

UN DECADE ON ECOSYSTEM RESTORATION

Research Article

Plant size and neighbourhood characteristics influence survival and growth in a restored ex-agricultural ecosystem

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Abstract

1. Restoring woody vegetation on degraded agricultural land is a widespread and common ecological restoration practice. However, highly variable plant survival and growth limit outcomes for many projects. Inconsistent reporting and monitoring of projects mean that an assessment of the relative importance of community-assembly processes is limited, particularly over longer timescales.
2. We use 7 years of monitoring data of nearly 2000 native trees and shrubs in a restoration project on ex-agricultural land in south-western Australia to test the potential effects of facilitation or competition from neighbouring plants, as well as look for patterns in their interaction with the attributes of individuals and species traits.
3. Overall, plant size was the strongest single predictor of survival and incremental growth. Individual plants in neighbourhoods with higher inter-generic basal area were more likely to survive, with this effect strongest in smaller individuals. When plants were larger, they were less likely to grow when in neighbourhoods with high intra-generic basal area. Taller-growing plants (higher species maximum height) were more likely to survive when individuals were small (basal area of 1–10 cm²), compared with shorter growing plants. Growth was also more likely in taller-growing plants, and this relationship increased with the size of the individual. Recruitment was very low, with just 148 new recruits recorded across the 42 plots over 7 years.
4. Maximizing the growth of plants in restorations in the early stages may promote survival and growth in the longer term. We also demonstrate that increased levels of inter-generic neighbouring plants may improve individual plant survival in the restoration of ex-agricultural land. As a result, we suggest tailoring direct-seeding methods to minimize clustering of congeneric individuals. We also highlight the need to find means of promoting recruitment for the long-term sustainability of restoration efforts.

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KEYWORDS

biodiversity, community assembly, competition, demography, ecological restoration, facilitation, neighbourhood, oldfield restoration, recruitment, vital rates

1 | INTRODUCTION

Ecological restoration targets continue to rise as we enter what the United Nations has declared the 'Decade on Ecological Restoration' (Fagan et al., 2020; GPFLR, 2019). Linking ecological theory to restoration practice to maximize desired outcomes will be a vital component in meeting these targets (Lindenmayer, 2020). One barrier to effectively linking theory to practice is the lack of sufficient planning, preparation and on-going monitoring of ecological restoration projects, particularly those at the landscape scale (Freudenberger, 2018; Lindenmayer & Likens, 2018). Moreover, the importance of the spatial context of an individual plant for its performance is infrequently investigated (Perring, Standish, et al., 2015; though see Canham et al., 2006; Charles et al., 2018; Gómez-Aparicio, 2009; Ibáñez & Rodríguez, 2020), further widening this gap between theory and practice. By overlooking the interactions of individuals through time, our understanding of the importance of community assembly dynamics in restoration may be obstructed (Coulson, 2020).

The densities and composition of planted species are directly manipulated in restoration projects, thus understanding how survival and growth of individual plants may be maximized through different assemblages is a highly practical means of enhancing restoration outcomes. Further, deepening the understanding of key mechanisms driving community assembly remains at the forefront of ecology more broadly (Lasky et al., 2014). The species identity, density, proximity and the size of neighbouring plants are important in understanding interactions between individuals (Chen et al., 2019; Harms et al., 2000; Johnson et al., 2012; Potvin & Dutilleul, 2009). Ecological theory predicts that competition from intraspecific neighbours should be stronger than from interspecific neighbours (Adler et al., 2018). Indeed, results from ecological syntheses show that interspecific competition is generally weaker than intraspecific competition in plant communities (Adler et al., 2018), though the negative influence of intraspecific neighbours is not universal (Goldberg & Barton, 1992; Gurevitch et al., 1992; Lasky et al., 2014). In a restoration setting, facilitation by nurse plants (Castro et al., 2002, 2004; Padilla & Pugnaire, 2006; Ren et al., 2008) can be a significant process shaping community assembly—particularly for woody plants facing water stress (Brooker et al., 2008; Cramer et al., 2008; Gómez-Aparicio, 2009; Ibáñez & Rodríguez, 2020; Padilla & Pugnaire, 2006). This prediction of facilitation by nurse plants suggests that in stressful environments there are benefits to growing close to other plants, including increasing water and nutrient availability in the soil, protection from herbivory and physical protection from other damaging processes such as wind exposure (Padilla & Pugnaire, 2006; Stachowicz, 2001). However, the density of plants in direct-seeded restoration projects often far exceeds natural stem densities (Perring,

Jonson, et al., 2015), which may result in detrimental overcrowding (Dwyer & Mason, 2018). Beyond competition for light and water, the increased densities of closely related species may compound the prevalence of natural enemies (pathogens, herbivores), increasing mortality (Comita et al., 2014; Mangan et al., 2010). Therefore, there is clearly a risk that high densities of stems in restoration projects may negate any nurse plant benefit, particularly where neighbouring plants are closely related to the focal stem.

Attributes of individual seedlings can have a major influence on survival and growth in restoration projects (Andivia et al., 2021; Gardiner et al., 2019; Grossnickle, 2012). Planted seedlings of subtropical rainforest species with larger initial sizes were found to accrue larger increments of growth (Gardiner et al., 2019). Tuttle et al. (1988) found that larger seedlings survived at higher rates under non-adverse conditions, but under adverse conditions, an increase in seedling height had a negative effect of seedling survival. Additionally, demographic relationships between both functional traits and neighbourhood dynamics are likely to be size dependent (Prado-Junior et al., 2017). Incorporating size alongside key functional traits is crucial for accurate investigations of survival and growth (Falster et al., 2018), though until recently has been rarely tested empirically (Falster et al., 2018; Gibert et al., 2016).

