RESEARCH ARTICLE

Look to seedling heights, rather than functional traits, to explain survival during extreme heat stress in the early stages of subtropical rainforest restoration

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Abstract

1. Ecological restoration is urgently needed to arrest and reverse land degradation, reinstate ecosystem services and recover threatened species. Tree planting is a commonly used strategy to restore forests; however, planted seedlings often experience low survival and slow growth during the establishment period. Critical evaluation of factors that lead to poor establishment is vital to improve practice but is often constrained by a lack of monitoring and reporting.

2. We took advantage of a large monitoring dataset (~7,000 native trees from 23 species) to interrogate an extensive suite of environmental conditions and plant characteristics that potentially contributed to poor survival and growth of seedlings in a restoration planting in southeast Queensland, Australia.

3. The initial height of planted seedlings strongly influenced survival and growth. Intermediate heights generally performed best and the optimal heights for different species were significantly but weakly modulated by functional traits including SLA, lamina area and leaf structure (compound vs. simple). Survival was lowest when seedlings were planted in high bulk density soils on hot days, and growth was fastest in plots with higher average elevation.

4. *Synthesis and applications.* In this large restoration experiment in Australia's subtropics, initial seedling height was a much stronger predictor of rainforest seedling survival than plant functional traits. We recommend planting rainforest seedlings between 25 and 35 cm tall, especially in restoration projects facing a high likelihood of hot weather during planting and establishment.

KEYWORDS
bulk density, land degradation, pasture, restoration, revegetation, riparian, tubestock

1 | INTRODUCTION

The global need for ecological restoration is highlighted by the United Nations' recent declaration of a decade of Ecosystem Restoration from 2021 to 2030 and other high-profile international agreements. In Australia, the Federal Government recently invested $42.65 million to plant 13.4 million trees by the year 2020 (Australian Government Department of the Environment & Energy,

2015) as part of the national strategy to prevent further loss of biodiversity (National Biodiversity Strategy Review Task Group, 2010). Such large investments make it crucial that restoration projects be cost-effective and achieve desired goals. Even if a project falls short of meeting goals, some amount of restored vegetation is likely to provide substantial ecological benefits compared to no intervention (Wortley, Hero, & Howes, 2013). A variety of factors can prevent projects from achieving their restoration goals (Rieger, Stanley, &

Traynor, 2014; Suding, 2011). Projects that aim to restore ecosystems to 'pristine' conditions can be infeasible from the outset if they ignore fundamental environmental changes that have occurred at a site (Hobbs, 2007). Changes in soil physical and chemical properties, and regional climate, can make the original state unattainable (Hobbs, Higgs, & Harris, 2009). Environmental conditions during and following restoration intervention will also influence project success (Hobbs, 2007). The aims and procedures of a project must therefore account for such challenges if the project is to succeed.

The establishment period is a critical bottleneck during restoration due to a range of biotic and abiotic stressors. Fast-growing grasses and forbs can suppress planted seedlings during initial phases (Cordell, Ostertag, Michaud, & Warman, 2016; Funk & Wolf, 2016; Suding, 2011) and herbivory can further reduce survival (Averett, Wisdom, Naylor, Rowland, & Endress, 2017; Davis et al., 2016; Opperman & Merenlender, 2000). Seedlings are especially vulnerable to extreme weather during planting and subsequent establishment periods (Hallett, Standish, Jonson, & Hobbs, 2014). For example, heat stress, drought (Martínez-Garza, Tobón, Campo, & Howe, 2011) and floods (Meli, Benayas, Ramos, & Carabias, 2015) can reduce survival substantially during these periods. Soil conditions can exacerbate the effects of extreme weather as well as having direct negative effects on seedlings establishment. For example, soil compaction can impede water infiltration and stunt root growth (Bassett, Simcock, & Mitchell, 2005; Willatt & Pullar, 1983).

The influence of environmental conditions on seedling survival also depends on characteristics of individual plants and species. Smaller seedlings typically have less developed root systems with lower capacity for water and nutrient uptake, and thus often exhibit reduced survival and growth under drought conditions (Close & Davidson, 2003; Martínez-Garza et al., 2011). Regardless of seedling size, species are known to differ substantially in their survival and growth rates. These differences should be captured, at least in part, by carefully selected functional traits, which are measureable attributes of plants that determine how they acquire and compete for resources and tolerate stressful conditions (McGill, Enquist, Weiher, & Westoby, 2006). Resource-acquisitive species rapidly acquire and use resources, and therefore exhibit fast growth but are susceptible to unfavourable weather such as droughts. More conservative species can tolerate certain stressors, but trade this tolerance for slower growth (Anderegg & HilleRisLambers, 2016).

This study focuses on the short-term outcomes of a restoration experiment embedded within a larger project that aimed to restore a corridor of riparian rainforest in Southeast Queensland, Australia. The experiment was designed to examine the trade-off in growth versus stress tolerance over the short term and long term, and hence species were selected to span a spectrum of functional strategies. The experiment was replicated across 1.5 km of formerly grazed alluvial floodplain that encompasses considerable variation in soil physical and chemical properties and micro-topography. In addition, planting took place over a 2-week period and temperatures on some days were well above average. Given this experimental design and abiotic context, this study asks the following questions:

1. How do temperature (on the day of planting) and soil variation influence early plant survival and growth during subtropical rainforest restoration?
2. How do the characteristics of individual plants and species influence early plant survival and growth during subtropical rainforest restoration?

