Pourewa models and 2024 for Pūkoro model. Survival was modelled as a Bernoulli variable. Predictors included covers of bare soil and dead vegetation on the ground, kikuyu cover at the lower and higher tiers, live vegetation cover, except kikuyu, at lower and higher tiers, total live vegetation at lower and upper tiers together, soil compaction, land slope and wetness, solar radiation, late-successional tree species and early-successional treatments (tree spacing, mixture and composition at Te Muri, Pūkoro and Te Pourewa, respectively). We performed a principal component analysis (PCA) on soil chemistry variables and included the

first three principal components (PC1-3; each explaining more than 10% of the variance) as predictors in the models. The mean and standard deviation of the three first principal components of the PCA on soil chemistry variables for each site were *Te Muri*: PC1: -0.07 ± 1.57 ; PC2: 0.12 ± 1.70 ; PC3: -0.08 ± 0.77 ; *Pūkoro*: PC1: 0.2 ± 1.55 ; PC2: -0.02 ± 0.94 ; PC3: 0.06 ± 0.86 ; *Te Pourewa*: PC1: 0.29 ± 1.28 ; PC2: -0.47 ± 1.22 ; PC3: -0.22 ± 0.86 . The total variance explained by the first three principal components was 78%, 70% and 73% for *Te Muri*, *Pūkoro* and *Te Pourewa*, respectively. We removed highly correlated continuous variables within each model (Pearson's pairwise correlation coefficient $R^2 \geq 0.7$; *corrplot* package; Wei & Simko, 2017). Correlation plots of retained continuous predictors are provided in Supporting Information (Figures S2–S4). To account for spatial autocorrelation, we included a polynomial trend surface regression within the models: $x + y + xy + x^2 + y^2 + x^2y + y^2x + x^3 + y^3$, where x and y are the late-successional tree coordinates. Incorporating these spatial terms helps capture broad-scale spatial patterns, such as unmeasured environmental gradients and heterogeneity, and thereby disentangles these background spatial effects from the ecological effects of interest. We implemented both spatial and non-spatial model for each site, including and excluding the spatial terms, respectively. Therefore, our base models included the late-successional tree species variable, the experimental treatment variable and all continuous predictors retained after the correlation analysis.

To test for the effects of the aforementioned predictors on survival, we performed a stepwise backward model selection procedure with likelihood ratio tests, selecting the model with the lowest log-likelihood as the final one (Neyman & Pearson, 1928a, 1928b). At each step, we calculated the significance of one term by comparing the models with and without it and retained it in the model if significant. We continued this process until all predictors have been tested. Thus, our final aster models contained only significant terms (terms in bold in Tables 2–4). We chose this approach for its ability to systematically identify the most important set of predictors, ensuring a parsimonious model that strikes a balance between goodness of fit and simplicity. Expected values and standard deviations of survival for significant predictor were calculated and visualized (*ggplot2* R package; Wickham, 2016) for a 'typical individual', that is, a hypothetical individual located at the centre of the site with arithmetic mean values for continuous variable. After the model selection procedure, we added and tested interactions between late-successional tree-species identity and the significant predictors, but no significant interactions were found. To compare the relative fit of the spatial and non-spatial models, we calculated Akaike's information criterion (AIC) for the full spatial model and non-spatial model after backwards selection, as well as for an intercept-only 'null' model including solely late-successional tree species as a categorical fixed effect and the latter model including the spatial term, following the R code from Waananen et al. (2024). AIC evaluates how well models capture information about the underlying processes influencing survival (Akaike, 1974). Because full spatial models had the lowest AIC (best case) at each site (Table S1), we present their results here (Tables 2–4; Figures 1–3). Results of non-spatial

TABLE 2 Backward selection results for spatial aster models for *Te Muri* using likelihood ratio tests.

Te Muri				
	Residual df	Test df	Deviance	<i>p</i>
Explanatory variables tested on the 3-year survival				
Base	31			
Bare soil	30	1	1.116	0.291
Dead material	29	1	8.116	0.004
Kikuyu at lower tier	29	1	0.487	0.485
Live vegetation at upper tier except kikuyu	28		0.440	0.507
Live vegetation at lower tier except kikuyu	27	1	2.164	0.141
Total live vegetation at lower & upper tiers	26	1	0.264	0.607
Soil compaction	25	1	2.720	0.099
Slope gradient	24	1	1.353	0.245
Topographic wetness index	23	1	1.489	0.222
Solar radiation	22	1	6.256	0.012
PC3: sodium (+), CEC (+)	22	1	1.174	0.279
PC2: calcium (+)	21	1	3.981	0.046
PC1: organic matter (+), total carbon (+), total nitrogen (+)	21	1	6.177	0.013
Early-successional tree spacing	19	3	11.36	0.010
Late-successional tree species	19	3	39.61	<0.001
Covariable tested on the 3-year survival				
Base	22			
Spatial effect ($x + y + x^2 + y^2 + xy + x^2y + y^2x + x^3 + y^3$)	13	9	55.21	<0.001

