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## RESEARCH ARTICLE

# Species wood density and the location of planted seedlings drive early-stage seedling survival during tropical forest restoration

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**Abstract**

1. The success of restoration projects is known to vary widely, with outcomes relating to numerous biotic and abiotic factors. Though many studies have examined the factors associated with long-term restoration success, few have examined which factors impact the establishment of restoration plantings.
2. In Australia's Wet Tropics, we used a large replicated restoration experiment to assess seedling survival for 24 native rainforest species commonly used in local restoration efforts. The experiment allowed for a rigorous assessment of the effects of species functional traits, planting conditions, and landscape- and local-scale biotic and abiotic factors on seedling survival. This study reports on seedling survival between three different time periods of 0–4, 4–9 and 9–31 months post planting.
3. The probability of seedling survival was influenced by multiple factors, varying in importance over time. Across the whole study period, seedlings with high wood density and which were planted closer to intact forest consistently displayed the highest probabilities of survival. Transient factors affecting seedling survival across the three time periods included plot aspect (0–4 months only), the identity of the planter and slope (4–9 and 9–31 months). Overall, species survival did not differ between the low (6 species) and high (24 species) diversity treatments, but was significantly lower in monocultures of *Flindersia brayleyana* by the end of the study.
4. We demonstrate that early-stage seedling survival depends on species wood density and planting location. Our results support the use of species with more conservative growth strategies when limited funds are available for follow-up plantings. High wood density species had significantly higher survival than lower wood density, early successional species typically used in rainforest restoration plantings.
5. *Synthesis and applications.* Our study highlights the importance of wood density and landscape structure to the initial survival of rainforest plantings. Factors influencing seedling survival shifted over time but, most importantly, our results highlight that, when planting into abandoned pastures, it may be preferable to select species with higher wood densities to maximize survival during the crucial early stages of establishment and growth.

**KEYWORDS**

functional traits, plantings, rainforest, restoration, revegetation, seedling establishment, succession, wood density

## 1 | INTRODUCTION

With the extensive loss of tropical forest over the last century and the current global increase in land abandonment (Cramer, Hobbs, & Standish, 2008; Munroe, van Berkel, Verburg, & Olson, 2013), ecological restoration to aid the recovery of degraded ecosystems is becoming increasingly important (Society for Ecological Restoration Science & Policy Working Group, 2002). Restoring tropical forested ecosystems commonly involves planting species to accelerate forest recovery (Chazdon, 2008). Despite the abundance of restoration theories and techniques, many restoration projects starting from abandoned pastures still fail to achieve desired goals (Lamb, Erskine, & Parrotta, 2005).

The large variability in outcomes among tropical forest restoration efforts is largely due to the many biotic and abiotic factors across spatial scales that impede early-stage seedling establishment and growth. Seedling establishment can be influenced by landscape-scale factors such as distance of plantings to established forest patches (Catterall, Kanowski, & Wardell-Johnson, 2008), slope, aspect (Nagamatsu, Seiwa, & Sakai, 2002) and soil fertility (Guariguata & Ostertag, 2001), but these factors have generally not been examined for early-stage seedling survival (but see Martínez-Garza, Tobon, Campo, and Howe, 2013). Local-scale factors of the planting site, such as competition with resident grass and weed species, may also impede seedling establishment (Holl & Kappelle, 1999; Hooper, Condit, & Legendre, 2002). Despite evidence of their importance, restoration efforts that focus on these factors still vary considerably in whether they are successful (Bechara et al., 2016; Dudley, Mansourian, & Vallauri, 2005).

To mitigate these factors, much attention has focused on species selection. Projects differ markedly in how species are selected, particularly in their consideration of species' phenologies, functional traits and responses to local environments. Species selection based on successional status (e.g. early, late secondary or mature species) is recommended under some restoration frameworks (Goosem & Tucker, 1995; Rodrigues et al., 2011), but has largely been untested in replicated planting experiments (but see Martínez-Garza, Bongers, and Poorter 2013). Other approaches, including species selection based on plant functional traits (Laughlin, 2014) have not yet been widely incorporated into restoration practice. These trait-based approaches are motivated in part by previous studies linking traits with increased survival and growth in restoration plantings and mature forests. For instance, Martínez-Garza, Peña, Ricker, Campos, and Howe (2005) recorded increased growth and survival of planted seedlings with increased variation in specific leaf mass, while Poorter et al. (2008) and Wright et al., (2010) found greater seedling survival for species with higher wood density and seed volume in mature-phase tropical forests. Additionally, comparisons of seedling establishment between monoculture and mixed diversity plantings have also been examined

(Piotto, 2008; Plath, Mody, Potvin, & Dorn, 2011), yet comparisons between low and high levels of diversity within mixed species plots in restoration plantings are still lacking.