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is in the inner southern suburbs of Brisbane, Queensland, Australia and is known locally as Oxley Creek Common (27°32′S 152°59′E, Figure S1). It is situated on an alluvial floodplain along a section of Oxley Creek, approximately 2 km from its confluence with the Brisbane River to the north. Rainfall averages 1,058 mm/year and is typically summer dominant with extended dry periods in late winter and early spring (July–September). Mean daily minimum and daily maximum temperatures are 14.4°C and 26.4°C, respectively (station number 40,211; Australian Bureau of Meteorology, 2017). Oxley Creek Common comprises infrequently inundated pasture and parklands on dermosols. Prior to European settlement, the areas adjacent to Oxley Creek most likely supported gallery notophyll vine forest (Regional Ecosystem 12.3.1; Queensland Herbarium, 2018). While the region receives less rainfall than is typically used to define rainforest in the tropics, this type of vegetation is commonly referred to as riparian subtropical rainforest in Australia.

Established in November 2016, the experiment was embedded within a larger project funded by the Australian Government's National Landcare Programme '20 Million Trees Round II'. Overall, the experiment aimed to test whether the long-term cost-effectiveness of forest restoration could be improved by designing planting mixes based on the functional traits of plants.

2.2 | Experimental design

2.2.1 | Species selection

A 'trait targets' approach (Laughlin, 2014) was used to generate two experimental assemblages with distinct trait profiles: a *fast* assemblage comprising more resource-acquisitive species, and a *hardy* assemblage comprising species with more conservative strategies (see Appendix S1). Each assemblage had 16 species and similar species evenness. *Fast* and *Hardy* assemblages each had eight species unique to them and the remaining eight were common to both assemblages, resulting in a total of 24 species. One species (*Jagera pseudorhus*) could not be sourced in time for planting, leaving 23 species in the present study (Table S1).

2.2.2 | Planting layout

The areas available for planting were mainly confined to a 50 m wide strip of alluvial floodplain (Figure S1) that was previously managed

as beef cattle pasture. To capture environmental variation across the site, and variation between grazing units (paddocks), a randomized block design that included 10 blocks distributed along the entire extent of the available planting area was implemented. Each block contained two plots to which the two mixes were randomly assigned. Each plot was 30 × 30 m with 400 trees planted in a grid at 1.5 m spacing. Paddocks containing plots were first fenced to exclude livestock, slashed approximately 2 months prior to planting and then sprayed with glyphosate 2–4 weeks prior to planting to suppress excessive grass and forb growth, as is standard restoration practice in the region.

Plants were sourced in 50 mm tubestock from a number of local nurseries but varied considerably in size within and among species (from 5 to 65 cm shoot heights, mean = 22 cm). The 400 plants per plot were pre-randomized at a separate location in the days before planting. Planting was undertaken between the 31st of October and 18th of November, 2016 at the beginning of the typical spring–summer growing season. Holes were pre-dug using motorized augers and a handful of water crystals were placed in the bottom of each hole at the time of planting and mixed with soil. Each plant was watered-in within an hour of planting. Supplementary watering was provided 1–2 times a week until mid-January 2017. Individual plants in each plot were mapped and their heights measured within 2 weeks of planting.

2.3 | Data collection

The survival of all plants was assessed 3.5 months after planting. Plants were considered dead if they had no visible living leaves, tips or shoots. The height of living plants was measured as the vertical distance from the ground to the live central apex. The exact number of days between planting and monitoring was recorded for each plot and used to calculate daily growth rates.

2.4 | Measuring environmental covariates

Maximum temperatures on the day of planting were obtained for each plot (Australian Bureau of Meteorology, 2017) to provide a measure of initial heat stress. Four soil samples were collected from each plot (one in the centre of each plot quarter) at a depth of 2–10 cm, making a total of 80 samples. Samples were passed through a 2-mm sieve and sent to the UQ Soil Analysis Laboratory to measure total ammonium and nitrate, plant-available phosphorus and potassium, as well as soil pH and electrical conductivity. Soil cores were taken immediately adjacent to sample locations to measure bulk density and gravimetric water content (GWC). This was undertaken during a dry period from the 4th of June to the 7th of June when the site had not received rainfall for over 2 weeks. Bulk density rings were 8.5 cm deep, with a radius of 6.5 cm, and were 'trimmed' so that the surface of soil was flush with the ring. Soil cores were weighed immediately in the field. Soil cores were then oven-dried for 48 hr at 105°C before being re-weighed. Bulk density (g/cm^3) was calculated as the mass of oven-dried soil divided by the volume of the soil at field condition, while the GWC was calculated as the weight of water in the core sample at field condition, divided by the dried soil weight (g/g).

A LiDAR-derived topographical raster was queried to estimate the elevation of individual plants (Source: QLD Government Remote Sensing Centre, Department of Science, Information Technology and Innovation). Plots were located on the raster using GPS points taken at each plot corner. Individual plant elevations were then extracted in using each plant's grid location within plots. From these data, we created two elevation variables. To capture plot-level variation in elevation, we calculated the mean elevation of plants in each plot. We also subtracted the plot-level minimum from each plant's elevation to describe the relative elevation of plants within plots (i.e. whether plants were on mounds or depressions).