Note: Residual and test degrees of freedom (df), deviance and corresponding *p*-value are given. *p*-values in bold are significant at the threshold of 0.05. Signs + or – in brackets indicate a positive or negative correlation with the corresponding PC.

models are presented in Supporting Information (Tables S2–S4; Figures S5–S7).

3 | RESULTS

3.1 | Modulating effects of species, tree density and environmental variables on tree survival at *Te Muri*

Late-successional tree survival after 3 years (2021–2023) varied significantly with species identity ($p < 0.001$), early-successional

TABLE 3 Backward selection results for spatial aster models for Pūkoro using likelihood ratio tests.

Pūkoro				
	Residual df	Test df	Deviance	<i>p</i>
Explanatory variables tested on the 3-year survival				
Base	29			
Bare soil	28	1	0.122	0.727
Dead material	27	1	3.143	0.076
Kikuyu at upper tier	26	1	0.521	0.470
Kikuyu at lower tier	25	1	0.671	0.413
Live vegetation at upper tier except kikuyu	24	1	1.013	0.314
Live vegetation at lower tier except kikuyu	23	1	1.305	0.253
Soil compaction	22	1	0.175	0.676
Slope gradient	21	1	2.402	0.121
Topographic wetness index	20	1	3.158	0.076
Solar radiation	19	1	0.012	0.913
PC3: CN ratio (-), magnesium (-)	18	1	0.001	0.971
PC2: pH (+), total base saturation (+)	17	1	0.012	0.914
PC1: total nitrogen (-)	16	1	6.899	0.009
Early-successional tree mixture	15	2	1.728	0.422
Late-successional tree species	13	2	10.93	0.004
Covariable tested on the 3-year survival				
Base	15			
Spatial effect ($x + y + x^2 + y^2 + xy + x^2y + y^2x + x^3 + y^3$)	6	9	31.24	<0.001

Note: Residual and test degrees of freedom (df), deviance and corresponding *p*-value are given. *p*-values in bold are significant at the threshold of 0.05. Signs + or - in brackets indicate a positive or negative correlation with the corresponding PC.

tree spacing ($p=0.010$), PC1 ($p=0.013$) and PC2 ($p=0.046$), that is, the first and second principal component of soil chemistry variables, solar radiation ($p=0.012$), dead vegetation cover at the lower tier ($p=0.004$) and in space ($p<0.001$; Table 2; Figure 1), at Te Muri. Survival was high for pūriri, rewarewa and tōtara (mean ± SE: 0.822 ± 0.052 , 0.746 ± 0.068 and 0.744 ± 0.071 , respectively) and was much lower for rimu (mean ± SE: 0.524 ± 0.086 ; Figure 1a). Late-successional tree survival was the highest at the 2-m spacing between early-successional trees (mean ± SE: 0.709 ± 0.065) and lower at the 1-, 3- and 4-m spacing (mean ± SE: 0.546 ± 0.076 ,

TABLE 4 Backward selection results for spatial aster models for Te Pourewa using likelihood ratio tests.

Te Pourewa				
	Residual df	Test df	Deviance	<i>p</i>
Explanatory variables tested on the 3-year survival				
Base	28			
Bare soil	27	1	2.304	0.129
Dead material	26	1	0.885	0.347
Kikuyu at lower tier	25	1	0.404	0.525
Live vegetation at upper tier except kikuyu	24	1	2.320	0.128
Live vegetation at lower tier except kikuyu	23	1	8.305	0.004
Total live vegetation at lower & upper tiers	23	1	0.268	0.605
Soil compaction	22	1	2.200	0.138
Slope gradient	21	1	3.433	0.064
Topographic wetness index	20	1	0.037	0.847
PC3: pH (-), potassium (+), magnesium (+)	19	1	0.028	0.868
PC2: pH (-), CEC (-), calcium (-), total base saturation (-)	18	1	2.789	0.095
PC1: organic matter (+), total carbon (+)	17	1	0.796	0.372
Early-successional tree composition	16	1	1.501	0.221
Late-successional tree species	13	3	46.73	<0.001
Covariable tested on the 3-year survival				
Base	16			
Spatial effect ($x + y + x^2 + y^2 + xy + x^2y + y^2x + x^3 + y^3$)	7	9	24.66	0.003

Note: Residual and test degrees of freedom (df), deviance and corresponding *p*-value are given. *p*-values in bold are significant at the threshold of 0.05. Signs + or - in brackets indicate a positive or negative correlation with the corresponding PC.