Two key functional traits relating to early growth are a species' maximum attainable height ('maximum height') and seed mass (Falster & Westoby, 2005; Kunstler et al., 2016; Moles & Westoby, 2004). Shorter plants are thought to trade off maximum height for faster early-stage growth rates to compete with taller but slower growing plants, by growing and reaching reproductive maturity sooner (Falster & Westoby, 2005). Seedlings from larger seeds, through their increased energy store, experience higher survival (Moles & Westoby, 2004). In direct-seeding restoration projects such as in the present study, larger seeded species have been shown to have the highest establishment rates (Ceccon et al., 2016; Palma & Laurance, 2015). However, the influence of this competitive advantage beyond the establishment stage is less clear (Moles & Westoby, 2004). We incorporate these key traits to investigate their relevance to growth and survival in a restoration setting.

Understanding the influence of plant size, species-level traits and neighbouring plants on individual plant survival and growth in restorations will increase our capacity to deliver desired restoration outcomes. Such studies are rarely possible given the limited resources allocated to monitoring of restoration projects beyond initial establishment, meaning that tracking the fate and growth of the same individuals through time is not often logistically possible (Coulson, 2020; Lindenmayer & Likens, 2018). We use 7 years of monitoring of individual stems in a landscape-scale restoration of

ex-agricultural land in south-western Australia to address the following questions:

1. How do individual plant size, neighbourhood and species-level functional traits influence survival and growth during the restoration of woody vegetation on ex-agricultural land?
2. How are the influence of plant neighbourhood and maximum height on survival and growth modulated by the size of the individual plant?

2 | MATERIALS AND METHODS

2.1 | Study area

The study site is located approximately 16 km southwest of Jerramungup, Western Australia, between the Fitzgerald River National Park and Stirling Range National Park ($-34^{\circ} 4' 52.2''$ S, $118^{\circ} 51' 18.8''$ E). The area receives approximately 400 mm of annual rainfall, with an average temperature of approximately 16° C. The local reference community includes tall eucalypt mallee, mallee heath, open mallee heath, low eucalypt woodland and tall woodland systems (Perring, Jonson, et al., 2015).

The 250-ha restoration site was direct seeded in mid-2008 with a diversity of seed mixes based on seven reference woodland communities informed by a soil and landscape survey (Jonson, 2010). Therefore, species composition and amounts of species' seeds varied across the site according to soil type and landscape position. As the project was part of a carbon capture contract, to ensure adequate biomass accumulation, a single species, *Eucalyptus occidentalis*, was planted as tubestock at a density of 350 stems/ha. In our data set, *E. occidentalis* comprises 79 individuals, whereas the 12 other seeded species of *Eucalyptus* comprise 414 individuals (Appendix S1, Table S1).

Across the site, established seedling densities within the first 3 years ranged approximately 1500–4300 stems/ha (Jonson, 2010). Young seedlings at the site were monitored prior to the current study and were shown to face strong establishment bottlenecks in the first summer after seeding (2008/09; Hallett et al., 2014). At 5 years, across the eight major vegetation associations, seeded and planted species range from 23 to 49 species (median 25) (Perring, Jonson, et al., 2015). Ongoing monitoring occurred in 42 plots, either $10\text{ m} \times 14\text{ m}$ or $20\text{ m} \times 14\text{ m}$. Both plot sizes consisted of 10 seeded rows spaced approximately 1.4 m apart. The larger plots were intended to sample sufficient individuals in more sparsely established areas. All living and dead stems were initially measured in 2011 (Hallett et al., 2014) and living stems were then monitored annually from 2013 to 2018 either at 10 cm or 1.3 m above ground level. Stems were measured to the nearest mm in diameter using callipers. All stems were individually identified along fixed transects within each of 10 planted rows in each plot (Perring, Jonson, et al., 2015). All surveys were conducted with the permission of the land managers, Greening Australia.

Species maximum height was obtained for each species from the Western Australian online flora database 'FloraBase' (Western Aus-

tralian Herbarium, 2020). These values are averages for each species across the varying range of conditions in which they occur. Where maximum height estimates have two values (e.g. "2 m–10 m (–15 m)"), we took the lower more conservative estimate.

Seed mass was obtained from the Seed Information Database (Royal Botanic Gardens Kew, 2020) and, for the subset of species for which it was available, from a local native seed supplier. Where we could obtain data from both sources—20 of 54 total species—we included an average. Local and Kew SID database measurements were on average within 20% of each other. For a small number of species ($n = 8$) for which no data were available, we used a genus average seed mass. The distributions of both species seed mass and maximum height traits for the top five most abundant genera are included in Appendix S1 (Figure S1).

2.2 | Neighbourhood calculations

We summed the basal areas of the inter- and intra-generic stems surrounding each focal stem at multiple radii (1–5 m) using spatial point patterns constructed with the 'spatstat' R package (Baddeley et al., 2015, 2020). In the case of individuals with multiple stems, the basal area was calculated for each stem and then summed. This results in the same outcome as using the quadratic mean of multi-stemmed individuals (Curtis & Marshall, 2000) to then calculate area. We use basal area as a measure of neighbourhood conditions as it integrates both the number of neighbouring plants and their size. We hypothesized that neighbourhood interactions would be the accumulation of stressors over time; therefore, for survival analysis, neighbourhoods were averaged for each stem over the census period. Where the radius partially fell outside the plot, we estimated the missing portion of the neighbourhood as the average intra- and inter-generic values for the plot as a whole and added this proportionally to the unknown portion. We did not use a measure of distance decay in our calculations, as there is no generalizable assumption for the rate at which the effects of neighbours ought to decay, particularly across many species.

