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Drivers of planted seedling survival and growth in a Mediterranean-climate woodland restoration experiment

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Abstract

Introduction: The restoration of degraded ecosystems is an important means of promoting and conserving biodiversity. However, restoration projects on average fail to reach target biodiversity levels within the time frames they are studied. Competition from non-native groundlayer grasses and forbs, potential facilitative effects of plant–plant interactions, and species-specific responses to these processes are all thought to be important in determining outcomes of tree and shrub-based restoration.
Objective: To quantify the effects of initial seedling height, herbicide application, nitrogen addition, starting soil conditions, soil depth (using distance to exposed bedrock as a proxy), and plot species richness on the survival and growth of seedlings in an experimental restoration project.
Methods: The survival and growth of over 11,000 individual trees and shrubs consisting of eight different species were measured over a 12-year period.
Results: We found that herbicide application had a lasting negative signature on the survival of plants and a positive effect on growth. In contrast, nitrogen addition had no significant effect on plant survival and growth. Larger seedling size was correlated with increased survival and growth more than 10 years after planting; however, these responses were species-specific. Importantly, approximately 50% of seedlings died over the 12-year monitoring period, and this mortality was concentrated in *Hakea lissocarpha*, *Banskia sessilis*, *Eucalyptus astringens*, and *Callistemon phoeniceus*.
Conclusion: Standard management practices such as weed control can have unintended consequences for plant survival. Initial seedling height strongly predicts survival and growth more than a decade after planting, meaning future restoration outcomes may be predicted based on early measurements.
Implications for Practice: The unexpected legacy effects of herbicide on planted seedling survival highlight the need for caution when integrating weed control in restoration programs and suggest that a staged restoration approach with spraying limited to before planting may be warranted. Species-specific failure rates highlight poorly performing species that could be the focus of more targeted research to avoid inadvertently homogenizing restored plant communities by focusing only on the "winners." Without understanding why some species consistently fail, restoration programs risk being unable to recover the full functional and compositional diversity of degraded ecosystems.

Key words: Acacia, basal area, biodiversity-ecosystem function, Eucalyptus, mortality, oldfield, soil fertility

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Introduction

Ecological restoration is an important means of promoting biodiversity and ecosystem functions in degraded areas (Benayas et al. 2009). However, on average, terrestrial restoration projects fail to reach the biodiversity levels of reference ecosystems, and outcomes are highly variable (Jones et al. 2018; Atkinson et al. 2022b). Despite recognition of these shortfalls, restoration projects are often only monitored over short time frames (Freudenberger 2018; Lindenmayer & Likens 2018), and most studies are observational rather than experimental, limiting researchers' ability to attribute causality (Shackelford et al. 2021). Furthermore, monitoring at the scale of individual plants tends to be lacking, which is problematic as this is the scale at which the interactive consequences of abiotic and biotic factors for survival and growth are realized (Coulson 2020). Here, we use a long-term restoration experiment, including monitoring of individual plants, to test some putative drivers of plant survival and growth in woodland restoration in southwest Western Australia.

Seedling size at planting is widely documented as a strong predictor of early survival and growth in restoration plantings, with larger seedlings often showing higher survival and growth (Gardiner et al. 2019; Atkinson et al. 2022*a*). Meta-analytical evidence across 86 species and 142 planting sites shows that planting larger seedlings consistently increases early survival in forest restoration worldwide, though the magnitude of this effect can vary with aridity and species traits (Andivia et al. 2021). Larger seedlings have also been shown to be more resistant to drought in plantings (Close & Davidson 2003; Martínez-Garza et al. 2013). Together, this evidence underscores the importance of seedling size as an important consideration for both restoration planning and when investigating survival and growth, while also highlighting that other variables such as environmental conditions can modulate these patterns.

Competition from a dense and persistent ground layer of vegetation (e.g. grasses and forbs) is often cited as hindering the establishment of tree and shrub seedlings in forests (Royo & Carson 2006) and abandoned agricultural land (Dorrough & Moxham 2005; Standish et al. 2007; Cramer et al. 2008; Royo & Carson 2008). Elevated levels of N and P can promote the growth of competitive ground layer plants therefore creating strong competition for light for native plantings (Dorrough & Moxham 2005). High levels of these nutrients can also lead to toxicity for some plant taxa (Lambers et al. 2015). More widely, airborne nitrogen deposition is considered a major threat to biodiversity globally due to its effects on competitive dynamics (Schoukens 2017; Stevens et al. 2018). While observational survey studies and experiments relating to elevated soil nutrients, especially from airborne pollution, are common across mature habitats (Maes et al. 2019; Bobbink et al. 2022; Weldon et al. 2022; Sanczuk et al. 2024), they are a rarity in partially restored woodland and forest studies. Control of competitive ground layer plants for restoration using herbicides is common to reduce the impact of competition on plant establishment in restoration (e.g. Hallett et al. 2014; Radford-Smith et al. 2021; Atkinson et al. 2022a), though is rarely done experimentally. Where weed control positively affects seedling success, the effect can be small. For example, just an 8% increase in probability of establishment success was observed for species in drylands in an international synthesis (Shackelford et al. 2021). In some cases, herbicide application intended to control competition and aid the survival and growth of planted species can cause inadvertent mortality through unintended exposure (Radford-Smith et al. 2021). To date, in a restoration context there has been few simultaneous manipulations of weed competition and elevated soil nutrients under field conditions (though see Cole et al. 2021; Wilson & Gerry 1995).