0.541 ± 0.082 and 0.490 ± 0.072 , respectively; Figure 1b). Late-successional tree survival increased with PC1 and decreased with PC2 (Figure 1c,d). PC1 was best represented by, and positively correlated with, organic matter, total nitrogen and carbon content in the soil, while PC2 was best represented by and positively correlated with calcium content (Figure S8). Late-successional tree survival also increased with solar radiation and dead vegetation cover (Figure 1e,f). Rimu consistently exhibited lower survival than other species across the gradients of early-successional tree spacing, PC1,

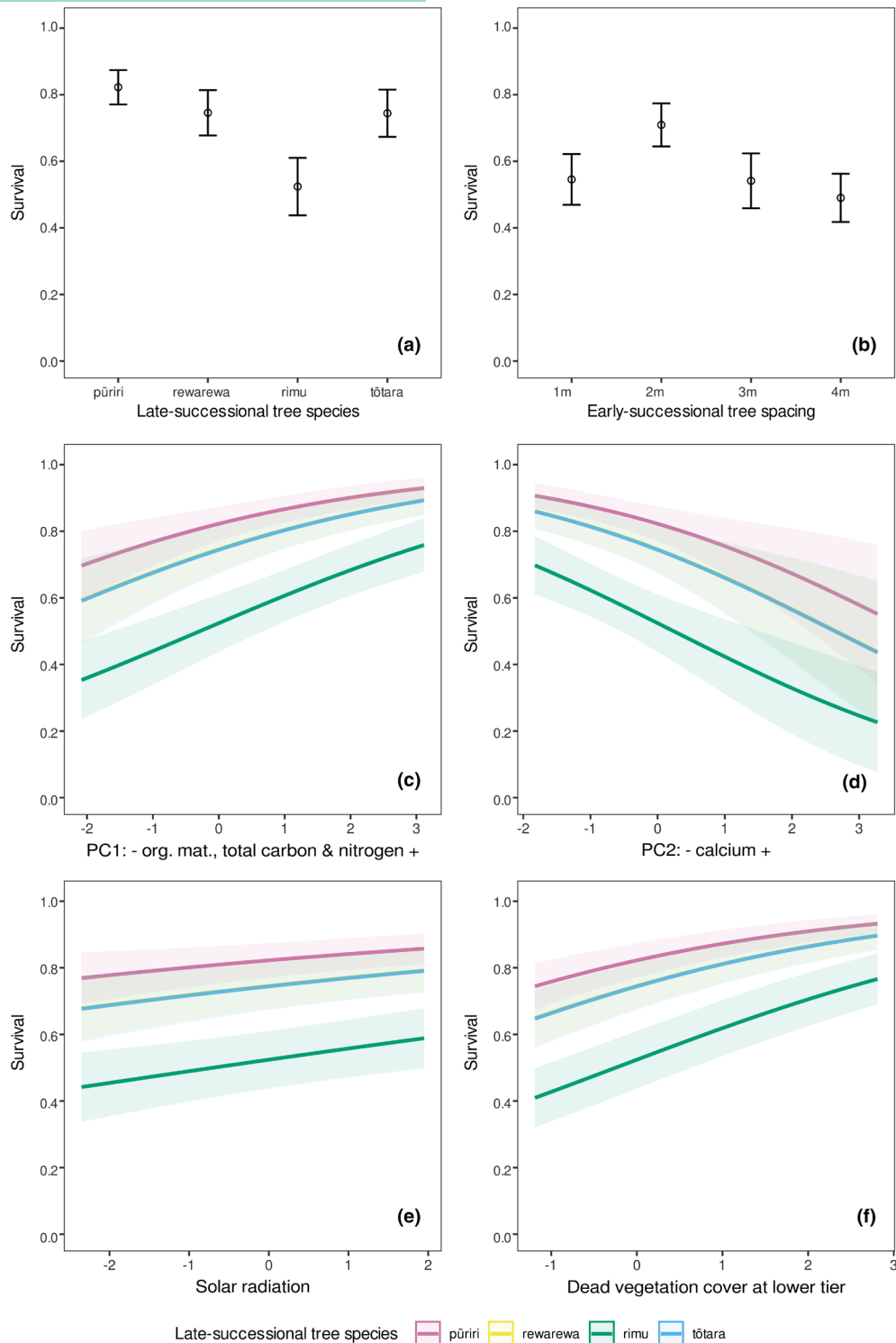


FIGURE 1 Predicted survival and 95% confidence intervals of the late-successional trees after 3 years for a typical individual at Te Muri in the aster model with a spatial term as a function of: (a) late-successional tree species; (b) early-successional tree spacing; (c) first principal component of soil variables (PC1), which positively correlated with organic matter, total nitrogen and carbon content in the