We chose to sum neighbourhood areas at the genus level to keep the analysis at a coarse level. That is, we expect that inter-generic differences between plants to be stronger than intra-generic (and therefore so too the differences in interactions). Further, the dominance of a few key genera in restoration plantings across Australia (*Eucalyptus*, *Acacia*, *Allocasuarina*, *Melaleuca*) means that this increases the capacity to generalize and broaden our findings across a wider range of ecosystems by considering the planting at this taxonomic level. Nonetheless, we also conduct the analysis at the species level, discuss any divergence from the genus-level neighbourhoods in effect and provide these comparisons in full in Appendix S3.

We limited the analyses to a 1 to 5 m radius due to the trade-off in data completeness and sample size. That is, with an increasing neighbourhood radii a larger proportion of the neighbourhood is unknown. We do not expect neighbourhood interactions to be approaching the larger ranges found in mature forests, given the restored site is still in early developmental stages. For instance, the average stem

diameter in the data set is 6 cm. Beyond a 5-m radius, the total percentage of the neighbourhood that would be required to be imputed from plot averages increases considerably (Appendix S1, Table S2). We chose to impute unknown neighbourhood portions rather than prune those stems from the data set in order to maximize the available sample size (see Appendix S1, Table S2 for loss in sample size with this approach). At 5 m, the average imputed portion of the neighbourhood is approximately 36%. However, we ran all models up to 10 m for comparison of any variation in the effects of variables but only include 1–5 m models in final model selection process (Appendix S2, Tables S1–S3). We also checked the sensitivity of our models to our method of neighbourhood imputation by re-running analysis with stems removed for which >50% of the neighbourhood was imputed. The results from these models did not qualitatively differ from our main results (Appendix S4, Tables S1–S3).

2.2.1 | Survival model

Plants were deemed dead if they had no visible living leaves or stems. We used a binomial mixed-effects model of survival during the period 2011–2018 ('survival model'). We only included plants established up until 2011—recruitment after this period was very low (148 recruits recorded across the 42 plots over 7 years). We accounted for possible size dependence of mortality by including a term for the maximum size (basal area) reached by each individual. We chose the maximum basal area reached as opposed to the average basal area (as for neighbourhood values), since we included this term to account for size-dependent mortality, for which we expect the largest size reached by an individual to be most important.

2.2.2 | Growth models

Due to the large number of live plants that did not record measurable growth during some census periods, we chose to first model the probability of a stem growing in a binomial mixed-effects model ('growth model') and then separately modelled incremental stem growth ('increment model') for stems that did grow, using a linear mixed-effects model. Growth was recorded from 2011 to 2013, and then annually until 2018. Growth increments were calculated as basal area increments (m^2 / growing days). Incremental growth was log-transformed to achieve an approximately normal distribution. As for the survival model, to allow models to fit random slopes for each species, we could only model species that recorded some variability in growth or increment.

2.3 | Statistical analyses

We included random effects in all models to account for several forms of non-independence in our data. We included a term for plot (global spatial autocorrelation), species (species-specific responses) and genus

(genus-specific responses). For growth models, we also included terms for stem identity (to account for repeated measurement of the same stem across multiple census periods) and year (to account for interannual variability in climate). We fitted random slopes in all models for size, allowing the size dependence of the relevant dependent variable to differ by species.

To assess potential local (within-plot) spatial autocorrelation, we tested the relationship between model residuals and x/y coordinates of individuals within plots in all our models using Moran's I (Cliff & Ord, 1973; Cocu et al., 2005; Jumars et al., 1977). We found that three plots from the survival model (7%), 14 plots from the binomial growth model (6%) and 26 plots from increment models (10%) exhibited significant spatial autocorrelation. To test the sensitivity of our models, we compared them to the same models but with these plots removed, and in no cases did this affect our overall results (Appendix S4, Tables S1–S3). Therefore, the models presented in the main results include these plots. We also re-ran our analyses with *E. occidentalis* removed from the data set to test any potential disproportionate effects this planted (compared with seeded) species may have on results, which showed no qualitative effect on models (Appendix S4, Tables S1–S3).

Explanatory variables were transformed to improve linearity with the response variables and to reduce the influence of a small number of very large values. In all models (survival and growth), stem diameter (preceding stem size in growth models and maximum size reached in the survival model), species maximum height and seed mass were log-transformed and neighbourhood values were square-root transformed. Following transformation, all explanatory variables were scaled by subtracting the global mean and dividing by the standard deviation.

To choose the presented neighbourhood distance, we compared five separate models using a neighbourhood radius of 1–5 m and assessed the best performing model using Watanabe–Akaike information criterion (wAIC).

Maximum height and seed mass are known to be correlated (Wright et al., 2010), though this is not always a strong relationship (Santini et al., 2017). We tested this correlation on our data set before including both variables in the same model and found no significant correlation ($R^2 = 0.038$, $p = 0.084$, Appendix S1, Figure S3).