Many landscape variables differ considerably within and between restoration projects, and these can also strongly impact the survival and growth of species in the restored plant community (Hillerislambers et al. 2012). While the landscape characteristics of many restoration sites are difficult or costly to manipulate (e.g. slope, aspect, and soil depth), the choice of where to plant seedlings within a varied landscape is relatively easy to incorporate into planning. For example, in some systems, shallower soils are related to drought mortality and height restriction in trees (Pracilio et al. 2006; Harper et al. 2009), suggesting plantings should generally target deeper soils. Therefore, soil characteristics relating to soil depth and moisture and resources may be important in understanding the survival bottlenecks and eventual growth of plantings. In our experiment, we expect that competition for water will play an important role in limiting seedling establishment owing to the summer drought typical of the Mediterranean climate, as will competition from ground layer grasses and forbs as outlined above.

Species richness in restoration plantings can reshape the competitive landscape experienced by individual seedlings, with cascading effects on survival and growth. Increasing the planted biodiversity of restoration projects is also often cited as potentially realizing greater benefits from restoration activities (Wright et al. 2009; Derhé et al. 2016; Andres et al. 2023), such as greater carbon sequestration and resilience to disturbance (Brancalion et al. 2017; Jochum et al. 2020; Standish & Prober 2020; Strassburg et al. 2020). A range of evidence suggests more diverse forests can be equally or even more productive than monocultures (Forrester & Bauhus 2016; Huang et al. 2018; Messier et al. 2022). Higher species richness may promote establishment through complementary resource use (Tilman et al. 1997; Loreau & Hector 2001), and through nurse plant effects (the latter is particularly relevant in arid systems; Callaway 1995; Padilla & Pugnaire 2006; Blondeel et al. 2024). Altering the species composition of planting should in theory be relatively straightforward, at least on a small scale (although can be constrained by seedling supply; Andres et al. 2024). Therefore, understanding how species richness of plantings shapes restoration outcomes is of high relevance to practice.

To fill the gap in our knowledge of the drivers of survival and growth of plants in restoration, we surveyed the effects of initial seedling height, herbicide application, nitrogen addition, starting soil conditions, soil depth (using distance to exposed bedrock as a proxy), and plot species richness on the survival and growth of trees and shrubs in a restoration planting in an experimental restoration project in Western Australia (Perring et al. 2012). We hypothesized that:

H1: Variation in native plant survival and growth is explained by seedling height at the beginning of the experiment, with larger seedlings having greater survival and growth.

H2: Native planted seedlings will have lower survival and growth under nitrogen addition treatments compared to control conditions, likely due to increased competition with ground layer species.

H3: Native planted seedlings will have higher survival and growth in herbicide treatments compared to controls due to decreased competition with non-native ground layer species.

H4: Nitrogen addition and herbicide treatments will have interactive effects, where positive effects of herbicide on seedling survival and growth are stronger under a high nutrient setting where uncontrolled ground layer species would reduce survival and growth.

H5: Native planted seedlings in plots with higher local soil nutrients will have lower survival and growth, and this effect will be due to increased competition (as in H2).

H6: Native planted seedlings in plots close to rocky outcrops will have lower survival and growth, likely due to shallower soils and resultant reduced access to soil water.

H7: Native planted seedlings will have higher survival and growth in plantings with higher species richness, likely due to resource use partitioning and reduced intraspecific competition.

Methods

Site and Experiment

The experiment was conducted at the Ridgefield Ecosystem Services Experiment, a biodiversity-ecosystem function restoration experiment in the fragmented agricultural landscape of southwestern Australia (at 32°29′S and 116°58′E) (Perring et al. 2012). The Ridgefield Ecosystem Services Experiment was designed to test diversity effects on multiple ecosystem services including carbon sequestration, biotic resistance to non-native invasion, nutrient cycling, soil erosion control, biodiversity maintenance, and pollination. The site was formerly used for agriculture including cropping and grazing until the beginning of the experiment in 2010. Ridgefield experiences a Mediterranean-type climate with the nearby long-term weather station at Pingelly recording a mean (1970–2025) January temperature of 32°C and an August mean temperature of 16°C, with winter-dominant rainfall and an annual average of 443 mm (Bureau of Meteorology 2026).

Nine plant assemblages of 110 individuals in each plot were replicated across 10 blocks, with two of those plant assemblages replicated across a further eight blocks. Each plot (approximately 530 m^2) constituted 11 planting lines, on contour, just over 2 m apart; see Fig. S1 for an example layout of a four species plot. Treatments were separated across two land use history types, grazing and cropping, which upon soil testing at the beginning of the experiment were shown to be different across a range of important soil structural and nutrient properties (Fig. S2; Perring et al. 2012). In the grazed area, treatments include a control (bare ground), a monoculture of *Eucalyptus loxophleba* subsp. *loxophleba* (Myrtaceae), and seven mixed plantings. Mixed treatments combined *E. loxophleba* with *E. astringens* (Myrtaceae), *Acacia acuminata* and *A. microbotrya* (Fabaceae), *Callistemon phoeniceus* and *Calothamnus quadrifidus* (Myrtaceae), and *Hakea lissocarpha* and *Banksia sessilis* (Proteaceae). These species were combined into treatments of 2, 4, 6, and 8-species mixes, with all treatment combinations including *E. loxophleba*, a keystone species of remnant vegetation in the region. In the cropped area, only control plots, monoculture plots, and 8-species mixes were included due to the limited area to ensure sufficient replication (Fig. S1).