The early stage of seedling establishment (typically between 1 and 3 years) is a strong predictor of mid-term performance of restoration plantings (Martínez-Garza, Bongers, et al., 2013; Montagnini, Gonzalez, Porras, & Rheingans, 1995). While seedlings during the initial stages of restoration plantings are highly susceptible to many biotic and abiotic factors, these impacts can be exacerbated by transplanting shock (Burdett, 1990) and poor planting conditions, such as inappropriate seedling handling and planting techniques (Grossnickle, 2005). Consequently, seedling mortality during the establishment phase can alter early successional trajectories and potentially lead to arrested forest recovery (Lamb, 2011).

The paucity of research into early-stage seedling establishment under different diversity planting regimes (Lamb & Lawrence, 1993), coupled with the distinct lack of monitoring of seedling survival and growth in many restoration projects (Kanowski, Catterall, Freebody, Freeman, & Harrison, 2010), underscores the need for more research into the factors that influence early-stage seedling establishment and future forest recovery.

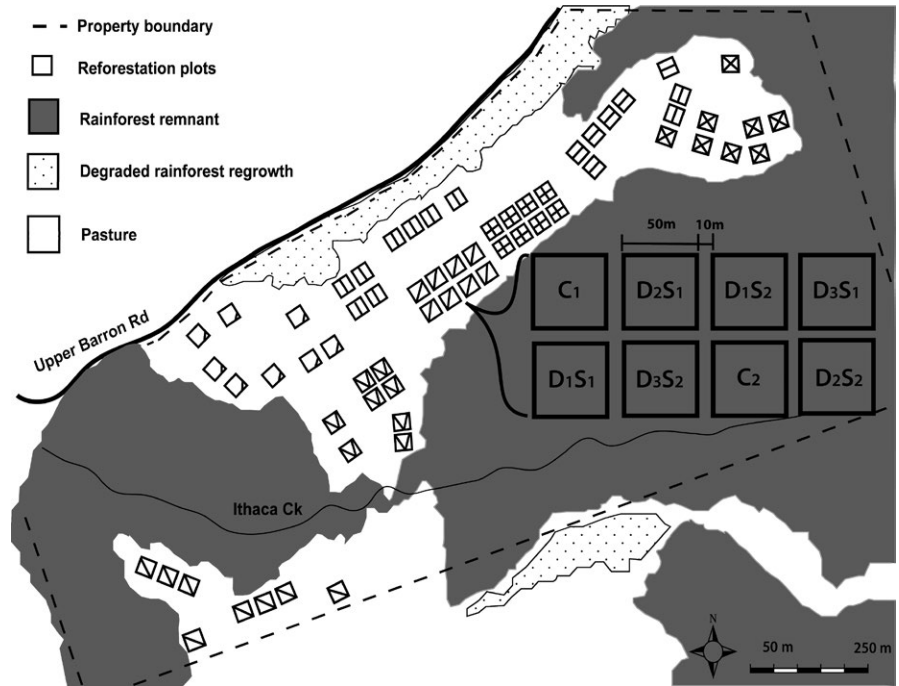
The aim of this study was to increase understanding of the factors influencing seedling survival, and how these factors change over time. We present survival data recorded during the first two and a half years of a rainforest restoration experiment in the Wet Tropics of Australia. The specific questions we ask are: (1) How important are landscape, site and planting conditions to seedling survival? (2) Do species functional traits explain variation in seedling survival? and (3) Do these factors change during the first two and a half years of seedling establishment? Given the wide range of factors that can influence early-stage seedling survival, we predicted a similarly large diversity of factors responsible for explaining survival patterns. In particular, we hypothesised that seedling survival will be highest on shallow slopes near forest, based on previous findings in the literature (Catterall et al., 2008; Nagamatsu et al., 2002). Due to the commonly observed relationship between the functional traits of species and seedling survival, we also hypothesised that species with high wood density and larger seed masses will have higher survival rates than species with low wood densities and small seeds (Baraloto, Forget, & Goldberg, 2005; Poorter et al., 2008).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This study was undertaken on the Thiaki Creek Nature Reserve (Figure 1), located on the southern Atherton Tablelands of far North Queensland, Australia (145°51'E 17°43'S), between 900 and 1,000 m

**FIGURE 1** Map of Thiaki Creek property. The restoration experiment consists of eight blocks, each containing eight 50 m × 50 m plots. Plots within a block are labelled with individual fill patterns. The eight treatments applied within each block were:  $C_1$  = no planted trees,  $C_2$  = no planted trees, herbicide addition,  $D_1$  = 1 species,  $D_2$  = 6 species,  $D_3$  = 24 species,  $S_1$  = 1.75 m spacing and  $S_2$  = 3.0 m spacing



elevation, with an average annual rainfall of 1,400 mm (Bell, Winter, Pahl, & Atherton, 1987). The underlying substrate is basaltic (Tracey, 1982) with a varied topography of narrow valleys surrounded by 15–45° slopes. The 181-ha reserve comprises 130 ha of primary and mature secondary rainforest, classified as *Endangered Regional Ecosystem 7.8.4*, Upper Barron complex notophyll vine forest (Bell et al., 1987) and 51 ha of abandoned pasture which was the focus of the restoration experiment established in January 2011. The pasture area had a consistent land use history (remnant forest cleared for grazing c. 50 years ago) and the pasture itself was relatively homogeneous in composition prior to planting.