soil; (d) second principal component of soil variables (PC2), which positively correlated with calcium content; (e) solar radiation; and (f) dead vegetation cover at the lower tier. N.b.: The regression lines for rewarewa and tōtara trees overlap.

PC2, solar radiation and dead vegetation, though late-successional species did not differ in how sensitive they are to those variables (non-significant interactions between species identity and

early-successional tree spacing ($p=0.985$), PC1 ($p=0.822$), PC2 ($p=0.919$), solar radiation ($p=0.299$) and dead vegetation cover ($p=0.075$)).

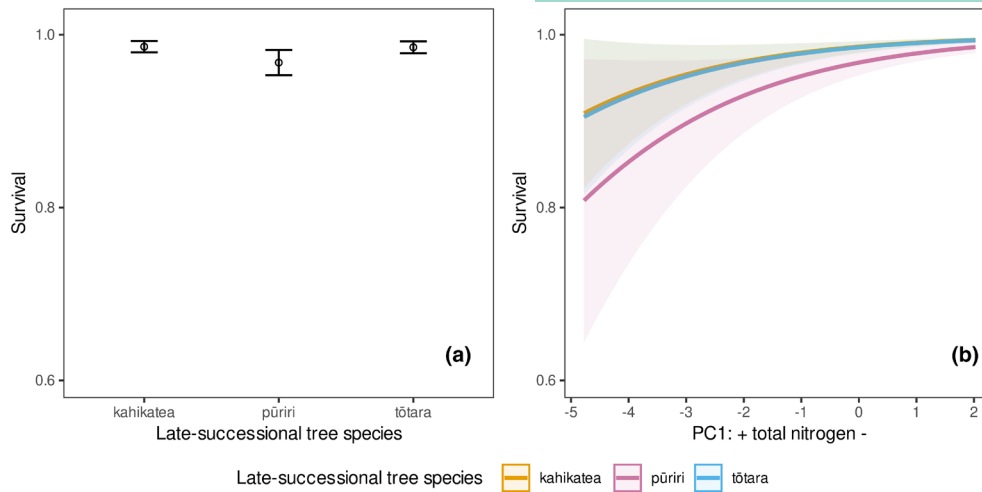


FIGURE 2 Predicted survival and 95% confidence intervals of the late-successional trees after 3 years for a typical individual at Pūkoro in the aster model with a spatial term as a function of: (a) late-successional tree species and (b) first principal component of soil variables (PC1), which negatively correlated with the total nitrogen content in the soil. N.b.: The regression lines for kahikatea and tōtara trees overlap.