2.5 | Seedling functional traits

Leaf, stem and root traits were measured on well-watered, sun-hardened seedlings of each species. Five replicate seedlings were sampled, except for three species that had four replicate seedlings. Three new, fully expanded leaves were selected from each seedling for measurement of SLA, leaf dry matter content (LDMC) and lamina area. Leaves with obvious herbivore or pathogen damage were avoided. After being cut from the stem, leaves were immediately weighed and scanned. The one-sided leaf area (mm^2) was obtained using ImageJ software, version 2.0.0 (Schneider, Rasband, & Eliceiri, 2012). Area and mass measurements of all leaves included petioles (simple leaves) or petiolules (compound leaves). Leaves were oven-dried at 60°C for 72 hr before being reweighed to obtain the leaf dry mass. SLA was calculated as the one-sided leaf area divided by the leaf dry mass (mm^2/mg), and LDMC as the oven dry mass divided by fresh leaf mass (mg/g).

Wood density was calculated as dry mass of wood per unit of volume (mg/mm^3). One wood sample was cut from the base of each seedling (average stem sample diameter of approximately 4 mm). Secondary phloem and bark were removed before volume was determined via water displacement (Perez-Harguindeguy et al., 2013). Wood samples were oven-dried at 105°C for 72 hr and then retained at room temperature for 1–2 min before weighing. Total root length and root volume were measured from fresh, washed root material, which was scanned for each seedling and analysed using WinRhizo image analysis software (Regent Instruments Inc.). Following a preliminary root wash, small samples of the finest living roots in each root system were selected and further washed in deionized water. All effort was made to select absorptive roots; however, some samples may have included structural or transport roots. Roots were scanned at 720 dpi using an EPSON Expression 11000XL LA2500 scanner (EPSON). Based on the estimated mean root diameter for each scanned sample, the overall mean (across species) was 0.3 mm, and species' means ranged from 0.193 for *Melaleuca bracteata* to 0.505 mm for *Toona ciliata*. Roots were then oven-dried at 60°C for 48 hr before weighing to obtain their dry mass. Specific root length (SRL) was calculated as root length divided by the root dry mass

(m/g) and root tissue density (RTD) was calculated as root dry mass divided by fresh root volume (mg/mm³).

Traits that were positively skewed were log-transformed (SLA and SRL) or square-root-transformed (lamina area) prior to analyses.

2.6 | Preliminary analyses of explanatory variables

Separate principal components analyses (PCA) were conducted on soil variables and seedling functional traits to assess correlations between variables. The first three components of the soil PCA explained 79% of the measured variation. Soil PC1 (41%) was negatively loaded by pH, and positively loaded by electrical conductance, phosphorus and nitrate, while the soil PC2 (23%) was positively loaded by ammonium and negatively loaded by potassium (Figure S2 and Table S2). Lastly, soil PC3 (15%) was negatively loaded by bulk density and positively loaded by gravimetric water content. The two elevation variables (mean plot elevation and relative elevation) were not included in the soil PCA because they did not directly describe physical or chemical properties of the soil.

The first three components of the functional trait PCA explained 83% of the variation in the seven measured functional traits. Trait PC1 (52%) described overall seedling economics and was positively loaded by log-transformed SLA and log-transformed SRL, and negatively loaded by LDMC, RTD and WD (Figure 1; Table S2). Trait PC2 (18%) was negatively loaded by square-root-transformed lamina area and positively loaded by leaf structure (compound = 1, simple = 0) and trait PC3 (13%) was positively loaded by leaf structure and square-root-transformed lamina area. Given the very strong correlations among the five 'economic' traits involved with trait PC1 (all Pearson correlations >0.5 or <−0.5), and strong contributions of the two remaining traits to the other axes, we chose to include only log-transformed SLA, square-root-transformed lamina area and leaf structure in subsequent statistical models to aid interpretation of results and to facilitate comparison with other trait-based studies. While square-root-transformed lamina area and leaf structure loaded on the same PC axes, their Pearson correlation was only −0.27.

2.7 | Statistical models of survival and height growth

Plant performance was measured as the probability of surviving to 3.5 months, and the height growth increments of surviving plants. Survival (1 = alive, 0 = dead) was modelled using a generalized linear mixed-effect model (GLMM) with binomial errors and logit link function. Random effects were included to account for the spatial nesting of plants within plots, plots within blocks and blocks within paddocks. Species was included as an additional random effect to account for the fact that members of the same species are likely to respond more similarly to each other than members of different groups.