## 2.2 | Experimental design

In January 2011, approximately 28,000 rainforest seedlings were row planted in a randomized complete block design consisting of eight blocks each containing eight 50 m × 50 m plots separated by a 10-m buffer zone. The experiment included a two-level planting density treatment: low-density (seedlings spaced 3 m apart) and high-density (seedlings spaced 1.75 m apart) and a three-level species diversity treatment (1, 6 and 24 species). The diversity treatment was phylogenetically nested with 24 local rainforest tree species from six common families: Lauraceae, Moraceae, Myrtaceae, Proteaceae, Rutaceae and Sapindaceae (Table S1). All monoculture plots were composed of *Flindersia brayleyana* (Rutaceae). We recognize that this decision prevented any general conclusions about seedling mortality in monoculture and thus deal with data on this species (and thus monoculture plots) separately from the higher diversity treatment plots. The multispecies “low-diversity” treatment included one species from each of the six focal families. The high diversity treatment included all 24 species, four species from each family and included all those species present in the low-diversity treatment. *Flindersia brayleyana* was used

in all three treatments. Within each experimental block, we assigned two control treatment plots, with no planted seedlings. Plots were randomly assigned treatments within each block (Figure 1).

Species were selected based on their commonality in local intact rainforest, availability in local nurseries and a suit of functional traits selected to match common successional stages. Specifically, we selected species in each focal family to span a broad range of trait values for the following traits: maximum tree height, wood density, dispersal vector, seed size and successional stage. Classifications of successional stages included early, late secondary and mature stage species. Early successional species are typically short-lived, fast growing, shade intolerant species and display both low wood density and small seed mass (Hopkins, Kikkawa, Graham, Tracey, & Webb, 1979). Mature stage species are shade tolerant, longer lived, slow growing species with high wood densities and large seeds (Hopkins et al., 1979). Early- and mature-stage species are functionally analogous with pioneer and non-pioneer species, respectively, as described by Whitmore (1989). Late secondary species display moderate growth rates and increasing shade intolerance with age (Hopkins et al., 1979) and are functionally equivalent to longer lived pioneer species (Whitmore, 1989).

Species from both 6- and 24-species diversity treatments were randomly assigned within rows in each plot. After cattle removal and prior to planting, the pasture was dominated by the exotic grass *Urochloa decumbens*. We applied a monocot-specific herbicide (Fusillade) along designated planting rows of all treatment plots (excluding one control plot in each block), leaving alternate rows of unsprayed grass to reduce the potential for run-off and erosion. Herbicide application within rows was continued every 6 months until August 2012. To avoid potential desiccation of seedlings, planting was conducted during the regional wet season. However, during planting in January 2011, a tropical cyclone off the eastern coast of the study region created unseasonably

dry weather during planting. No rainfall was recorded at the planting site until 5 days after the planting was complete. Seedlings were planted without fertilizer application by professional planters using standard forestry industry techniques. Seedlings were not manually watered after planting. The identity and location of planted seedlings was recorded along each row in all plots.

### 2.3 | Explanatory variables

Slope and aspect of the plots were measured using a clinometer and compass respectively. We measured the distance from the centre point of plots to the nearest surrounding forest fragments using ArcGIS (ESRI, 2006). The identity of the person responsible for planting individual seedlings (hereafter referred to as planter identity) and the day until first rain were also recorded (plots differed in the time between planting and rainfall). Wood density estimates for all planted species were obtained from Chave et al. (2009) and Zanne et al. (2009). Dry seed mass values were obtained from the literature and the Royal Botanic Gardens Kew Seed information database (Royal Botanic Gardens Kew, 2017). Maximum adult height values and dispersal vectors were obtained from Cooper and Cooper (2004). The complete list of explanatory variables examined in this study can be found in Table S2.

### 2.4 | Data collection

To minimize edge effects within experimental plots, the survival of seedlings was recorded only in a central 25 m × 25 m subplot within each treatment plot. Seedling status was recorded by visual inspection, with seedlings deemed to be dead if there was pronounced stem desiccation, no leaves and/or the seedling could not be located. Seedling survival was assessed at 6-month intervals starting 4 months after planting in April 2011 until July 2013.

### 2.5 | Statistical analysis

Seedling survival (binary response, 1 = living, 0 = dead) was modelled as a function of planting regime, landscape- and site-scale variables, and species' functional traits (Table S2) using generalized linear mixed-effect models with logit link function and binomial error distribution. Block and plot (nested within block) and family and species (nested within family) were included as random effects in all models. Two-way interactions between functional traits (wood density, seed mass and maximum tree height) and plot slope, distance to forest and day until first rain were included in all models to test for species-level differences in their responses to different factors. Plot aspect was not included in any interactions due to the uneven distribution of south-facing (31%) compared to north-facing plots (69%). While wood density, seed mass and maximum tree height were included as species-level variables, they likely also vary by family. As such, we first ran a variance component analysis which indicated that c. 35% of variance in both wood density and seed mass occurred between families and 65% within families (Table S3), though much of the within-family variation was driven by two families—Lauraceae and Proteaceae for

wood density and Lauraceae and Moraceae for seed mass (Figure S1). Thus, our wood density and seed mass variables captured both species and family level differences. Variation in maximum tree height occurred entirely within families (Table S3). Before fitting models, there was no evidence of correlation among explanatory variables (Pearson's product-moment correlation, Table S4).