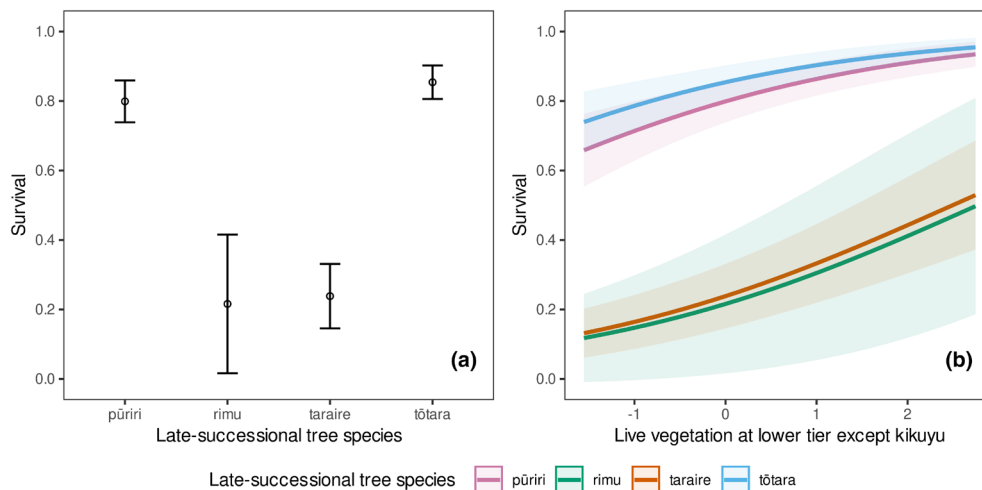


FIGURE 3 Predicted survival and 95% confidence intervals of the late-successional trees after 3 years for a typical individual at Te Pourewa in the aster model with a spatial term as a function of: (a) late-successional tree species and (b) live vegetation cover, except kikuyu, at the lower tier.

3.2 | Modulating effects of species and soil chemistry on tree survival at Pūkoro

Late-successional tree survival after 3 years (2022–2024) varied significantly with species identity ($p=0.004$), PC1, the first principal component of soil chemistry variables ($p=0.009$), and in space ($p<0.001$; Table 3; Figure 2), at Pūkoro. Survival was very high for all species (mean \pm SE for kahikatea: 0.986 ± 0.007 , pūriri: 0.968 ± 0.015 , tōtara: 0.985 ± 0.007 ; Figure 2a). Late-successional tree survival increased with PC1 (Figure 2b), which was best represented by and negatively correlated with total nitrogen and carbon content, organic matter and cation exchange capacity of the soil (Figure S9). No significant interaction was observed between species identity and PC1 ($p=0.349$) nor was the experimental treatment

(stature and relative drought tolerance of early-successional trees) significant ($p=0.422$).

3.3 | Modulating effects of species and live neighbouring vegetation on tree survival at Te Pourewa

Late-successional tree survival after 3 years (2021–2023) varied significantly with species identity ($p<0.001$), live vegetation cover, except kikuyu at the lower tier ($p=0.004$), and in space ($p=0.003$; Table 4; Figure 3), at Te Pourewa. Pūriri and tōtara had high survival (mean \pm se: 0.799 ± 0.060 and 0.854 ± 0.048 , respectively), while rimu and taraire had much lower survival (mean \pm se: 0.216 ± 0.200

and 0.238 ± 0.093 , respectively; [Figure 3a](#)). Late-successional tree survival increased with live vegetation cover at the lower tier ([Figure 3b](#)). Rimu and taraire had consistently lower survival compared to the two other species across the live vegetation cover gradient. No significant interaction was observed between species identity and live vegetation cover ($p=0.522$) nor was the experimental treatment (composition of early-successional trees, reflecting their seed dispersal mode) significant ($p=0.221$).

4 | DISCUSSION

Our study addresses critical knowledge gaps in forest restoration and the conditions that facilitate the introduction of late-successional tree species into agricultural lands designated for restoration. Our analyses revealed that seedling survival varied among late-successional species and was influenced by factors such as early-successional tree density, vegetation cover, solar radiation and soil chemistry. Survival also varied spatially, as ecological and environmental factors, such as soil fertility and vegetation cover, are influenced by underlying geographical features like topography, elevation and hydrology, creating inherent spatial structure.

4.1 | Most late-successional tree species' survival was high when planted simultaneously with early-successional species

Late-successional tree species showed significant differences in survival ([Figures 1a, 2a and 3a](#)) in our study. Pūriri, tōtara, rewarewa and kahikatea exhibited high survival, whereas rimu and taraire showed much lower survival. Although our experimental design does not provide a comparison between simultaneous and non-simultaneous planting of late- and early-successional trees, our results based on 1840 trees clearly demonstrate that four out of six late-successional tree species exhibited high survival rates when planted alongside early-successional species. Therefore, even in the absence of a control treatment, these findings suggest that this approach could be effective for some late-successional species. In this sense, they challenge the prevailing view in forestry that early-successional trees should be planted ahead of late-successional ones (Hilderbrand et al., 2005; Laughlin & Clarkson, 2018; but see also Bechara et al. (2016) and Corbin and Holl (2012) for alternative perspectives). From a practical perspective, planting early- and late-successional trees simultaneously also appears to greatly reduce the resource requirements: it is more efficient on labour time/costs and logistics to do one planting session for both late- and early-successional trees than it is to spread these across two staged sessions. Nonetheless, further research is required to compare the impact of simultaneous versus staggered planting of early- and late-successional species across a wider range of species with different ecological requirements and traits.