In total, there were 10 blocks within the grazed area (90 plots excluding unplanted plots) and 8 blocks within the cropped area (16 plots excluding unplanted plots). Blocks within the two major land use histories were separated based on surface (0–10 cm) soil texture (ranging from loamy sand to light medium clays), soil moisture at the time of site preparation (ranging from 9 to 22%), and aspect (ranging from north facing, through west to south facing).

Nursery-grown seedlings of the eight species were planted on 14th–16th August 2010 in a restricted random design, to ensure the same treatment composition but not necessarily identical neighborhoods, thus avoiding hidden treatment effects (Huston 1997). Prior to planting, the entire site was sprayed with glyphosate to reduce weed biomass. Seedlings were approximately 8 months of age at planting. Subsequent checks of the planting ensured the accuracy of species identification, and thus the location and identities of all 11,660 planted individuals were known. In August 2011, any dead individuals were replaced with new plants to maintain desired species mixes.

Nitrogen deposition and weed control treatments were initiated randomly in a split–split plot design on 6 July 2011 (i.e. subplots were weed control only, nitrogen deposition only, weed control and nitrogen deposition combined, or no treatment; Fig. S1). Nitrogen was applied by hand as dry ammonium nitrate four times per year at the equivalent of 10 kg N ha^{-1} yr^{-1}, though was reduced from quarterly to triennially from 2017 to 2019. This rate was chosen to mimic atmospheric nitrogen deposition rates projected for the region in 2050 (Phoenix et al. 2006). The nitrogen deposition treatment stopped in 2019 (i.e. after 9 years of simulated nitrogen deposition). The herbicide treatment consisted of foliar spraying of non-native herbs and grasses two times per year. In winter and spring, subplots were treated with a mixture of Glyphosate 470, metsulfuron, pulse surfactant, and a red dye marker. Blanket spraying was required to control these weeds and consisted of 2–4 L of solution applied in each subplot depending on total weed cover (approximate application rate therefore 4–8 L/ha Glyphosate

470, 20–40 g/ha metsulfuron). Additionally, two spot-spray treatments were applied to control patches of summer-active weeds (e.g. *Citrullus amarus* Schrad.). The first in December 2012 using Triclopyr 600 (66 mL per 100 L) and the second in December 2014 using Glyphosate 470 (1.3 L per 100 L) and Garlon 600 (66 mL per 100 L). Per-subplot application rates varied for these latter spot-spraying treatments. The December 2014 treatment was the final herbicide application (i.e. after 4 years of weed control). Lastly, prior to planting, the entire site was sprayed with simazine and Glyphosate 470 at rates of 2 and 1 L/ha, respectively.

Field Measurements

Individuals were resurveyed in April 2022. Survival and diameter were measured for every living tree in each plot. Trees were measured at breast height, and multi-stemmed shrubs and small seedlings were measured approximately 10 cm from the ground (DBH and d10, respectively). We then converted all measurements to basal area to account for multiple-stemmed individuals, which were common in the mallee-form eucalypt and the shrubs.

For analysis, we excluded all individuals in the first and last planting lines, and individuals in positions 1 and 10 on all remaining planting lines to avoid edge effects. Individuals on the sixth planting line were treated as the edge between split plot treatments and these individuals were also excluded from analyses (see Fig. S1). Many of the large *E. loxophleba* trees had resprouted from epicormic buds in the intervening period since establishment. These resprouted individuals were recorded as alive but noted as having resprouted, and any living stems were measured.

Principal Components of Soil

We measured baseline soil variables of each plot in August 2010, including pH, electrical conductivity, carbon, nitrogen, phosphorus, sulfur, and exchangeable aluminum, calcium, magnesium, potassium, and sodium to capture the starting soil conditions faced by seedlings (Perring et al. 2012). We reduced these 11 variables to two dimensions using principal components analysis, with the two main axes explaining 59.1% of the variation in the data. PC1 was positively loaded by carbon, nitrogen, phosphorus, conductivity, calcium, potassium, and sodium, which we consider primarily a soil fertility axis (Fig. S2). PC2 was negatively loaded by soil pH and magnesium and positively loaded by aluminum and sulfur, which we interpret as a soil acidity and chemical stress gradient. In addition to direct measurements of soil properties, we used the distance of each tree to the nearest rocky outcrops as a proxy for soil depth, based on the assumption that proximity to rocky outcrops is associated with shallower soils (DPRID 2026). At the plot level, we took direct measurements of soil depth and moisture. We found the distance to rocky outcrops was correlated with soil depth with an r^2 of 0.54.

