

# Seedling growth responses to species-, neighborhood-, and landscape-scale effects during tropical forest restoration

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**Abstract.** Central to the success of restoration plantings within abandoned pastures is the appropriate selection of species that can establish and grow rapidly to form canopies to suppress grasses. However, species selection can be difficult, largely due to combinations of biotic and abiotic factors operating across multiple spatial scales that can affect seedling growth rates. Using a large replicated restoration experiment in Australia's Wet Tropics, we evaluated seedling growth rates of 24 native rainforest species commonly used in local restoration efforts over the first 31 months post-planting. We investigated the influence of landscape, site, and planting conditions on early-stage seedling growth and whether functional traits and surrounding neighborhood density and composition explain variation in seedling growth rates. Seedling growth rates were influenced by numerous stem-, species-, plot-, and climate-level factors, with the strength of these effects strongly dependent on the size of the seedling. Specifically, species with low wood densities and larger seeds grew faster. In response to plot-scale and climate factors, larger seedlings consistently displayed faster growth, demonstrating the benefits of initial seedling size for seedling success. Our study highlights that early-stage seedling growth can be influenced by many factors, operating across multiple spatial scales. Importantly, we demonstrate that planting larger seedlings may improve seedling growth and that developing strategies to increase the survival of fast-growing low wood density species is crucial for ensuring that plantings can achieve canopy closure quickly, improving early to mid-term trajectories of tropical forest recovery.

**Key words:** functional traits; plantings; restoration; seedling establishment; seedling growth; tropical forests; wood density.

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## INTRODUCTION

There is a growing need for restoration in tropical landscapes as deforestation rates continue to increase around the globe (Chazdon 2008). A common theme to many restoration approaches is the use of natural forest recovery processes as a theoretical benchmark when deciding which

species to plant in a given project (Lugo 1997, Holl and Aide 2011). As such, species across a range of successional stages with diverse functional strategies linked with growth and mortality tradeoffs are often selected based on their responses to the suite of biotic and abiotic conditions found within and around planting sites (Lamb 2011). For example, many restoration

plantings on ex-pasture sites contain fast-growing, short-lived pioneer species, together with slower growing, longer-lived non-pioneer species. The intent of this approach is to use pioneer species to accelerate canopy formation and suppress competition from resident grass species, while preparing for their subsequent replacement by slower growing species over time (Goosem and Tucker 1995, Bechara et al. 2016).

Despite the continual development of restoration approaches, species selection is a persistent topic of debate (Lamb et al. 2005), largely due to many factors that can affect planted species performance. These factors operate across multiple spatial and temporal scales and impact different measures of performance, including survival and growth. Climatic conditions may influence species growth rates, such as high levels of irradiance (Kobe 1999, Celis and Jose 2011) typical of ex-pasture sites, and local rainfall patterns (Bristow et al. 2005, Wishnie et al. 2007). Edaphic conditions may also influence early growth performance (Webb et al. 2005, Bare and Ashton 2016) along with the context of the site, including the proximity to adjacent forest fragments (Muñiz-Castro et al. 2006, Catterall et al. 2008, Ley-López et al. 2016), slope, and aspect (Nagamatsu et al. 2002).

At the species level, plant functional traits can determine growth responses to many environmental factors (Valladares et al. 2007, Ostertag et al. 2015). These responses are often trait specific, for example, smaller seed mass (Baraloto et al. 2005, Martínez-Garza et al. 2013a), heavier leaf mass (SLM; Martínez-Garza et al. 2005), and lower wood density (Erskine et al. 2005, Nguyen et al. 2014) have all been observed to positively relate to growth rates of planted species. Functional differences between neighboring plants in resource acquisition strategies may also impact growth rates, particularly in mixed species plots (Piotto 2008). However, these patterns can vary considerably, with species planted in mixed plots experiencing increased (Montagnini et al. 1995, Erskine et al. 2006), decreased (Piotto et al. 2003), or no difference in growth (Plath et al. 2011) compared to species planted in monocultures, which could reflect species-specific responses to diversity treatments (Grant et al. 2006). Interactions between seedlings and surrounding vegetation can also influence growth, via competition from both resident grasses

(Hooper et al. 2002) and between planted species (Erskine et al. 2005). The interactions between seedlings within local neighborhoods can influence both individual and neighborhood growth (Li et al. 2014, Setiawan et al. 2017) and vary with density (Uriarte et al. 2004) and species composition (Potvin and Dutilleul 2009).