The low survival of rimu and taraire can be attributed to the combined effects of the species' ecological traits and

environmental conditions at the afforestation sites. Specifically, rimu is intolerant of seasonal drought and prefers moist, nutrient-poor soils (Dawson & Lucas, 2016; [Table 1](#)). As such, the farming history of Te Muri and Te Pourewa, which most likely enriched the soil, and the severe summer 2019–2020 drought likely strongly hindered the establishment of rimu. Similarly, the low survival of taraire is likely due to its susceptibility to seasonal drought and soil compaction from past agricultural use; these factors were highlighted by Myers and Court (2013; [Table 1](#)) as key limitations to its establishment. These considerations align with Martínez-Garza et al. (2005), Löf et al. (2014) and Osorio-Salomón et al. (2021), who investigated the survival of mid- and late-successional species introduced to early-successional environments or degraded sites in tropical and temperate climates and attributed survival differences to species-specific fundamental niches, functional traits and environmental interactions.

4.2 | A 2-m spacing between early-successional trees maximizes seedling survival of late-successional tree species

Our analysis revealed an important trade-off concerning the spacing (i.e. density) of early-successional trees and its impact on the survival of late-successional trees. Late-successional tree survival peaked at 2-m spacing between early-successional trees ([Figure 1b](#)), while survival was lower at 1, 3 and 4 m. A two-meter spacing strikes a compromise between shading, competition, and resource availability for late-successional species. At smaller spacings (e.g. 1 m), early-successional trees may create excessive shading or compete for resources with late-successional tree seedlings, thereby inhibiting their growth and survival (Pacala et al., 1994). At wider spacings (e.g. 3 and 4 m), while competition might be reduced, the more open canopy could lead to increased exposure to environmental stressors and less favourable microclimatic conditions for the late-successional trees, such as drought and high temperatures (Dupuy & Chazdon, 2008; Facelli & Pickett, 1991; Vázquez-Yanes & Orozco-Segovia, 1992). Since three of the four late-successional tree species used to test the spacing effect (i.e. Te Muri site) are rather shade-intolerant (Dawson & Lucas, 2016; [Table 1](#)), our results highlight the importance of balancing shelter and light for successful tree establishment.

Our results on the spacing effect, based on 833 late-successional trees, have significant implications for forest management and restoration. Ecologically, a 2-m spacing regime promotes high seedling establishment and survival of late-successional species, which in turn contributes to the forest's ability to maintain a natural balance and ecological functioning, supporting its long-term viability and resilience. Economically, a 2-m spacing regime decreases initial tree costs due to lower early-successional tree density compared with smaller spacings. This minimizes the need for thinning, but may incur higher weed control costs due to increased open space allowing more weed growth. This finding aligns with the Timata Method, which recommends a 2-m spacing for early-successional

trees (Dewes et al., 2022) and with Clark et al. (2008), who showed that common walnut (*Juglans regia* L.) survival exceeded 99% when planted in a 2-m × 2.5-m grid of nurse trees in England, although they did not test other spacings. In contrast, Sakai et al. (2009) reported that a nurse tree grid of 2 m × 8 m in Thailand supported the highest survival of a late-successional tree species, while 2 m × 4 m resulted in the lowest. Finally, Nord-Larsen and Meilby (2016) found no effect of nurse tree density on late-successional species biomass (*Fagus sylvatica* L. and *Quercus robur* L.) in Denmark. Future research shall thus aim to examine if a 2-m spacing is appropriate across species with different functional traits, shade tolerance and climatic and environmental requirements.

4.3 | Vegetation cover supports seedling survival of late-successional tree species

In our study, cover of neighbouring dead and live vegetation positively influenced late-successional tree survival at two sites, Te Muri and Te Pourewa (Figures 1d and 3b, respectively). Dead vegetation cover had a significant effect on seedling survival at Te Muri only. Dead vegetation cover was lowest at Te Muri compared to Pūkorokoro and Te Pourewa (mean ± SD at Te Muri: 26.44 ± 22.20, Pūkorokoro: 39.61 ± 19.83, Te Pourewa: 37.40 ± 24.98). This suggests that variation in dead vegetation cover may only significantly affect seedling survival at low cover levels. At higher levels, such as observed at Pūkorokoro and Te Pourewa, variation in dead vegetation cover did not lead to significant differences in seedling survival. This is possibly because an overall high cover of dead vegetation may act as an insulating layer, reducing and buffering abiotic variation (e.g. temperature and moisture) across the environment, and thus reduce drastic shifts in ecological conditions. Live vegetation only had a significant impact on seedling survival at Te Pourewa. The intermediate level of cover (%) of live vegetation at Te Pourewa compared to Te Muri and Pūkorokoro (mean ± SD: at Te Muri: 42.77 ± 30.42, Pūkorokoro: 33.30 ± 20.24, Te Pourewa: 37.07 ± 22.55) suggests that the significant effect of live vegetation cover at Te Pourewa was likely driven by site-specific factors, such as moisture retention, nutrient availability and reduced competition from invasive species (Martínez-Garza et al., 2005; Osorio-Salomón et al., 2021; Pozo Inofuentes & Säumel, 2022). Lastly, the community composition at Pūkorokoro, that is, its specific arrangement or makeup of herbaceous plant species, may have been particularly conducive to tree seedling survival (e.g. through positive interactions and by creating shade, shelter and reduced competition)—as indicated by the high survival rate and greatest cover of dead vegetation among all sites—potentially explaining the lack of a significant supporting effect of vegetation cover.