Data Analysis

To examine factors influencing plant survival, we fitted a binomial mixed-effects model using "*glmmTMB*" (Brooks et al. 2024), including fixed effects for initial seedling height (2011 height) interacting with species (H1), the main and interactive effects of herbicide and nitrogen treatments (H2–H4), soil PCA axes 1 and 2 (H5), distance to rocky outcrops (H6), and planted species richness (H7). We used a binomial model for modeling survival as our response was dead (0) or alive (1). We included random intercepts for plots nested within blocks to account for similarity in environments faced by species in close proximity. We ran an identically structured linear mixed model to test the effects of these variables on growth, measured as log-transformed basal area. We excluded both *B. sessilis* and *H. lissocarpha* from our main models due to the high mortality which prevented robust estimation of their survival and growth relationships. We ran the models including these species to ensure this did not change any of the main or interactive effects (Tables S2 & S3). All continuous variables were mean centered for both models.

We fitted an identically structured Gaussian spatial mixed model to predict survival and growth using the same fixed and random effect structure using "*spaMM*." This approach used a spatially structured random field with a Matérn covariance function based on individual coordinates in universal transverse mercator (meters). We found limited evidence for spatial autocorrelation using spatial mixed-effects models. The estimated range parameter ρ, which describes the point at which spatial autocorrelation becomes negligible, was 0.02 m for survival and 0.48 m for growth. As both were well under 1 m, we interpret this as strong evidence there is no strong spatial autocorrelation detected using this method. A subsample of 10,000 samples from the distance matrix used in these models is shown in Figure S3, and given these negligible effects, we present the non-spatial glmmTMB mixed models described above in the results.

In a post hoc analysis, we tested the sensitivity of our results to an additional term in the growth model of the plot-level density of surviving individuals in 2022 as a coarse proxy of potential plot-level density effects. We did not do the same for survival as these metrics were intrinsically confounded.

All analyses were conducted using R v. 4.5.1 (R Core Team 2020).

Results

Over the period 2010–2022, 5594 out of 11,660 individuals were recorded as dead. A large number of living individuals (1492) had resprouted (Fig. 1). Resprouting was almost entirely concentrated within *Eucalyptus loxophleba*, with approximately 25% of individuals total having resprouted after dieback (Fig. 1). *Banksia sessilis* (Proteaceae), *Hakea lissocarpha* (Proteaceae), and *E. astringens* (Myrtaceae) all experienced very high rates of mortality whereas *Acacia acuminata* (Fabaceae) and *Callistemon phoeniceus* (Myrtaceae) showed the highest rates of survival.

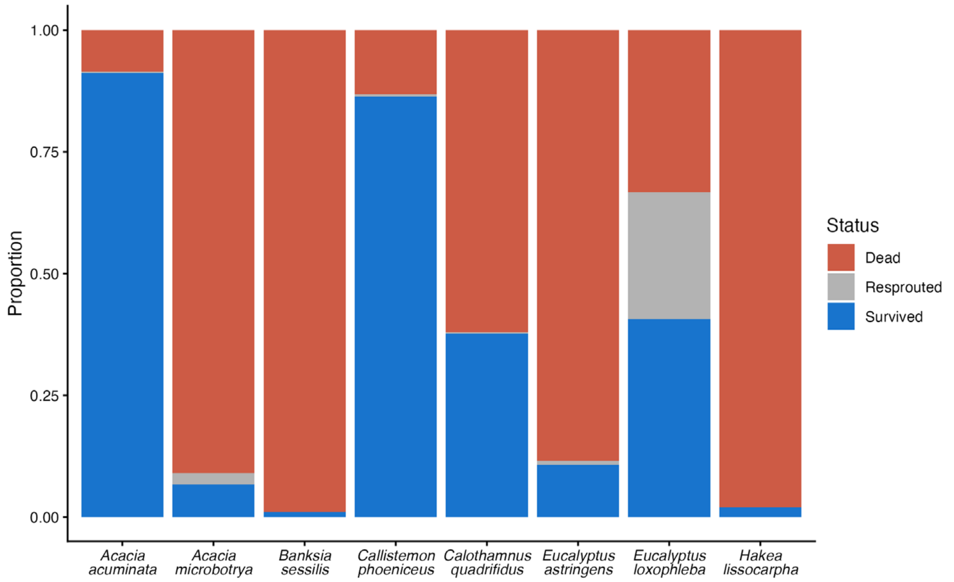

Figure 1. Each species' overall mortality and survival by 2022, including the number that had dead main stems but had resprouted from basal, epicormic, or underground buds.