The survival model included both environmental and plant-related variables as fixed effects. Environmental variables included
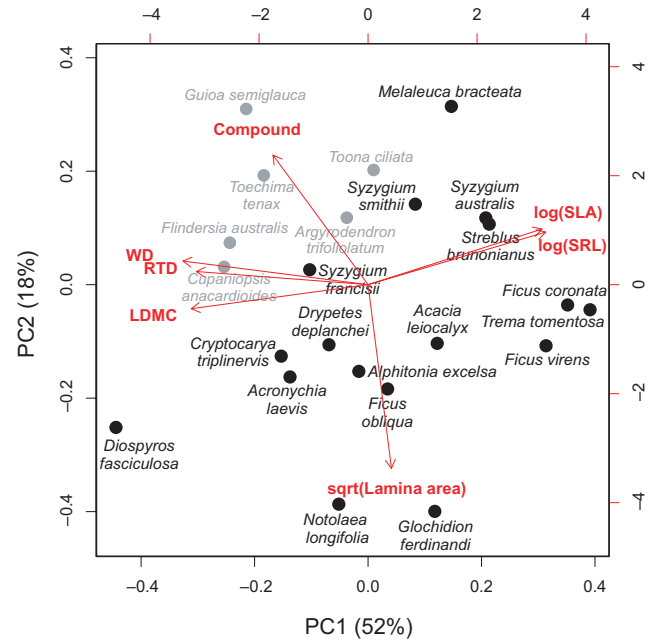

FIGURE 1 Biplot of the principal component analysis conducted on the seven functional traits measured on all study species. The first two principal components are plotted showing the location of each species and the arrows for each trait indicating the loadings. Species with simple leaves are shown in black and those with compound leaves are shown in grey. Refer to Table S2 for detailed loadings

the maximum temperature on the day of planting (herein maximum temperature), the plot-scale average elevation, the relative elevation of each stem within plots and the first and third soil principal components. We did not include soil PC2 because it was strongly correlated with plot-level mean elevation. We also included two-way interactions between maximum temperature and the soil and elevation variables to allow temperature effects on survival to vary depending on soil characteristics or the elevation of seedlings. The plant-related variables included the initial height of seedlings and the three selected functional traits, log-transformed SLA, square-root-transformed lamina area and leaf structure (compound = 1, simple = 0). Seedling height was square-root-transformed to reduce the influence of occasional very tall seedlings. We also included a quadratic term for seedling height because exploratory plots indicated that height–survival relationships were not necessarily monotonic. Thus, we included square-root-transformed seedling height and seedling height to fit the quadratic relationship. Two-way interactions between seedling height (linear and quadratic terms) and trait variables were included to allow species' traits to modulate the shape of the height–survival relationships for each species. We also included random slopes for species with respect to seedling height (linear and quadratic terms).

Height growth of surviving seedlings was calculated as $(\text{height}_{t_{1i}} - \text{height}_{t_{0i}})/(t_{1i} - t_{0i})$ and expressed as cm/day, where t_{0i} was the date that seedling i was initially mapped and measured and t_{1i} is the date that seedling i was re-measured. Plants that were leaning
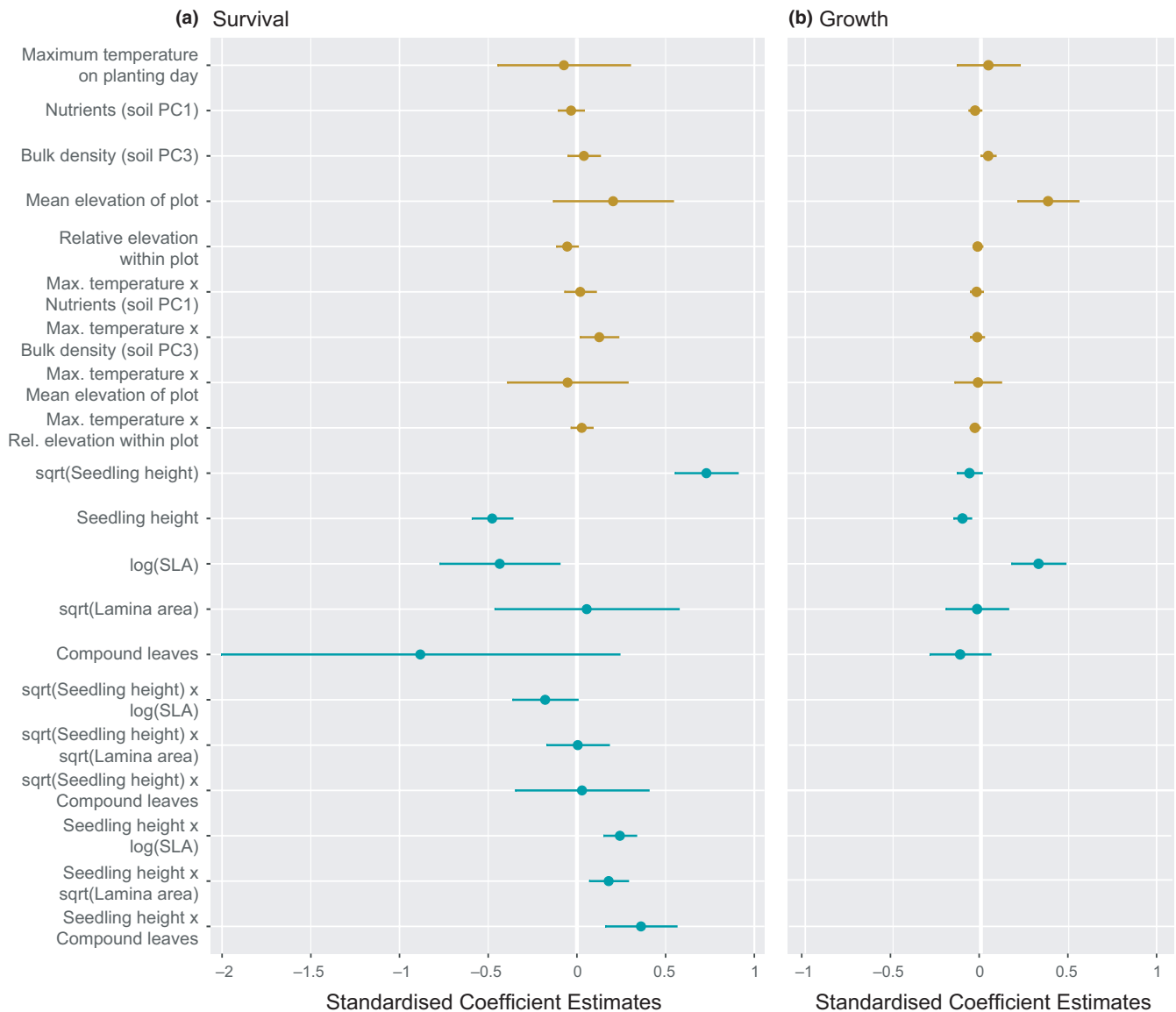
FIGURE 2 Coefficient plots for (a) the binomial GLMM of survival and (b) the LMM of square-root-transformed height growth rates (cm/day). Points are standardized coefficient estimates and bars are associated 95% confidence intervals. Terms with bars not overlapping zero can be interpreted as statistically significant. Points and bars in gold indicate terms involving environmental variables (soil and weather variables) and points and bars in green indicate terms associated with plant characteristics (initial seedling height and trait variables)