All statistical analyses were conducted using R Version 3.6.3 via RStudio Version 1.2.5033. All models were fit as Bayesian mixed models using the R package 'brms' (Bürkner et al., 2020). For each model, we used four Markov chains with 3000 iterations including a 1500 iteration warm-up. We used the Bayes marginal and conditional R^2 (Gelman et al., 2019) to describe the variance explained by the models. Equations for all models are included in Appendix S5. All models use weakly informative prior distributions, meaning they are similar to linear mixed-effects models.

Bayesian inference does not produce a traditional frequentist p -value to test significance of model variables (and therefore the ability to describe results as 'significant' or 'non-significant'). Instead, we use the 'probability of direction' (pd) which is the probability that an effect operates in a particular direction, which we calculated using the bayestestR package (Makowski et al., 2019, 2021). The pd can range

from 0.5 to 1, with a pd of >0.975 being analogous to a p-value of <0.05 (Makowski et al., 2019).

2.3.1 | Survival data set

A total of 1715 individuals were monitored for survival from 2011 to 2018. Of these, 649 plants died in the 7-year sampling period, an overall mortality rate of approximately 35% (Table S1). The highest levels of mortality occurred in 2014–2015 with the loss of nearly 200 plants across all plots in each year. Before and after this period, mortality was consistent between 60 and 100 plants per year across all plots.

The model of survival included 52 species, largely from the families Fabaceae, Myrtaceae, Casuarinaceae and Proteaceae. Dominant genera included *Acacia* (26%), *Allocasuarina* (8%), *Calothamnus* (11%), *Eucalyptus* (33%) and *Melaleuca* (17%).

2.3.2 | Growth data set

A total of 1866 individuals were measured over the study period, yielding 8989 separate increment measurements. Over the 7 years, 5814 were positive growth increments (65%).

The binomial model of positive growth included 54 different species, from the same families included in the survival model. Dominant genera include *Acacia* (21%), *Allocasuarina* (7%), *Calothamnus* (13%), *Eucalyptus* (36%) and *Melaleuca* (17%).

3 | RESULTS

3.1 | Probability of survival

The survival model using a 5-m radius ranked higher than all other radii (1–4 m) when assessed with wAIC (Appendix S1, Table S4). We found a positive and highly certain relationship between inter-generic neighbourhood basal area and survival (pd = 1, Figure 1; see Table 1 for all pd values for all models). In contrast, the effect of increasing intra-generic neighbours was weak and less certain (pd = 0.897, Figure 1). There was a strong positive relationship between plant size and survival (pd = 1, Figure 1).

The interactions between maximum stem size and inter-generic neighbourhood with stem survival and between stem maximum stem size and maximum height were highly certain (pd = 0.987, Figures 1 and 2). These interactions indicate that larger plants attained a high survival probability, regardless of neighbourhood, whereas smaller plants were nearly twice as likely to survive when in neighbourhoods with high inter-generic basal area (pd = 0.980, Figure 2b). In contrast, an increase in intra-generic neighbours did not modulate size-dependent survival (pd = 0.505, Figure 2a). Species' maximum height interacted with maximum stem size such that taller growing species attain high rates of survival at relatively small stem sizes, compared to

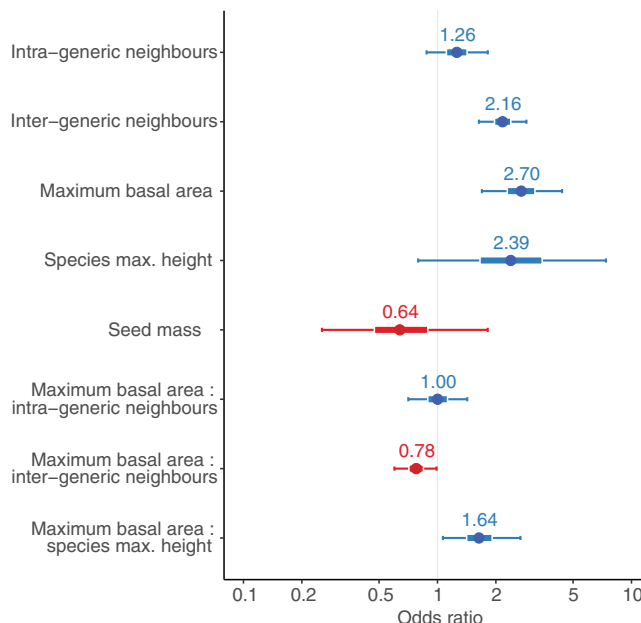


FIGURE 1 Odds ratios from the binomial mixed model of survival from 2011 to 2018. Points indicate the median posterior probability; the thicker part of the bar is 50% credibility interval and the thinner portion 95%. Neighbourhoods are the sum of basal areas within a 5-m radius of each focal stem. All coefficients have been log-transformed, except for neighbourhood values, which are square root transformed. Red and blue coefficients correspond to a median posterior probability below and above one, respectively. Neighbourhoods are the sum basal area of inter-generic and intra-generic stems within 5 m of each focal stem. The odds ratio is the odds of surviving, with an increase in each respective variable

TABLE 1 Probability of direction (pd) for each model term in each model. Values ≥ 0.975 are bolded, as these are analogous to a frequentist p-value of ≤ 0.05

Model term	Survival	Probability of growth	Growth increment
Intrageneric neighbours ^a	0.897	0.810	0.969
Intergeneric neighbours ^a	1.000	0.515	0.892
Individual size ^b	1.000	1.000	1.000
Species max. height	0.941	1.000	1.000
Species seed mass	0.813	0.565	0.524
Intrageneric neighbours ^a × individual size	0.505	0.998	1.000
Intergeneric neighbours ^a × individual size	0.980	0.760	0.964
Species max. height × size	0.987	1.000	0.812

^aNeighbourhood area refers to the sum basal area of neighbouring plants within 5 m in survival and growth increment models and 4 m in probability of growth model.