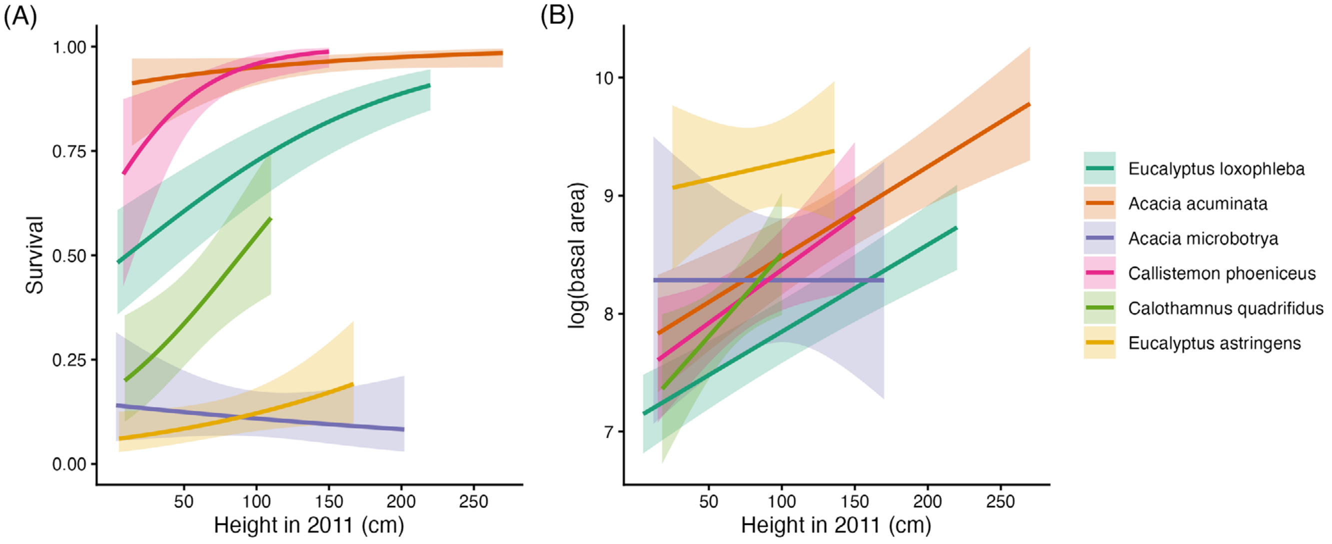

Figure 2. Relationship between individual height during the first census in 2011 and survival (A) and growth (B) for each species in 2022. Shaded envelopes show 95% CIs. We excluded *Banksia sessilis* and *Hakea lissocarpha* from these models due to high mortality resulting in mostly zeroes for the model of survival and very few basal area measurements for the growth model. Comparison models of six and all eight species are in Tables S3 and S4.

Consistent with our first hypothesis, the strongest predictor of survival was initial seedling height, with a strongly positive relationship (odds ratios [OR]: 1.55; 95% CI: 1.38–1.74, $p \leq 0.001$). This corresponds to roughly 60% higher odds of survival for seedlings one standard deviation larger in height at planting. In addition, initial seedling height was a good predictor of growth (Est: 0.30, CI: 0.21–0.38, $p \leq 0.001$), with one standard deviation increase in height equating to, on average, 35% greater basal area in mature trees and shrubs.

However, the general relationship between size and both survival and growth was highly variable among species in line with our expectation (H1; Fig. 2). Interestingly, we found that for both *Acacia* species, seedling height was not strongly linked to survival, either high survival in *A. acuminata* or low survival in *A. microbotrya* (Table S2). Equally, in Eucalyptus and the two Myrtaceous shrubs, we found a strong size–survival relationship, but again with overall very different survival curves (Table S2; Fig. 2A). Growth, on the other hand, followed a roughly similar relationship across species, with a positive relationship between starting seedling height and basal area growth to 2022, with the exception of *A. microbotrya*, which showed a flat relationship (Fig. 2B).

Counter to our second hypothesis, we found no evidence for a lasting effect of 9 years of regular nitrogen addition on survival or growth (OR: 1.06, CI: 0.88–1.28, $p = 0.56$; Est 0.00, CI: −0.13 to 0.12, $p = 0.96$; Figs. 3A & 4A).

Counter to our third hypothesis, native plants in herbicide plots had 24% lower odds of survival than did native plants in plots without herbicide (OR: 0.75, CI: 0.63–0.91, $p = 0.003$; Fig. 3B). However, consistent with our third hypothesis, herbicide had a positive effect on growth (Est 0.24, CI: 0.12–0.37, $p \leq 0.001$; Fig. 4B), with about 5% higher growth under herbicide treatments. Interestingly, we found no evidence for an interactive effect of nitrogen and herbicide on either growth or survival (H4; Tables S2 & S3).

The only detected relationship with soil conditions was soil PC2 positively interacting with growth (H5; Est = 0.08, CI = 0.02–0.14, $p = 0.005$; Fig. 4D), though this effect was small and associated with high variability. Consistent with H6, we found a positive effect of the distance to rocky outcrops on individual survival (OR: 1.42, CI: 1.12–1.79, $p = 0.006$; Fig. 3E). However, we found no relationship between distance to rocky outcrops and growth (Est = 0.06, CI = −0.05 to 0.16, $p = 0.28$; Fig. 4E).

Lastly, we found no strong relationship between planted species richness and survival (OR: 0.88, CI: 0.75–1.03, $p = 0.108$; Fig. 3F) but a positive effect on growth (Est 0.14, CI: 0.04–0.25, $p = 0.006$; Fig. 4F), partially supporting H7.