over, had their tops snapped or died back were excluded from the growth analysis. Any remaining negative daily height increment values were also excluded. As such, the growth model examines the performance of seedlings that survived and experienced positive growth. Height growth was square-root-transformed to approximate a normal distribution and modelled using a linear mixed-effects model (LMM). The growth model included the same fixed and random effects as the survival model, with the exception of two-way interactions between seedling height (linear and quadratic terms) and trait variables.

All statistical analyses were undertaken in R 3.2.0 (R Development Core Team, 2017). The survival GLMM and growth LMM were fitted using the glmer and lmer functions, respectively, from the lme4 package (Bates, Mächler, Bolker, & Walker, 2015).

3 | RESULTS

The overall probability of surviving the first 3.5 months was 0.45. The *Hardy* mix had a slightly higher overall probability of survival (0.46) than the *Fast* mix (0.42), but this difference was not significant when assessed in a simple binomial GLMM ($p = .063$). Individual species survival probabilities ranged from 0.11 (*Toona ciliata* and *Toechima tenax*) to 0.87 (*Acacia leiocalyx*), while growth rates ranged from 0.02 (*Toechima tenax*) to 0.45 cm/day (*Acacia leiocalyx*; Table S1).

3.1 | Survival

The survival model had a marginal R^2 of 0.13 (deviance explained by fixed effects alone), indicating that the fixed effects explained
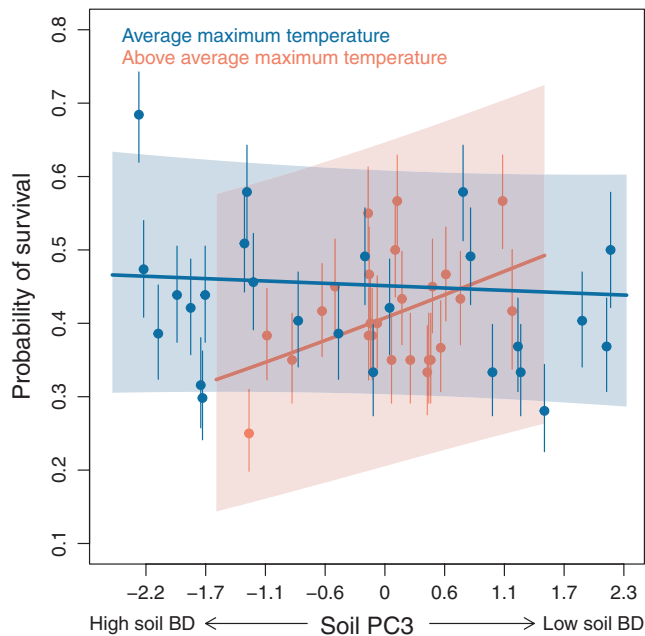
FIGURE 3 Plot from the survival model showing the interaction between soil PC3 (bulk density) and the maximum temperature on the day of planting. Soil PC3 is plotted against the probability of survival, with separate fitted lines (and associated 95% confidence intervals) for planting days with average maximum temperatures (29.5°C) and those with above average temperatures (32.5°C). The underlying points and standard error bars shown for each relationship were calculated from 25 bins of observed binary data

relatively small amounts of variation in survival. The only significant term involving environmental variables in the survival model was the interaction between maximum temperature and soil PC3 (Figure 2a). This interaction indicated that the probability of survival for seedlings planted in compact soils was lower when they were planted on hot days (Figure 3). We found a strong overall hump-shaped (concave quadratic) relationship between the initial height of seedlings and the probability of survival (Figure 2a), and the shape of this relationship was modulated to some extent by functional traits. In particular, interactions between each trait and the quadratic height term were all significant. For species with simple leaves, hump-shaped curves were narrowest for low SLA, small-leaved species and broadest for high SLA, large-leaved species (Figure 4). For species with compound leaves, curves tended to be boarder and have taller optimal heights. To assess how well

these fixed-effect relationships matched observed height–survival relationships for each species, we fitted a simple GLMM to each species separately and only included a quadratic height term if it was significant. When modelled separately, only 8 of the 23 species had significant quadratic terms, while most of the remaining species had positive monotonic relationships (Figure 4). Furthermore, the conditional R^2 (representing deviance explained by both fixed and random effects) was 0.41, much higher than the marginal R^2. And as such, height–survival relationships fitted using species-specific random effects matched the observed data much more closely than those using fixed effects (Figure 4).