^bSize in survival models = maximum size of the individual; in growth models, it is the preceding stem size.

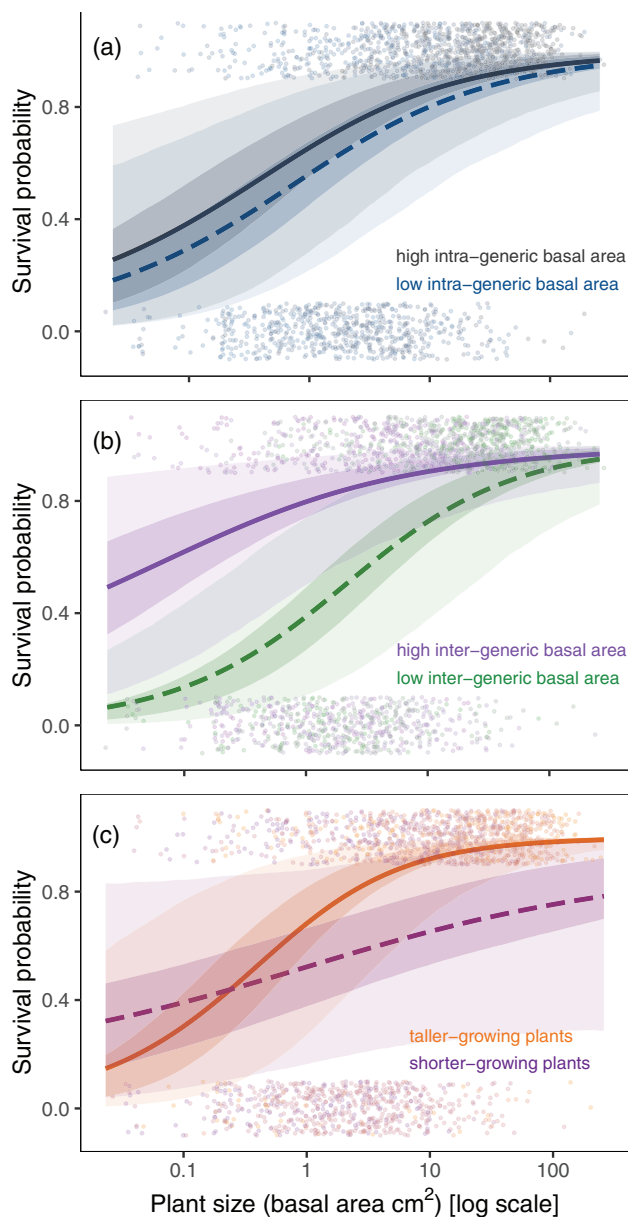


FIGURE 2 Interactions from the binomial survival model between log-transformed plant size (measured as the sum basal area of the individual) and (a) inter-generic neighbourhood (square root transformed), (b) intra-generic neighbourhood (square root transformed) and (c) maximum height (log-transformed). 1 = survived the period 2011–2018. Points are the raw data but are jittered to aid their visibility. Darker envelopes are 50% credibility intervals and lighter envelopes are 95%. Neighbourhoods are the sum basal area of inter-generic and intra-generic stems within 5 m of each focal stem. Prefixes ‘high/taller’ and ‘low/shorter’ in colour-coded captions correspond to +1 (solid line) and –1 (dashed line) standard deviation from the mean of each respective moderator variable

smaller growing species which show a linear size–survival relationship ($pd = 0.987$, Figure 2c). The marginal R^2 (fixed effects only) of the survival model was 0.26, and the conditional R^2 (including random effects) was 0.69. The variance captured by each random effect is detailed in Appendix S2 (Table S1).

The direction of the inter-specific neighbourhood effects in the survival model is the same as in the models using intra-generic neighbourhoods. However, the effect of an increase in neighbouring intra-specific basal area was negative and highly certain compared to intra-generic neighbourhoods, which had no effect (Appendix S3, Table S1).

3.2 | Probability of positive growth

The binomial growth model using a 4-m radius ranked higher than all other radii (1–3, 5 m) when assessed with wAIC (Appendix S1). Using this model, we found that larger plants were less likely to record positive growth ($pd = 1$, Figure 3). By contrast, species maximum height had a positive effect on the odds of growth ($pd = 1$). The effect of seed mass on the probability of growth was weak and uncertain ($pd = 0.565$).

A highly certain ($pd = 0.998$) but relatively weak interaction between plant size and neighbourhood intra-generic basal area indicated that the negative effect of plant size on growth probability was marginally weaker for large plants in neighbourhoods with a lower intra-generic basal area (Figure 4a). There was no interactive effect between the level of inter-generic basal area and plant size ($pd = 0.760$, Figure 4b). The interaction between plant size and species maximum height revealed that the negative effect of plant size on growth probability was stronger for shorter growing species than for taller growing species ($pd = 1$, Figure 4c).

The marginal R^2 of the full binomial growth model was 0.12, and the conditional R^2 was 0.16. The variance captured by each random effect is detailed in Appendix S2 (Table S2).