The survival model had a marginal r^2 of 0.43 and a conditional r^2 of 0.52, indicating that the included terms explained a considerable proportion of the variation in survival, noting that

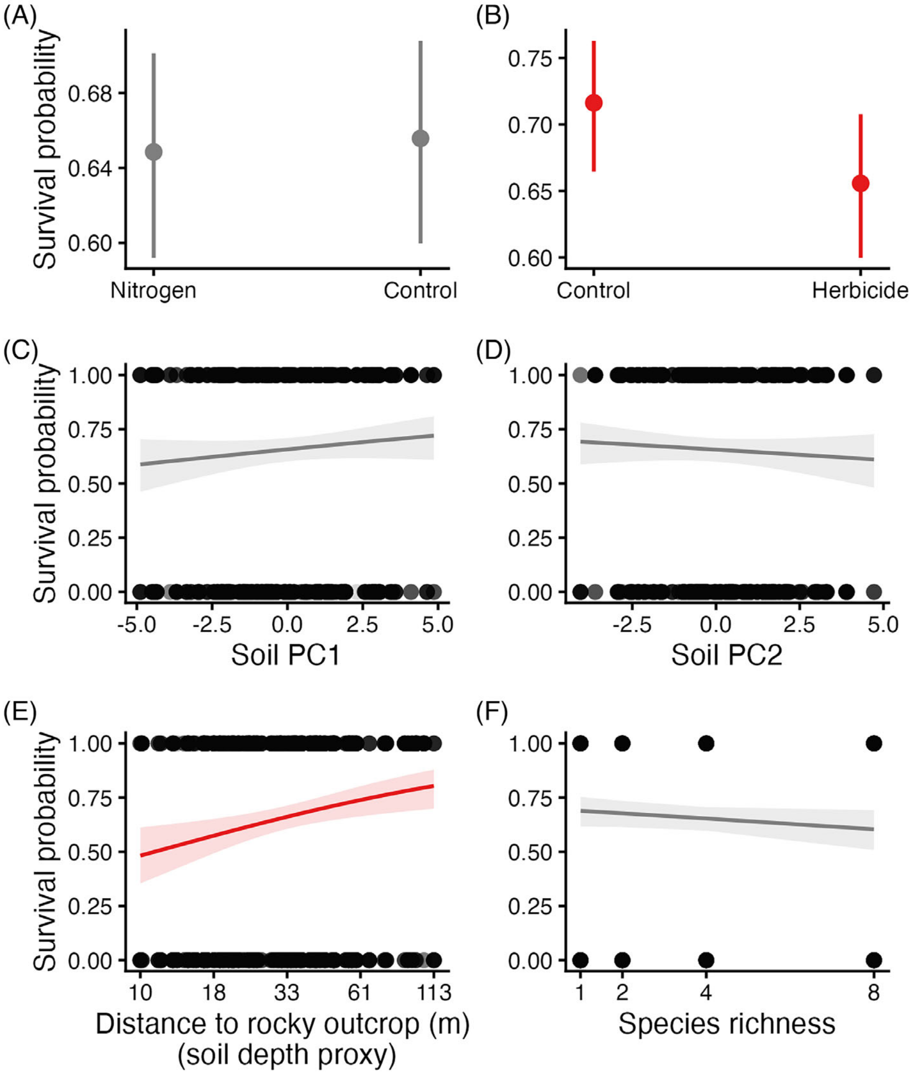

Figure 3. Predicted survival probabilities from the six-species model. Plots show the effect of (A) nitrogen addition, (B) herbicide application, (C) soil PC1, (D) soil PC2, (E) distance to rocky outcrop (soil depth proxy), and (F) species richness. Raw data points are overlaid with transparency to aid visualization. Non-significant predictors are denoted using gray point estimates or gray regression lines.