3.2 | Growth

The marginal R^2 of the growth model was 0.27 (around double that of the survival model despite having fewer terms) and the conditional R^2 was 0.57. The mean elevation of plots was significantly and positively related to height growth (Figure 2b). The interaction between maximum temperature (on planting day) and relative elevation was also significant. This interaction indicated that growth was slower for seedlings planted on hot days, especially if they were planted in high positions within plots, compared to lower positions.

Initial seedling height and log-transformed SLA also significantly influenced height growth (Figure 2b). Acquisitive species predictably had faster growth than conservative species, but no other trait variable was related to growth. The relationship for seedling height was again quadratic, indicating that seedlings with intermediate initial heights grew faster than smaller and larger seedlings.

4 | DISCUSSION

Suboptimal outcomes are common in restoration (Hobbs, 2007; Suding, 2011), but are rarely critically evaluated using empirical data or within the context of a randomized experimental design to reveal barriers impeding restoration. We found that survival and growth of planted seedlings were influenced by planting day temperature and soil properties, and depended on initial seedling height and species. In particular, the overall relationship between initial height and survival was hump-shaped, indicating optimal seedling heights between 25 and 35 cm (for the purpose of surviving hot planting conditions). Species varied in the shape of their height–survival relationships and

FIGURE 4 Fitted relationships between the probability of survival and the initial seeding height (cm) for each of the 23 species examined in this study. Species are located approximately in trait space formed by log-transformed SLA (x-axis) and square-root-transformed lamina area (y-axis) for species with simple leaves (a) and compound leaves (b). Orange curves are predictions from the full survival model using the trait values of each species and fixed-effect model coefficients. All other explanatory variables were held at their mean values when plotting these 'trait-based' predictions. Red curves are species-specific predictions from the full survival model using the trait values of each species and each species' random-effect coefficients. Black curves are relationships fitted to each species separately in simpler GLMMs with square root (initial seedling height) as the sole fixed effect, unless the quadratic height term was significant in which case the quadratic was fitted (as indicated by *). Grey points are observed binary data that have been jittered to show trends. Black points and standard error bars were calculated from seven bins of observed binary data to indicate how the raw data fit each relationship. The solid portions of curves indicate the limits of observed seedling heights for each study species. The grey envelope shows the 25–35 cm height range. The number of observations used for each species is included in parentheses