Contrary to expectations, the invasive kikuyu grass' cover did not significantly hinder the survival of late-successional trees at any site. It is possible that the early-successional trees provided enough shade to effectively reduce kikuyu growth (personal observation; see Hooper et al., 2002), preventing it from having a negative impact on late-successional seedlings. While our study does not provide

evidence on this effect, it calls for further investigation to evaluate the potential of using early-successional tree planting to reduce invasive grass cover, offering a more cost-effective alternative to the labour-intensive eradication of invasive species in restoration projects (Hulme, 2006).

4.4 | Abiotic variability alters seedling survival of late-successional tree species

Our analyses revealed contrasting relationships between soil nutrient-richness and late-successional tree survival across sites. At Te Muri, survival was higher in microhabitats with greater total nitrogen and carbon and organic matter, but lower in those with higher calcium content (Figure 1c,d; Figure S5). In contrast, at Pūkorokoro, survival was higher at lower total nitrogen, carbon, organic matter and cation exchange capacity (Figure 2b; Figure S6).

The results for Te Muri align with the common assumption that higher nitrogen, carbon and organic matter typically enhance tree survival (Grigal & Vance, 2000). Given that calcium is essential for plant growth (Baribault et al., 2012; Kobe et al., 2002; McLaughlin & Wimmer, 1999), the negative relationship between survival and soil calcium at Te Muri may result from particularly high calcium levels compared to the other sites (mean ± SD at Te Muri: 7.29 ± 2.21, Pūkorokoro: 4.10 ± 1.85, Te Pourewa: 6.91 ± 2.51 [me/100 g]). High calcium levels increase soil pH, limit nutrient availability (McLaughlin & Wimmer, 1999) and can disrupt the symbiotic relationship between trees and mycorrhizal fungi, impairing nutrient uptake. Trees adapted to infertile acidic soils, such as rimu (Adams & Norton, 1991; Dawson & Lucas, 2016), are likely particularly sensitive to such conditions, driving higher mortality.

At Pūkorokoro, however, nutrient-poor conditions seemed to offer advantages, despite late-successional species planted at this site typically preferring fertile soils (Dawson & Lucas, 2016; Table 1). Such conditions often support slow-growing plant communities (Berendse, 1998), possibly allowing tree seedlings to establish more effectively than in nutrient-rich conditions dominated by fast growers. They may also harbour specific microbial communities (Siles & Margesin, 2016; Teste et al., 2021) that favour late-successional species. Similar patterns have been observed in other ecosystems, such as the temperate Appalachian mountains (Bao & Nilsen, 2015) and tropical Seychelles (Schumacher et al., 2009).

At Te Muri, late-successional tree survival also increased with higher solar radiation. Increased solar radiation enhances photosynthesis, leading to better nutrient acquisition and faster growth (Dong et al., 2012; Kašpar et al., 2024), which may ultimately improve survival. Our results reflect the shade intolerance of three of the four late-successional species planted at Te Muri (Dawson & Lucas, 2016; Table 1), as this trait makes species more reliant on higher solar radiation for their physiological processes, growth and survival compared to shade-tolerant species. Solar radiation at Te Muri (mean ± SD: 481,944.25 ± 48,810.75 [Wh/m²]) was, however, lower than at Pūkorokoro (mean ± SD: 525,593.19 ± 54,976.22 [Wh/m²]; n.b. solar