Seedling survival was analysed separately for three time periods representing early-stage survival (0–4, 4–9 and 9–31 months post planting). Due to low seedling survival within the first 4 months, the density of planted seedlings within plots changed considerably, thus density was excluded as an explanatory variable from all mixed-effects models. Monoculture treatment plots (containing *F. brayleyana*) were excluded from analyses due to lack of variation in family and functional traits. Separate analyses were conducted for *F. brayleyana* survival across all plots as it was the only species included in a monoculture treatment. Maximal models containing all relevant explanatory variables for each time period were simplified by removing non-significant terms (determined by Wald Z tests) one at a time. Data analysis was conducted using the R statistical software package version 3.3.3, using the lme4 package (Bates, Maechler, & Bolker, 2011; R Development Core Team, 2010). Post hoc tests of pairwise treatment differences were conducted for *F. brayleyana* seedling survival using the glht function in the multcomp package (Hothorn, Bretz, & Westfall, 2008).

## 3 | RESULTS

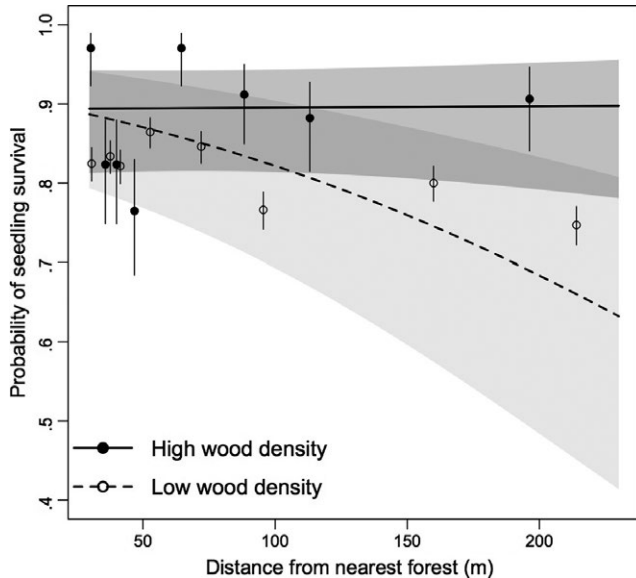
### 3.1 | Overall seedling performance

Of the 6,657 seedlings for which data were collected in this experiment, only 3,544 survived (53.2%) to 31 months post planting. Overall probability of seedling survival varied by family, with species from Moraceae having the highest probability of survival (0.7) and Lauraceae (0.33) the lowest (Table S5). Survival probability differed considerably between species within families as well (Table S5) with *Stenocarpus sinuatus* (0.87), *Rhodamnia sessiliflora* (0.8) and *Guioa lasioneura* (0.8), the top surviving species, and *Cryptocarya oblata* (0.09) and *Melicope jonesii* (0.09) experiencing the lowest survival.

### 3.2 | Factors affecting seedling survival

Seedling survival was affected by multiple factors, and the relative importance of these factors changed through time. At 0–4 months, seedling survival was marginally higher in south-facing than north-facing slopes, with significantly higher survival in plots close to forest fragments than those further from forests. This distance effect was most pronounced for low wood density species (Figure 2, Table S6). Survival of *F. brayleyana* in monoculture, low- and high-diversity plots over the same period was best explained by slope, with greater seedling survival on steeper slopes (Figure S2 and Table S7).

For the 4- to 9-month period, seedling survival was best explained by species' wood density, slope, distance to forest and planter identity (Table S8). Like the preceding time period, seedling survival decreased with distance from forest fragments (Figure S3). Seedling survival declined