The effect of an increase in intra-specific neighbours on the probability of growth was positive and more certain compared to intra-generic neighbours (Appendix S3, Table S2). By contrast, an increase in inter-specific neighbours had a negative effect on growth (compared with no effect in inter-generic models).

3.2.1 | Growth increments

In the increment model, a 5-m radius outperformed all other radii (1–4 m) when assessed with wAIC (Appendix S1). Taller growing species accrued larger increments of growth ($pd = 1$), as did larger individuals ($pd = 1$, Figure 3). We found no strong effect of increasing intra-generic basal area on incremental growth rate ($pd = 0.969$, Figure 3). Seed mass had no effect on growth rate ($pd = 0.524$).

The interaction between plant size and intra-generic basal area showed that growth increments were larger in large plants where neighbourhoods had a lower intra-generic basal area, though this effect was very small ($pd = 1$, Appendix S1, Figure S2). However, the size–increment relationship was not strongly related to a change in the neighbouring inter-generic basal area (0.964, Appendix S1, Figure S2). The interaction between plant size and species maximum height showed that, compared to shorter growing species, taller growing species accrue larger growth increments regardless of size, though the probability of the direction of this effect was low ($pd = 0.812$, Appendix

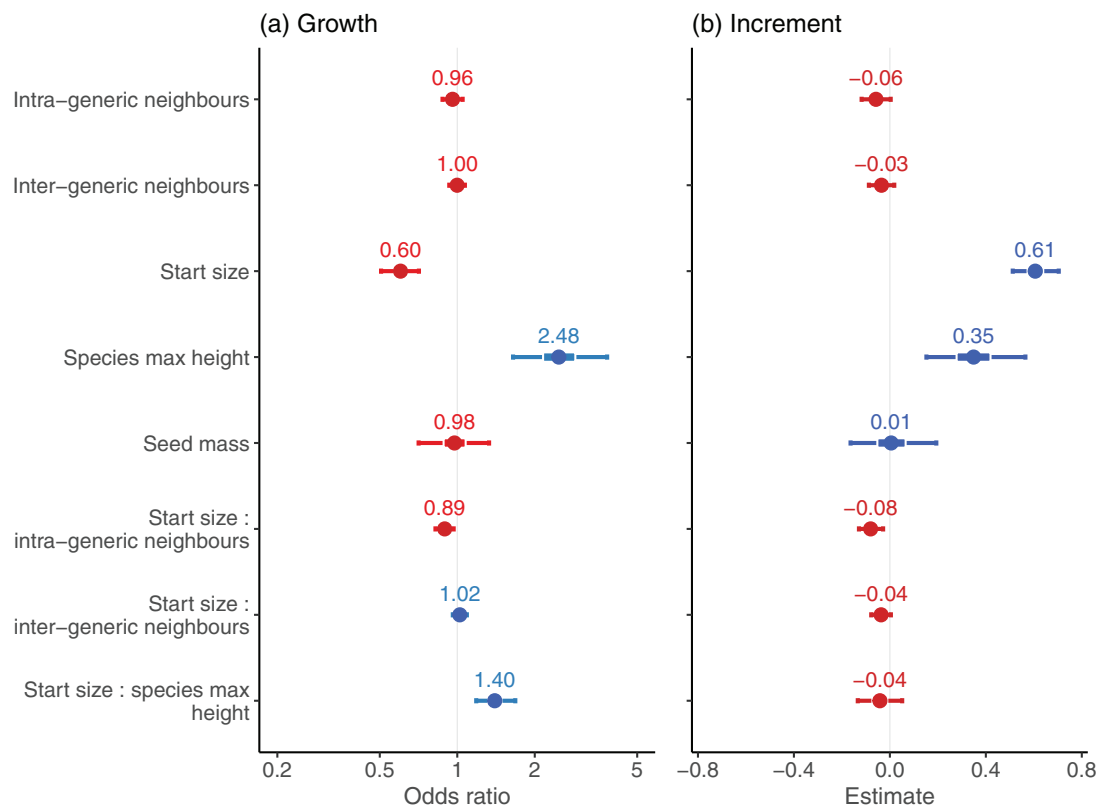


FIGURE 3 Model results showing (a) odds ratios from the binomial model of plants that did or did not record measurable growth, and (b) regression coefficients from the growth increment model. Points indicate the median posterior probability; the thicker part of the bar is 50% credibility interval (not visible for all coefficients) and the thinner portion 95%. Neighbourhoods are the sum of basal areas within a 4-m radius for (a) and 5 m for (b). All coefficients have been log-transformed, except for neighbourhood values, which are square root transformed. Red and blue odds ratios/estimates correspond to a median posterior probability below and above one, respectively. The odds ratio is the odds of recording positive growth, with an increase in each respective variable

S1, Figure S2). The marginal R^2 of the increment model was 0.30 and the conditional R^2 was 0.55. The variance captured by each random effect is detailed in Appendix S2 (Table S3).

The negative direction and certainty of increasing intra-generic basal area was not present when using intra-specific neighbourhoods (Appendix S3, Table S3). By contrast, the negative direction and certainty of inter-specific neighbours was stronger compared to inter-generic models (Appendix S3, Table S3).

The direction of all effects from all models was consistent at neighbourhoods from 1 to 10 m, though generally confidence of estimates widened as neighbourhood radius increased (Appendix S2).