radiation was removed from the model for Te Pourewa, as it was highly correlated with other variables) where radiation had no significant effect. Solar radiation at Te Muri and Pūkorokoro corresponded to a coefficient of variation of ~10%, indicating moderate within-site variability and generally open conditions with limited shading or complex topography, consistent with field observations. The effect of solar radiation on survival appears logarithmic rather than linear: changes in survival are most noticeable at low radiation levels, while at higher levels, additional radiation has little impact. This suggests both a minimum threshold needed for tree growth and an upper limit to what trees can utilize for photosynthesis. Because trees were still small in our study, neighbourhood shading was likely minimal, so excluding it probably did not affect our results. As trees grow and shading intensifies, especially in the densely planted early-successional grid, its influence on light availability and solar radiation will increase, and future studies should account for it, particularly in the Te Muri experiment with variable spacing. Altogether, these findings emphasize the need for species- and site-specific considerations in forest restoration efforts to ensure that the right species are planted in the right location. For instance, shade-intolerant species should be prioritized for planting in fully exposed, well-lit (micro-)sites, such as the north face of a hill in the Southern Hemisphere, while shade-tolerant species should be prioritized in other (micro-)sites.

5 | CONCLUSIONS

Our study, investigating the conditions that promote seedling survival in the afforestation of agricultural lands designated for restoration, revealed two key findings. First, we showed that some late-successional tree species can achieve high survival when planted simultaneously with early-successional species, suggesting that late-successional species do not necessarily need to be planted later in succession. Given that species identity, environmental and ecological conditions significantly influenced seedling survival, our study provides empirical evidence for future research aimed at developing a framework for identifying the functional characteristics of late-successional tree species suited to this approach (Aerts & Honnay, 2011; Loureiro et al., 2023).

Second, our research showed that a 2-m spacing between early-successional trees optimized late-successional tree survival, a result consistent with existing literature (Clark et al., 2008; Dewes et al., 2022). We recommend that future forest restoration projects explore the impact of a 2-m early-successional tree spacing on late-successional species' survival and gather evidence on whether this spacing is optimal across different tree species, shade tolerances, functional traits, species' climatic and environmental requirements and project locations. Finally, while our results do not provide direct evidence, they suggest that planting early- and late-successional trees together may offer a potential cost-effective strategy for mitigating the impact of invasive grass species on late-successional seedlings. This approach warrants further investigation to assess its effectiveness.

AUTHOR CONTRIBUTIONS

Sarah Bürli, Bradley S. Case, David Hall and Hannah L. Buckley conceived the ideas and designed methodology; all authors collected the data; Sarah Bürli analysed the data; Sarah Bürli led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Akaike's information criterion (AIC) from aster models for late-successional trees' survival after three years per site.

Table S2: Backward selection results for non-spatial aster models for Te Muri using likelihood ratio tests.

Table S3: Backward selection results for non-spatial aster models for Pūkoro-koro using likelihood ratio tests.

Table S4: Backward selection results for non-spatial aster models for Te Pourewa using likelihood ratio tests.

Figure S1: AUT Living Laboratories program forest restoration experiment site locations within the context of the greater Auckland Region, and within Aotearoa New Zealand.

Figure S2: Pearson correlations between continuous predictors retained in the final Te Muri model.

Figure S3: Pearson correlations between continuous predictors retained in the final Pūkoro-koro model.

Figure S4: Pearson correlations between continuous predictors retained in the final Te Pourewa model.

Figure S5: Predicted survival and 95% confidence intervals of the late-successional trees after three years for a typical individual at Te Muri in the aster model without a spatial term as a function of: (A) late-successional tree species, (B) third principal component of soil variables (PC3), which positively correlated with the sodium content and the cation exchange capacity of the soil, (C) solar radiation, (D) topographic wetness index, and (E) dead vegetation cover at the lower tier.

Figure S6: Predicted survival and 95% confidence intervals of the late-successional trees after three years for a typical individual at Pūkoro-koro in the aster model without a spatial term as a function of: (A) late-successional tree species, (B) first principal component of soil variables (PC1), which negatively correlated with the total nitrogen content in the soil, (C) slope gradient, (D) live vegetation cover, except kikuyu, at the lower tier, and (E) dead vegetation cover at the lower tier.

Figure S7: Predicted survival and 95% confidence intervals of the late-successional trees after three years for a typical individual at Te Pourewa in the aster model without a spatial term as a function of: (A) late-successional tree species, (B) live vegetation cover, except kikuyu, at the lower tier, and (C) bare soil cover at the lower tier.

Figure S8: Biplot of the principal component analysis (PCA) of soil chemistry variables at Te Muri.

Figure S9: Biplot of the principal component analysis (PCA) of soil chemistry variables at Pūkoro-koro.

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