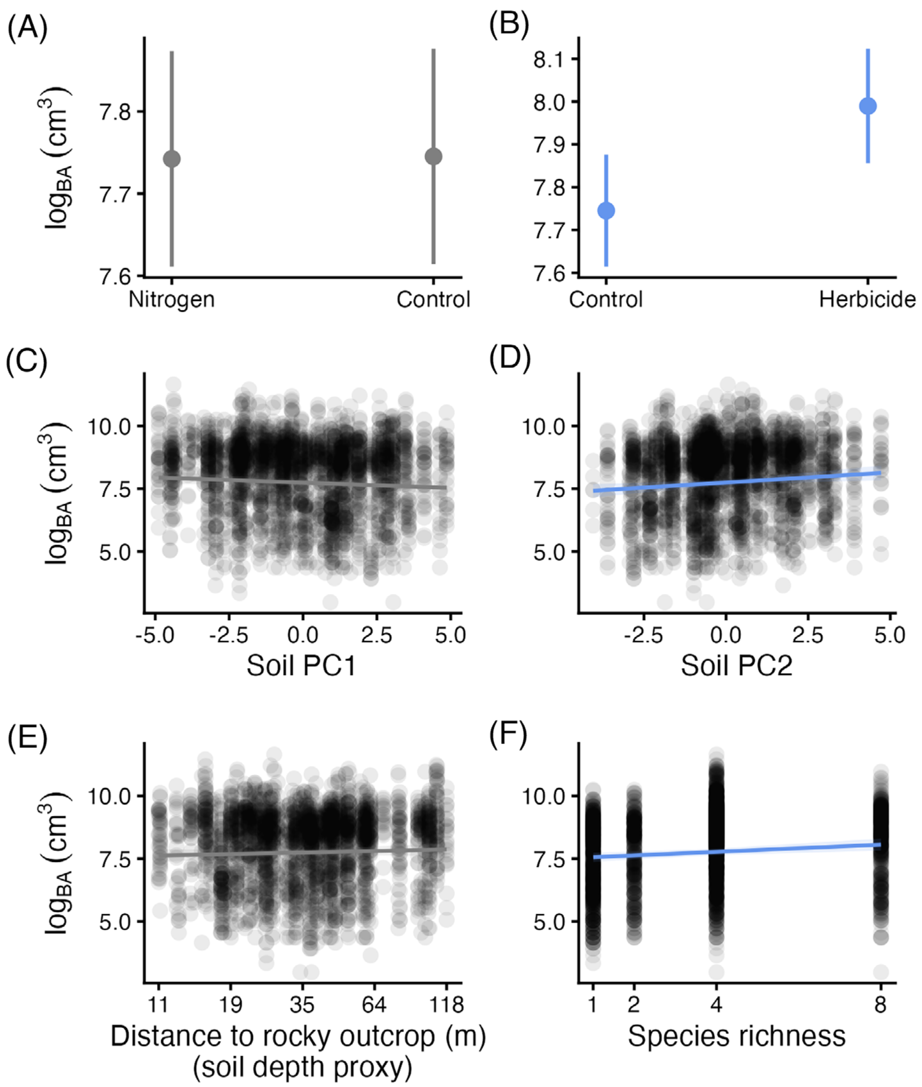

Figure 4. Predicted growth, measured as log-transformed basal area (log[BA] cm^3) in 2022, from the six-species model. Panels show the effect of (A) nitrogen addition, (B) herbicide application, (C) soil PC1, (D) soil PC2, (E) distance to rocky outcrop (soil depth proxy), and (F) species richness. Raw data points are overlaid with transparency to aid visualization. Non-significant predictors are denoted using gray point estimates or gray regression lines.

we included a fixed effect for species in our model specification. The growth model had a marginal r^2 of 0.16 and a conditional r^2 of 0.26, indicating the weaker predictive capacity of these same variables for growth.

In response to the post hoc analysis of the relationship between plot-level plant survivorship and growth, we found no relationship between the density of individuals in plots in 2022 and the growth of individual plants, and no change to the significance or not of other variables (Table S4).

Discussion

Twelve years into a tree and shrub restoration experiment, we found that the size of planted individuals (after 1 year of field growth or replants) was an important factor in explaining individual survival and growth, supporting our first hypothesis. Annual herbicide application in the first 4 years had a negative impact on plant survival but a positive effect on growth. Nitrogen addition for 9 years did not affect growth or survival, and local variation in soil conditions was not strongly related to either survival or growth, except for the distance of individuals to rock outcrops. Our results highlight that long-term experiments can reveal how some management techniques with good intentions (e.g. weed control) can have perverse outcomes, and that a stronger understanding of the species-level biology of valued species for restoration is needed to better improve their performance.

Our finding that height just 1 year after planting is a good predictor of survival 12 years later aligns with the results of restoration experiments in other biomes and on other continents (Martínez-Garza et al. 2013; Tsakaldimi et al. 2013; Anton et al. 2015; Gardiner et al. 2019; Atkinson et al. 2022a).

Species-specific responses to survival, however, did not obviously relate to the size of the species, with congeners with similar characteristics such as height and life form showing mixed responses. For example, the tall growing *Eucalyptus* species showed both low, size-agnostic survival, and high, size-specific survival, the same being true of *Acacia* species and the two Myrteaceous shrub species *Callistemon phoeniceus* and *Calothamnus quadrifidus*. This result has practical management implications, including that optimizing seedling size at planting might be a means of ensuring the survival of target species. Interestingly, however, we found that this positive interaction was not consistent among all species, with a weaker relationship between size and growth in the species experiencing the most mortality. Non-positive relationships were only evident in species that had suffered extremely high mortality.

Herbicide application was positively related to growth and negatively related to survival, albeit moderately, suggesting either that it promotes growth among seedlings by reducing competition with ground layer weeds or simply that inadvertent mortality to a subset of seedlings from spraying reduces overall competition between juvenile seedlings. Spraying of weeds at the time of planting or seeding has long been considered to have benefits to restoration outcomes (Ashby 1997), but our results support recent research that found unintended negative effects of herbicide use for grass control on woody plant survival in restoration (Radford-Smith et al. 2021). In addition, a recent global synthesis found limited effects of herbicide application on plant establishment in global dryland restoration (Shackelford et al. 2021). Our data suggest a staged approach to restoration (Bakker et al. 2018) may benefit seedling establishment where possible whereby herbicides are applied before planting to control weeds and blanket spraying after planting is minimal or avoided altogether.