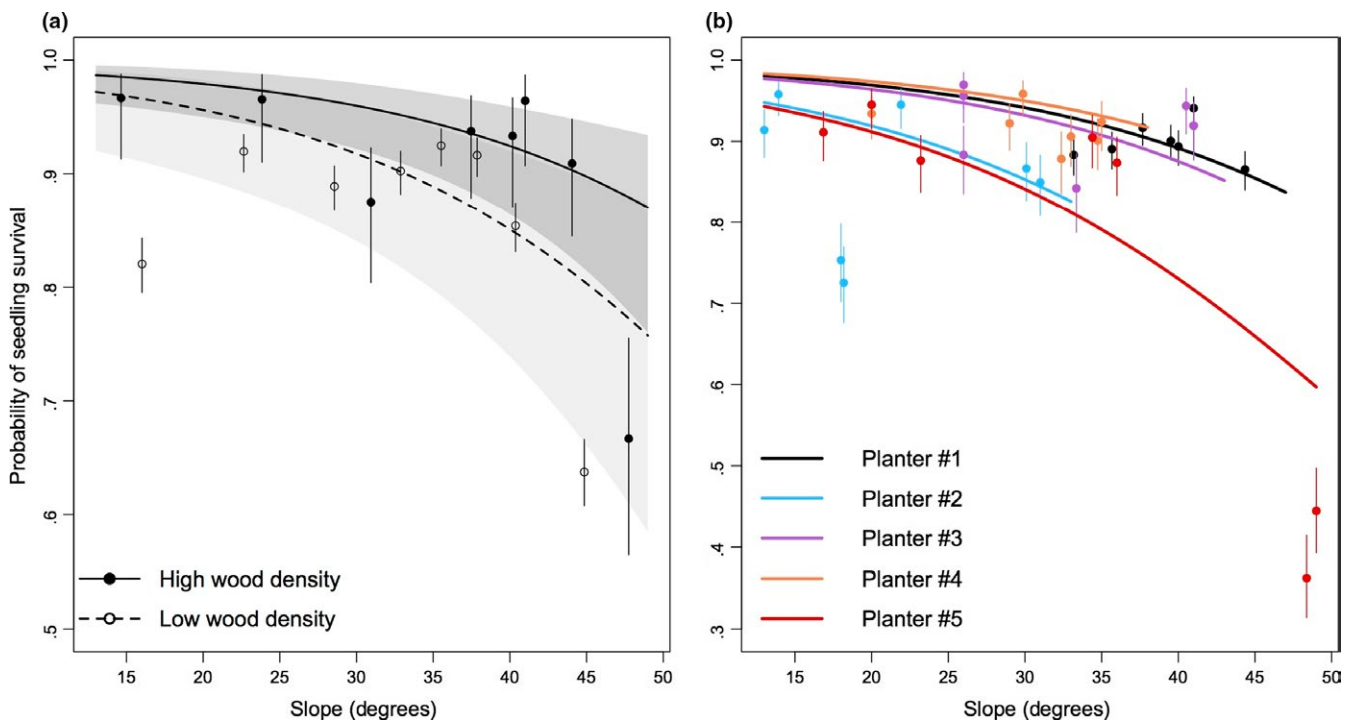
**FIGURE 2** Probability of seedling survival for the 0- to 4-month time period in relation to distance to nearest forest fragment (m) with high and low levels of species' wood density ( $\text{g}/\text{cm}^3$ ). Fitted line values for low and high wood density are 0.38 and 0.84  $\text{g}/\text{cm}^3$  respectively. Points for high and low wood density were calculated from the upper and lower third of wood density values respectively. Bars are associated SEs on the probability scale. Shaded bands represent 95% confidence intervals

with increasing slope, and was lower for species with low wood density (Figure 3a), though there were no significant interactions between wood density and other variables during this time period. Survival also varied significantly among planters (Figure 3b). No explanatory variables proved to be good predictors of *F. brayleyana* survival during this time period.

During the final 9–31 months, survival was best explained by distance to forest, planter identity and the interaction between slope and wood density (Table S9). The significant interaction between wood density and slope (Figure 4a) indicated that high wood density species survived better on shallow slopes, but on steep slopes all species experienced similarly low survival, regardless of wood density. Similar to the previous time periods, survival varied among planter identity, but the order of planters changed through time (planter 5 had lowest survival during 4–9 months, whereas planter 1 had lowest survival during 9–31 months, Figure 4b). *Flindersia brayleyana* survival during the final period was best explained by the diversity treatment (Table S10), with survival significantly lower in monocultures than in the 6- and 24-species treatments (Figure 5, Table S11). Apart from wood density, no other functional trait explained variation in seedling survival over the 31-month observation period.