4 | DISCUSSION

Our results provide evidence consistent with a facilitative relationship of neighbours on survival at the early stages of woody vegetation restoration after agriculture, and no evidence for competition-driven mortality (Castro et al., 2002, 2004; Padilla & Pugnaire, 2006). Our results do not show any negative effects of increasing inter-generic basal area on survival, and no effect in either direction of increasing intra-generic basal area, contrary to general patterns in the liter-

ature (Comita et al., 2014). Distance- and density-dependent mortality is generally stronger at wetter sites (Comita et al., 2014), as well as in regions of higher net primary productivity (LaManna et al., 2017). Therefore, it might be expected that these positive neighbourhood effects may dissipate in restoration projects conducted in more productive or wetter sites compared to the landscape of the current study.

There was no clear relationship of increasing intra-generic basal area and odds of growth or incremental growth. While forests with higher evenness and species richness are generally more productive than are less diverse forests (Liang et al., 2016; Zhang et al., 2012), such a relationship was not evident in a meta-analysis of restoration plantings of forest species on ex-agricultural land in Australia (Staples et al., 2019). Importantly, we did not find evidence of a trade-off in growth when neighbours were from other genera, supporting the advocacy for continuing to incorporate or even increase genus-level diversity in future restoration projects (Schneemann & McElhinny, 2012; Standish & Prober, 2020). In addition, we found support for the survival effects using specific-level neighbourhoods compared to our main genus-level results. The divergence in growth results at this finer taxonomic resolution may be a result of the fact that there are many more low-scoring intra-specific neighbourhoods compared to intra-generic. That is, stems were likely to have little or no neighbouring stems of the

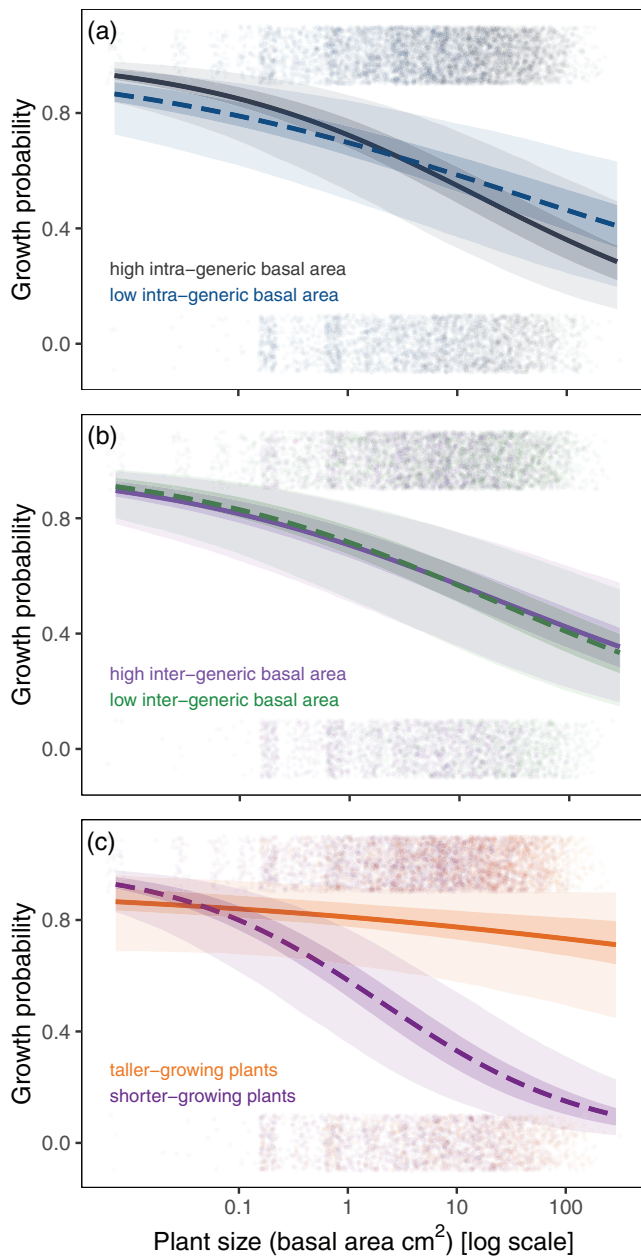


FIGURE 4 Interactions between log-transformed plant size (measured as the sum basal area of the individual) and (a) intra-generic neighbourhood, (b) inter-generic neighbourhood and (c) maximum height from the binomial growth model. 0 = did not record measurable growth and 1 = did record growth. Points are the raw data but are jittered to enable the distribution of data to be seen more clearly. Darker envelopes are 50% prediction intervals and lighter envelopes are 95% prediction intervals. Neighbourhoods are the sum basal area of inter-generic and intra-generic stems within 4 m of each focal stem. Prefixes ‘high/taller’ and ‘low/shorter’ in colour-coded captions correspond to +1 (solid line) and –1 (dashed line) standard deviation from the mean of each respective moderator variable

same species, but often had neighbours of the same genus. In these less common instances of co-occurring with conspecifics, the positive relationship with growth could be due to microsite conditions highly suitable for the species.

There was a positive relationship between species maximum height and both individual survival and growth, indicating that selecting diverse mixes of taller growing species could overcome hurdles to survival and maximize growth. In many woodland communities, this approach would be at odds with the aim of restoring a reference community, where much of the diversity occurs in the ground layer (Cramer et al., 2004; Hobbs & Yates, 2000; Keith, 2006; Kirkpatrick et al., 1995). Yet, in the most challenging restoration sites where barriers to establishment and survival are strong, such a strategy may assist in kick-starting restoration by providing a canopy structure under which arriving species could establish. However, some consideration must be given under such a strategy to avoid creating communities dominated by only the tallest growing species from a reference community. That is, such an approach if taken to the extreme could result in high levels of competition from the tallest species suppressing the establishment of shorter growing species.