(a) Species with simple leaves
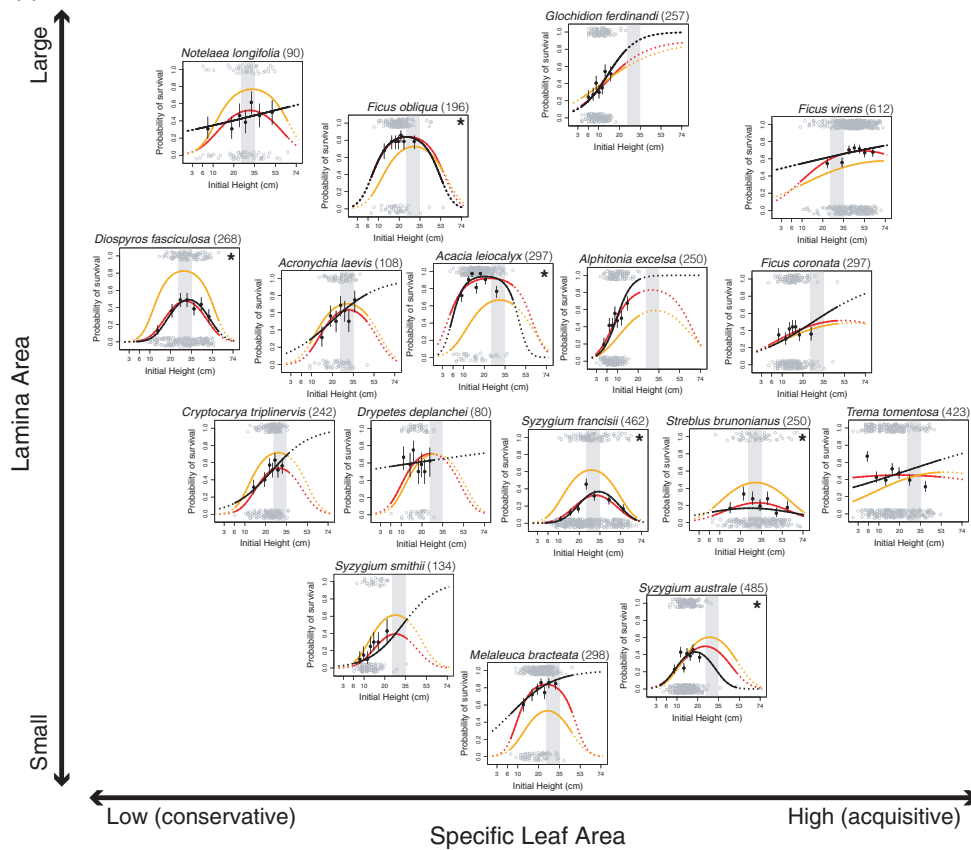
(b) Species with compound leaves
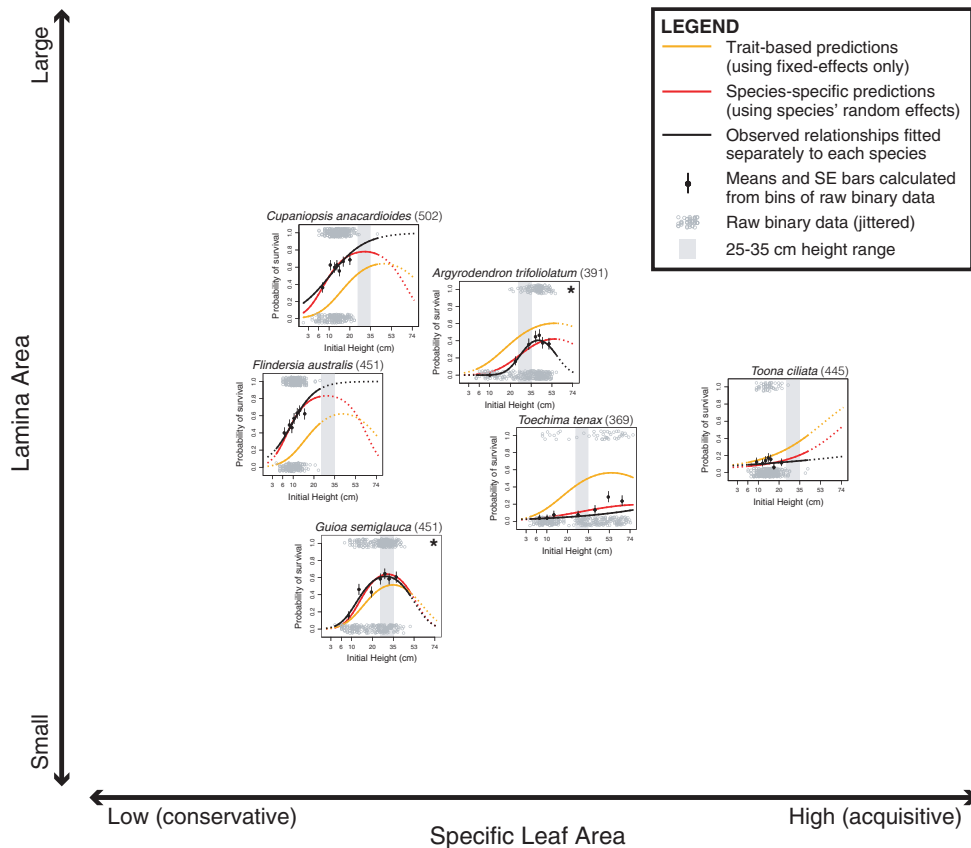
some of this variation was explained by three easy-to-measure functional traits. Growth was predictably faster for species with acquisitive seedling leaf economics. Environmental variables had significant but weaker effects on survival and growth than seedling heights.

4.1 | How does environmental variation influence plant survival and growth during subtropical rainforest restoration?

The influence of soil bulk density and micro-topography on early plant performance has been highlighted in previous restoration studies (Cheesman, Preece, Oosterzee, Erskine, & Cernusak, 2018; Douterlungne et al., 2015; Martínez-Garza, Campo, Ricker, & Tobón, 2016; Martínez-Garza et al., 2011). The survival of seedlings in high bulk density soils is likely reduced because compaction can physically restrict root growth (Bassett et al., 2005; Skinner, Lunt, Spooner, & McIntyre, 2009), reduce water infiltration and retention (Chyba, Kroulík, Krištof, Misiewicz, & Chaney, 2014; Ekwue & Harrilal, 2010) and, consequently, limit plant available water (Archer & Smith, 1972). Similarly, seedlings planted on mounds may have reduced water availability as water moves to depressions, a process that is likely exacerbated on high bulk density soils due to reduced infiltration (Ekwue & Harrilal, 2010). It is also well understood that temperature can directly influence the growth and survival of seedlings (Baumber et al., 2017; Close & Davidson, 2003; Dordel, Seely, & Simard, 2011). Importantly, however, effects of these variables might also emerge through interactions.

In this study, the effect of hot planting days on survival depended on soil bulk density. While seedlings were watered multiple times immediately following planting, compact soils could have reduced the ability of seedlings to respond to acute heat stress. It is also possible that the combination of heat and compact soils resulted in shallower planting due to planter fatigue, which would have exposed seedling surface roots to extreme temperatures. Previous studies have identified planter effects, often relating reduced growth or survival to a lack of planting experience (Charles et al., 2018; Close & Davidson, 2003; Vogt, Watkins, Mincey, Patterson, & Fischer, 2015). While planting effects may be possible in our study, we did not record information on planter experience nor changes in planting quality and so cannot explore these factors further.