We expected that nitrogen addition would increase weed competition, but that herbicide would cancel that effect. However, we found no evidence to support either hypothesis. The added nitrogen may have been rapidly utilized by relatively dense non-native ground layer grasses (though less likely in the herbicide plots) or preferentially absorbed by the dominant *Eucalyptus* species which are known to deplete soil N (Mallen-Cooper et al. 2022). In addition, given we intended to mimic atmospheric N deposition, our overall rate of fertilization was low compared to some nutrient addition experiments (e.g. the Nutrient Network applies N at a 10 times higher rate; Borer et al. 2014). This may explain why the N fertilization treatment had no effect on survival and growth. In addition, soil N was already relatively high across plots. More surprising was that underlying soil fertility, as reflected by PC1, did not appear to relate to survival or growth of native seedlings. This finding was unexpected given the particularly low levels of soil P in south-west Western Australia, where this study was conducted (Viscarra Rossel & Bui 2016) and since high soil phosphorus is often cited as a negative pressure on native plants in Western Australia (Lambers et al. 2015).

It is possible that baseline soil measurements from the start of the experiment do not fully reflect soil conditions later in the study due to temporal change. However, we used these initial values because they characterize the conditions experienced during the earliest stages of restoration. Baseline soil properties are most relevant for understanding early size-survival and size-growth relationships, which is when we expected to be the most influential for shaping the longer term outcomes of plantings. Understanding how surface soil properties have changed since planting may be important for further investigations on the development of ecosystem services underpinned by survival and growth of planted individuals.

Anecdotally, we observed limited seedling recruitment of planted species in the plots, whether from seedbank or planted species reaching reproductive maturity. This may in part reflect the legacy of agriculture at the site as elsewhere in the wheatbelt region, where native seedbanks are depleted and elevated soil nutrient levels persist (Parkhurst et al. 2021). However, it should also be noted that some recruits were removed early in the experiment (until 2014) in an effort to maintain the experimental mixes. Nonetheless, the evidence suggests little recruitment has taken place since this time. Evidence from other mixed *Acacia* and *Eucalyptus* restoration plantings suggests recruitment could be rare, even in the longer term (Atkinson et al. 2022a, 2023). Recruitment and replacement of individuals in restored eucalypt woodlands remains an important issue for ongoing restoration efforts.

Planted species richness was positively associated with tree and shrub growth. However, whether this is an effect of complementarity or simply a byproduct of decreased density-dependent competition is difficult to disentangle, as with the herbicide treatment effects. Nearly all *Hakea lissocarpha* and *Banksia sessilis* seedlings failed to establish, meaning that the surviving Myrtaceae and Fabaceae trees and shrubs had grown for 8 or 9 years under lower densities in these species' mixes compared with monoculture and other mixed stands. However, in our post hoc analysis, we found the density of individuals in plots surviving in 2022 was not related to growth and did not override the positive effects of species richness or herbicide. While this additional analysis attempted to unpack potential plot-level density dependence, analyses of neighborhood density and individual-level density dependence may reveal further insights into drivers of growth and mortality. Nonetheless, our results of varying species richness showed no apparent negative trade-off between survival or growth and some evidence of a small positive effect of diversity on growth. Therefore, our precautionary recommendation would be to diversify restoration plantings in these environments to promote growth—which our results show is tightly linked to long-term survival.

We interpret the positive relationship between distance to rocky outcrops and seedling survival as reflecting increased access to soil moisture in deeper soils away from rocky outcrops. The positive relationships between distance from exposed rocks with both soil depth and moisture have been shown elsewhere (Li et al. 2014), and our data on soil depth was correlated with this distance to rock outcrop. However, given the complexity of surface water flows, this warrants further investigation. This finding is particularly relevant given the drying trend in the region since the early 2000s, and especially over the last two decades (Mastrantonis & Bourne 2025), following a historically wetter-than-average twentieth century (O'Donnell et al. 2021). Plants in this study have therefore experienced water stress conditions well above the long-term regional average, highlighting the critical role that soil moisture and the region's hot dry summers play in determining the survival and growth of native woody species in restoration projects.

With nearly half of the planted seedlings lost over 12 years, our study has demonstrated a lasting legacy of herbicide applied in the 4 years after initial planting, alongside the roles of initial seedling height and spatial variation in environmental conditions in shaping plant survival and growth. While we were surprised by the limited role of soil fertility in shaping outcomes, it may have contributed to the early failure of two Proteaceous species to establish. It is highly plausible that in this ecosystem water limitation is more important than nutrient availability, obscuring soil fertility effects. Although labor intensive, precise restoration that accounts for species placement within the landscape and plant size may be an important means of improving individual survival and, therefore, restoration success. Our findings underscore the magnitude of effort required to restore native woody vegetation in Mediterranean-climate systems.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Average soil values, standard deviation and minimum and maximum values across all plots at the beginning of the experiment (July 2010).

Table S2. Comparison between survival models with *Banksia sessilis* and *Hakea lissocarpha* included and removed.

Table S3. Comparison between growth models with *Banksia sessilis* and *Hakea lissocarpha* included and removed.

Table S4. The six-species survival and growth models from Tables S2 and S3.

Figure S1. Location of the Ridgefield Multiple Ecosystem Services experiment within Australia (A), and the arrangement of plots and individuals (B).

Figure S2. Principal components 1 and 2 of a principal components analysis of soil variables.

Figure S3. Matérn correlation by distance for survival (a) and growth (b) models.

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