We found that smaller stems were more likely to grow, yet survival and growth increments were highest in larger stems. Many of the dominating *Acacia* species were likely reaching the end of their natural lifespan, meaning that only the smaller, younger shrubs were actively growing by the end of the study period. For example, growth is known to slow considerably in *Acacia pulchella* (a shrub) from 5 to 6 years of age onwards (Monk et al., 1981). The same species was shown in a restoration following bauxite mining to have reduced growth in disturbed soils with lower mycorrhizal infectivity (Jasper et al., 1989). The prevalence of this species and other similarly shorter lived and short-statured species are likely driving the negative relationship between individual size and growth.

Many of the taller species in this study are from the genus *Eucalyptus* (Appendix S1, Figure S1, Table S1), 95% of which produce underground lignotubers that can provide greater tolerance of and recovery from extreme heat and drought (James, 1984; Moore, 2015). Lignotubers on *Eucalyptus cinerea* begin formation within 6 months (Graham et al., 1998). The lignotuber may in part explain the interaction between maximum height and survival, where once established *Eucalyptus* seedlings and trees are less likely to die from drought and heat stress compared to the other genera in the study. This capacity to recover from adverse conditions may also explain the interaction between species maximum height and growth.

We found no evidence for a relationship between seed mass and survival or growth. Seed mass can have lasting effects on seedling establishment in restoration in the study region, likely due to seed resources affecting summer drought survival (Hallett et al., 2011). In our case, however, seed resources were likely exhausted for most species given many were approximately 3 years old at the beginning of the study period (Moles & Westoby, 2004). Our results support the notion that the benefit to establishment afforded to larger seeded species following germination does not explain longer term survival or growth in restoration plantings.

Our results also indicate that the relevant neighbourhood distance to consider the effect of diversity on survival and growth is relatively large (4–5 m) in this semi-arid environment. This could be driven by the fact that a key facilitative mechanism of neighbours in stressful environments include physical protection from adverse climatic conditions such as strong desiccating winds (Stachowicz, 2001). Such interactions in smaller plants may operate across larger spatial scales compared to underground interactions. Alternatively, these interactions may scale relative to the individual size of neighbours.

Future research could extend the range of traits used to explain plant survival and growth, to increase understanding of the usefulness of traits to explain demographic changes in these novel environments. For instance, lower wood density was related to increased growth rates in a tropical rainforest restoration (Charles et al., 2018), and meta-analysis has shown specific leaf area (SLA) to be positively correlated with early-stage growth (Gibert et al., 2016). This correlation at later stages of development is mixed, with one recent study encouraging the use of leaf:wood allometry (specifically the ratio of leaf mass to stem mass in branches) alongside leaf and wood traits (Gray et al., 2019). A range of additional under-investigated traits may provide further insights into variation in ecological restoration outcomes (Moles, 2018; Wright et al., 2010). Widening the range of measured traits may also enable the linking of traits to recruitment to shed light on the low levels of new recruits measured. For example, Dwyer and Mason (2018) found that recruiting plants following experimental thinning of regenerating brigalow (*Acacia harpophylla*) forests in Queensland, Australia, were those that are readily bird dispersed. Given that the restoration of ex-agricultural land through direct seeding is a common restoration method across the world, future investigations into dispersal and recruitment limitations will be of broad interest to restoration ecologists and practitioners.

4.1 | Implications for future restoration

Previous studies at Peniup have shown that genetically diverse populations of some species have been successfully established (Millar, Anthony, et al., 2019; Millar, Coates, et al., 2019), which is an important goal of restoration. However, successful restoration projects are also characterized by their capacity to persist (Wilsey, 2020). We found that recruitment was very low, with just 178 recruits recorded in total across the 7 years and 42 plots. Many species in this restoration may be reaching the end of their expected lifespan, and as such, mechanisms to promote recruitment will be vital in replacing the diversity as plants continue to die. While difficult logistically to enact at scale (Murcia et al., 2016), burning and thinning are known to promote recruitment and growth in restoration projects elsewhere (Dodson & Peterson, 2010; Dwyer & Mason, 2018; Gonsalves et al., 2018; Towers & Dwyer, 2021; Young et al., 2015).

Our results show that higher levels of inter-generic neighbours in direct-seeded vegetation may improve survival, particularly in smaller stems. Taller statured plants were more likely to survive and grow compared with shorter growing plants, and growth increments were neg-

atively related to an increase in intra-generic neighbour density. Our results support restoration efforts in similar landscapes that tend to focus on planting key canopy and sub-canopy species. Unfortunately, however, our data set shows little evidence of recruitment in the understorey, despite large rates of mortality in many species. Our results suggest that direct seeding of seed mixes of tall and small plant species from a range of genera at a fine scale is likely to be a key practical manipulation that practitioners can apply to maximize survival and improve future restoration outcomes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

JA, JD and DF conceived the ideas and developed the statistical models. DF and RS were involved in plot survey design and data collection and curation. JA analysed the data. JA led the writing of the manuscript with AM, DF, JD, RS and SB contributing critically to drafts, and giving final approval for publication.

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