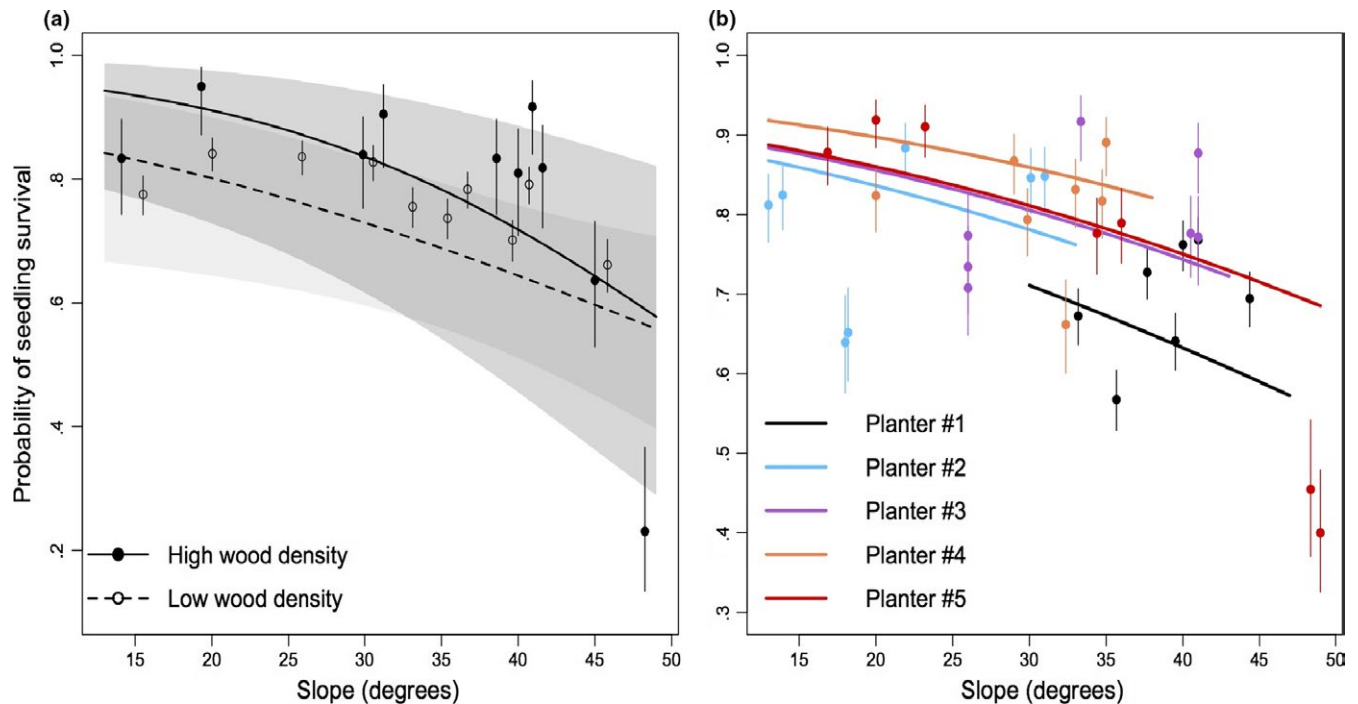
## 4 | DISCUSSION

The probability of seedling survival during early-stage restoration was influenced by multiple interacting landscape and biological factors,

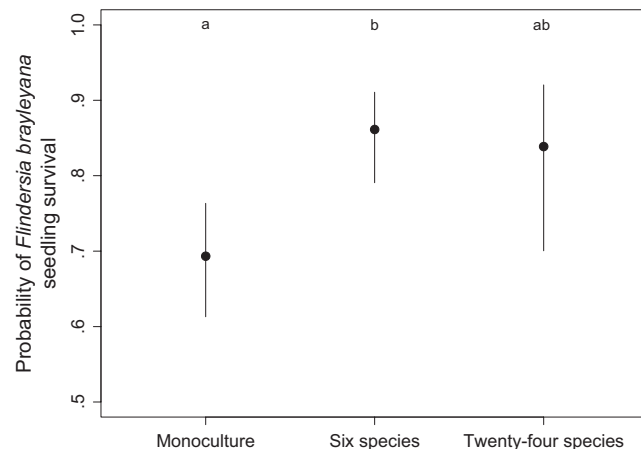


**FIGURE 3** Probability of seedling survival 4–9 months post planting in relation to slope ( $^{\circ}$ ) and (a) wood density ( $\text{g}/\text{cm}^3$ ) and (b) planter ID, with separate lines fitted for each planter ID. Fitted line values for low and high wood density are 0.38 and 0.84  $\text{g}/\text{cm}^3$  respectively. Points for high and low wood density were calculated from the upper and lower third of wood density values respectively. Shaded bands represent 95% confidence intervals. Points for planter ID are mean probabilities calculated from seven bins of ordered binary values. All bars are associated standard errors on the probability scale





**FIGURE 4** Probability of seedling survival 9–31 months post planting in relation to slope (°) and (a) wood density ( $\text{g}/\text{cm}^3$ ) and (b) planter ID, with separate lines fitted for each planter ID. Fitted line values for low and high wood density are  $0.38$  and  $0.84 \text{ g}/\text{cm}^3$  respectively. Points for high and low wood density were calculated from the upper and lower third of wood density values respectively. Shaded bands represent 95% confidence intervals. Points for planter ID are mean probabilities calculated from seven bins of ordered binary values. All bars are associated standard errors on the probability scale



**FIGURE 5** Probability of *Flindersia brayleyana* seedling survival in relation to species diversity treatments 9–31 months post planting. Points are mean probabilities calculated from each treatment and bars are the corresponding 95% confidence intervals. Letters denote significantly different groups ( $p < .05$ ), based on pairwise post hoc tests (Table S8)

with the strength of some factors changing over time. Only wood density, a species-level predictor, and the distance of plantings to forest fragments consistently influenced seedling survival throughout the 31-month observation period. Overall, seedlings with high wood densities planted near intact forest patches had the greatest probability of survival. This positive wood density effect suggests that when planting into abandoned pastures it may be preferable to include species

with higher wood densities to maximize survival during the crucial early stages of establishment and growth.