The growth of surviving seedlings was significantly slower in lower lying plots, most likely due to temporary waterlogging and associated reductions in water absorption, transpiration and growth rates compared to plants in more elevated plots (Delgado, Zúñiga-Feest, & Piper, 2018).

4.2 | How do the characteristics of individual plants and species influence plant survival and growth during subtropical rainforest restoration?

Seedling attributes are well understood to influence initial growth and survival in revegetation settings (Grossnickle, 2012). Many studies have reported that initial seedling height positively correlates with survival and growth of seedlings. Poor performance of small seedlings is generally attributed to the disturbance of root systems during planting (Close & Davidson, 2003; Martínez-Garza, Bongers, & Poorter, 2013) or suppression by recolonizing weeds (Cordell et al., 2016; Douterlungne et al., 2015). Instead of the increasing monotonic relationships between seedling height and survival reported in other studies (e.g. Kabrick, Knapp, Dey, & Larsen, 2015), we found strong support for an overall hump-shaped relationship (Figures 2a and 4), strongly suggesting intermediate 'optimal' seedling heights for surviving extreme planting temperatures. The reduced survival and growth of larger seedlings may, in part, be due to stock being pot-bound, as 'root circling' in pots reduces anchorage as well as nutrient and water uptake (Allen, Harper, Bayer, & Brazee, 2017; South, Harrisa, Barnett, Hainds, & Gjerstad, 2005). Given that all plants were supplied in 50 mm planting tubes, larger seedlings probably also had lower root:shoot ratios, and thus a reduced capacity to supply water to transpiring foliage under stressful, open pasture situations (Close, Beadle, & Brown, 2005; Grossnickle, 2012).

It should be noted that only eight of the 23 species had significant quadratic height–survival relationships when modelled alone. The strong quadratic relationship in the overall survival model occurred because many species with apparently monotonic relationships only included seedlings that spanned the lower half of the height range. When all species were modelled in a single GLMM, information was borrowed from species that spanned the full height range (the effect of partial pooling in multi-level models; Gelman & Hill, 2007), including a number of species with strong hump-shaped relationships. While it would have been ideal for all species to span a similar height range, sharing of information across species during model fitting provided conservative estimates of optimal heights for all species.

Significant interactions between trait variables and initial seedling heights explained species' differences in optimal seedling heights to some extent. Low SLA species had a narrower range of predicted optimal heights than those with high SLA, as did species with simple leaves compared to those with compound leaves. However, the result for compound leaves was influenced by two species with very low survival probabilities (*Toona ciliata* and *Toechima tenax*; Figure 4) and weakened when these species were removed (not shown). In general, trait effects on optimal heights were small in absolute terms, and most species were predicted to have highest survival with initial shoot heights between 25 and 35 cm tall.

Interestingly, species with more conservative traits did not consistently have high survival in this study. This is counter to reported trait-vital rate relationships in natural systems (Anderegg & HilleRisLambers, 2016; Markesteijn, Poorter, Bongers, Paz, & Sack, 2011) and a recent trait-based restoration study in the Australian tropics reporting a positive relationship between seedling survival and wood density (Charles et al., 2018). It is possible that seedling mortality due to planting stress, mishandling or a decline in planting quality (as previously discussed) could have obscured trait–survival relationships. More consistent with theoretical and empirical expectations (Shipley, Vile, Garnier, Wright, &

Poorter, 2005), the growth of surviving seedlings was strongly and positively related to SLA. Thus, once seedlings overcome stresses associated with planting, commonly measured functional traits such as SLA are effective at predicting species' performance in restoration settings, especially if traits are measured on seedlings instead of adult plants (Gibert, Gray, Westoby, Wright, & Falster, 2016).

4.3 | Implications for restoration

This study identified the antagonistic effects of planting in compact soils on hot days, as well as the importance of planting seedlings at optimum sizes (25–35 cm tall) to increase survival during the establishment period. Clearly, planting should be avoided on days with high maximum temperatures. However, it is also recognized that forecasts can be uncertain for the lead-times required to make planning decisions, and the ability to modify decisions upon new information can be limited (Hobday, Spillman, Eveson, & Hartog, 2016). For example, if planting is delayed due to extreme conditions, it may not be possible for nurseries to hold stock for long periods, and it may be difficult to reschedule planting or maintenance teams. Even if stock can be held, seedlings will likely develop taller shoots and thus be more susceptible to transplant shock when eventually planted. Due to the complexity of coordinating projects, and with record-breaking temperatures predicted to occur more frequently in Australia (CSIRO & Bureau of Meteorology, 2015) and elsewhere, it is reasonable to believe that many future restoration projects will experience similar conditions to those presented here. This highlights the need to either make better use of evidence-based strategies that improve planting success when environmental conditions are highly uncertain or develop implementation strategies that enable necessary flexibility to delay restoration projects when adverse environmental conditions arise (Hagger, Dwyer, Shoo, & Wilson, 2018).

AUTHORS' CONTRIBUTIONS

L.S. and J.M.D. designed the experiment, supervised its implementation and collected baseline mapping and plant height data. R.G. conducted all remaining fieldwork with support from L.S. and J.M.D. R.G. and J.M.D. analysed the data. R.G. wrote the first draft of the manuscript with input from L.S. and J.M.D. J.M.D. revised the manuscript for journal submission.

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SUPPORTING INFORMATION

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