#### 4.1 | Effects of functional traits on seedling survival

Throughout this study, wood density had a consistently positive effect on seedling survival. Our results are consistent with seedling survival-growth trade-offs identified in other tropical rainforest species (Chave et al., 2009; Poorter et al., 2008), with higher wood density species displaying higher survival than species with lower wood densities, at the expense of slower growth (Kraft, Metz, Condit, & Chave, 2010; Nascimento et al., 2005). The very high levels of light and heat exposure typically experienced in open tropical pasture may favour species with higher wood densities that typically have reduced risk of xylem implosion under water stress than low wood density species (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001; Sperry, Meinzer, & McCulloh, 2008). Contrary to our expectations, seed mass did not explain variation in early-stage seedling survival. Surprisingly, we observed a negative relationship between seed mass and survival (a relationship also found by Martínez-Garza, Bongers, et al., 2013), although this relationship was non-significant. This result is counter to survival patterns observed in plantings (Baraloto et al., 2005) and mature forests (King, Davies, Tan, & Noor, 2006), whereby larger seed mass is correlated with higher survival rates in seedlings.

Despite strong evidence of a survival-growth trade-off in tropical trees, early successional species with low wood densities are often selected for restoration projects under the assumption that restoration

plantings follow the same recovery trajectory as naturally regenerating forests, notably that early successional species start the regeneration process and later successional species move in to replace them once fast growing early successional species have created a closed canopy and start to die out (Palmer, Ambrose, & Poff, 1997). However, there is increasing evidence that restoration projects do not always follow this trajectory (Griscom & Ashton, 2011; Lamb, 2011). Though early successional species are clearly important in the natural regeneration of many forest systems, our results (along with others; Bonilla-Moheno & Holl, 2010; Hooper et al., 2002; Montagnini et al., 1995) suggest that they may not be the best choice for planting-based forest restoration. Rarely are funds sufficient for supplementary plantings in restoration planting projects (Chazdon, 2008; Holl & Aide, 2011) and natural recruitment can be slow in plantings undertaken in open pasture (Florentine & Westbrooke, 2004). If plantings rely heavily on early successional species with fast growth and high mortality rates, canopies may never actually form, or may reopen over time as plants senesce and recruitment fails to fill gaps. Our results suggest that when restoration funding is limited, planting high wood dense species with slower growth rates may help to maximize mid-term restoration success.

#### 4.2 | Effects of distance to forest on seedling survival

Seedling survival decreased with distance from forest fragments throughout the observation period. Air temperature, vapour pressure deficit and soil temperature can increase with distance from forest (Pareliussen, Olsson, & Armbruster, 2006). Forest edges can provide intermittent shading throughout the day and this reduction in sun exposure and evaporation may provide a more suitable microhabitat for survival and/or growth of young seedlings (Duncan & Duncan, 2000). This is likely important for both early and late successional species in reducing stress levels as discussed above. The impact of distance from forest was stronger for species with low wood densities, further supporting our conclusion that reliance on early successional species with lower wood densities may reduce the likelihood of restoration success in exposed restoration sites.

There is some evidence that herbivore pressure can increase with distance to forest as well, though this appears somewhat system-specific (Myster & McCarthy, 1989; Ostfeld, Manson, & Canham, 1997). While herbivore damage was not directly measured in our experiment, herbivory was not observed to be substantial in any of our experimental plots (L. Charles, T. Smith pers. observ.). Given that many global forest restoration efforts are conducted in abandoned pastures, the effect of planting distance from adjacent forests on seedling mortality is relevant regardless of the root cause. The lower probability of seedling survival in exposed pastures highlights the importance of targeted management schemes, such as enrichment plantings expanding out from existing fragments, or selecting species with appropriate physiological adaptations for use further away from forest fragments.

#### 4.3 | Effects of slope on seedling survival

Consistent with previous studies (Daws, Pearson, Burslem, Mullins, & Dalling, 2005; Nagamatsu et al., 2002), during the 4- to 9-month time

period, seedlings planted on steep slopes experienced lower survival compared to seedlings planted on shallow slopes (Figure 3a). This trend became more pronounced with time for all species (Figure 4a). Typical factors associated with steeper slopes include increased water run-off (Snyman & Van Rensburg, 1986), soil erosion and reduced water retention (Meyer & Wischmeier, 1969). At this site, grass strips were intentionally retained to minimize erosion and run-off. Observed increases in seedling mortality on steeper slopes, however, suggest that either these strips were ineffective or that other abiotic factors caused negative associations with slope. To further investigate why mortality was higher on steep slopes at this site, we conducted post hoc linear regression analyses of soil samples collected from each experimental plot. In this analysis, we found no relationship between slope and soil temperature, pH, electrical conductivity or available nitrogen (Figure S4). It is, or course, possible that unmeasured soil factors created the observed slope effect, such as historical nutrient run-off, erosion and compaction associated with initial forest clearing and decades of cattle grazing. In addition, planting may have been more difficult on steep slopes, resulting in suboptimal planting techniques, which likely explains some of the variable performance of individual planters. The planter-mediated effect could also have been exacerbated by drier conditions on steep slopes where drainage and soil moisture holding capacity are probably lower, factors not measured here but worth assessing in the future. As we did not score "planting quality" per individual tree, it is hard, however, to disentangle such effects. Regardless of the cause, this finding is particularly important for tropical restoration given that many passive and active forest recovery projects are located on steep terrain (Asner, Rudel, Aide, Defries, & Emerson, 2009). Again identifying local species that survive and grow on steep slopes may be key to improving success rates of rainforest restoration.

#### 4.4 | Effects of aspect on seedling survival

Consistent with previous studies (Armesto & Martinez, 1978), we found a significant (though weak) relationship between aspect and seedling survival during the first 4 months post planting, with the probability of seedling survival marginally higher on south-facing slopes (Table S6). North-facing slopes in the southern hemisphere consistently experience more direct solar radiation than south-facing slopes (Tian, Davies-Colley, Gong, & Thorrold, 2001) which can increase surface temperature and moisture evaporation (Monteith, 1965) and lead to less favourable environments for planted seedlings (Turton & Freiburger, 1997). However, in the absence of both west- and east-facing plots in our experimental landscape, we advise that these results do not give a full picture of seedling performance across more topographically heterogeneous landscapes. The aspect result may also reflect differences in light tolerance among our study species, a trait we did not assess. While there is evidence that seedling light tolerance can impact survival rates within plantings (Augsburger, 1984), many species are able to acclimate to high-light conditions (Loik & Holl, 1999). Given that these species-specific responses have largely been untested in restoration experiments, and given our strong wood density results, future studies of species-specific responses to high-light conditions are clearly warranted.



## 4.5 | Effects of planter on seedling survival

Following the first 4 months post planting, the probability of seedling survival was somewhat dependent on who planted the seedling (planter identity; Figures 3b and 4b). The absence of a planter effect in the first time period is surprising given past research quantifying planter effects (Rietveld, 1989). The cyclone-induced dry period during planting may have masked short-term planter effects, by inducing immediate stress responses in all seedlings following planting, regardless of planter identity. Past studies have found that poor planter technique can damage roots and reduce root contact with the soil, which causes a reduction in a plant's ability to obtain water many months after planting (Burdett, 1990; Grossnickle, 2012). The professional planters used in this study included a mix of experienced planters (5+ years planting experience) and novices (mostly backpackers with <1 season of planting experience). Though we did not quantitatively evaluate planter background, our qualitative observations were that experienced planters were noticeably better tree planters. Our results suggest that if using untrained planters, training and quality control measures are worthwhile to improve seedling survival.

## 4.6 | Effects of diversity treatments on seedling survival

There was no observed effect of planting diversity on seedling mortality. When analysed separately, however, the probability of *F. brayleyana* seedling survival across all three diversity treatments was significantly lower in the monoculture plots than in the six species diversity plots (Figure 5), at least during the latest time period. This result contrasts with past studies comparing survival between monoculture and mixed species plantings within the neotropics (Piotto, Viquez, Montagnini, & Kanninen, 2004; Plath et al., 2011; Potvin & Gotelli, 2008). Seedling mortality in monoculture stands can result from increased herbivore or pathogen susceptibility (Jactel, Brockerhoff, & Duelli, 2005), though no obvious herbivores and pathogens were evident in our plots. Past studies have suggested that mortality in monocultures is species-specific and thus our monoculture treatment cannot be generalized beyond *F. brayleyana* (Forrester, Bauhus, & Khanna, 2004). Results for this species are important, however, as *F. brayleyana* is commonly used in low-diversity timber plantations and more diverse restoration plantings.

## 5 | CONCLUSIONS

Restoration projects can be expensive and labour-intensive, with no real guarantee of success. This situation is further impeded by the lack of large-scale, controlled studies of seedling performance in diverse types of restoration projects. Our study demonstrates that seedling survival is influenced by both biological and landscape factors, some of which are persistent, while others are transient. In particular, we show that planted species and sites (context, slope, aspect) can be carefully selected to maximize early-stage seedling establishment, and to reduce the probability of delayed forest recovery. We found no evidence that planting large numbers of species (24) improved seedling

survival rates early in planting establishment, despite higher diversity being advantageous in later successional stages and being an increasingly common approach to restoration plantings in Australia's tropics (and further afield). Our results also suggest that to maximize seedling survival in the first few years post planting, it is important to use experienced planters, use a high proportion of species with high not low wood densities (or species known to be robust to local planting conditions), and where possible, select restoration sites adjacent to existing forest patches. Though this experiment took place in Australia's wet tropics, many of our findings are likely applicable to other tropical systems, given that our results were robust across a diversity of tropical tree families. Understanding the temporal shift in the influence of species and site selection on seedling establishment can aid in the development of targeted management strategies both before and post planting to maximize restoration success.

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## AUTHORS' CONTRIBUTIONS

M.M.M. conceived and designed the research. L.S.C., T.J.S. and S.C. collected data. L.S.C., J.M.D., P.M. and M.M.M. analysed data. L.S.C. and M.M.M. led the manuscript writing with substantial contributions from J.M.D. and input from P.M., S.C. and T.J.S. All authors approved final publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.t1rv6> (Charles et al., 2017).

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