Seedlings and young saplings are particularly vulnerable to many of these effects (Grime and Curtis 1976, Camargo et al. 2002), which can be exacerbated by post-planting stress (Burdett 1990), further lowering their resilience and survival (Khurana and Singh 2002, Martínez-Garza et al. 2013b). In combination, it is perhaps unsurprising that many restoration plantings within abandoned pastures experience delays in canopy closure, resulting in arrested forest recovery (Lamb et al. 2005) and may be especially difficult for projects with limited funding to support extended grass and weed management (Webb et al. 2005, Catterall and Harrison 2006). Therefore, understanding the growth responses of species to the biotic and abiotic factors in planting sites is critical to predict early to mid-term trajectories of forest recovery (Martínez-Garza et al. 2013a) and future interactions between planted species (Callaway and Walker 1997). While many studies have examined some of these factors in planting experiments, few studies have examined how combinations of these factors affect early-stage seedling growth rates under differing density and diversity plantation regimes (but see Holl et al. 2011).

The aim of this study was to identify factors that influence seedling growth rates during the first three years after planting. The specific questions we ask are (1) How important are landscape, site, and planting conditions to seedling growth rates? (2) Do species functional traits explain interspecific variation in seedling growth rates? and (3) Are the growth rates of seedlings influenced by the density and composition of surrounding seedlings? Given the well-documented link between species growth rates and functional traits within previous restoration plantings (Martínez-Garza et al. 2013a, Nguyen et al. 2014), we predicted that species with low wood densities and small seeds would have faster seedling growth. We also expected growth rates to be influenced by climatic factors, with faster seedling growth during summer wet seasons (Bristow et al. 2005, Wishnie et al. 2007).

## METHODS

### Study site

The study was undertaken on the Thiaki Creek Nature Reserve (Fig. 1), located on the southern Atherton Tablelands in far North Queensland, Australia (145°51' E 17°43' S), between 900 and 1000 m elevation. The topography comprises narrow valleys surrounded by 15–45° slopes, with an underlying basaltic substrate (Tracey 1982). The region has distinct wet (November–April) and dry (May–October) seasons, with an annual rainfall of 1940 mm (Cheesman et al. 2018). The 181 ha reserve comprises 51 ha of abandoned pasture which was the focus of the restoration experiment established in January 2011, bordered by 130 ha of primary and mature secondary rainforest, classified as Endangered Regional Ecosystem 7.8.4, Upper Barron complex notophyll vine forest (Bell et al. 1987). The pasture area has a consistent land use history (remnant forest cleared for grazing approximately

50 yr ago), and the pasture itself was relatively homogeneous in herbaceous plant species composition prior to planting.

### Experimental design

In January 2011, approximately 28,000 rainforest seedlings were row planted in a randomized complete block design consisting of eight blocks each containing eight 50 × 50 m plots separated by a 10-m buffer zone. The experiment included a two-level planting density treatment: low-density (3 m grid spacing) and high-density (1.75 m grid spacing) and a three-level species diversity treatment (one, six and 24 species). The diversity treatment was phylogenetically nested with 24 local rainforest tree species from six common families: Lauraceae, Moraceae, Myrtaceae, Proteaceae, Rutaceae, and Sapindaceae (Appendix S1: Table S1). *Flindersia brayleyana* (Rutaceae) was used in all monocultures and as one of the species in the six and 24 species treatments as well. Monoculture plots (those

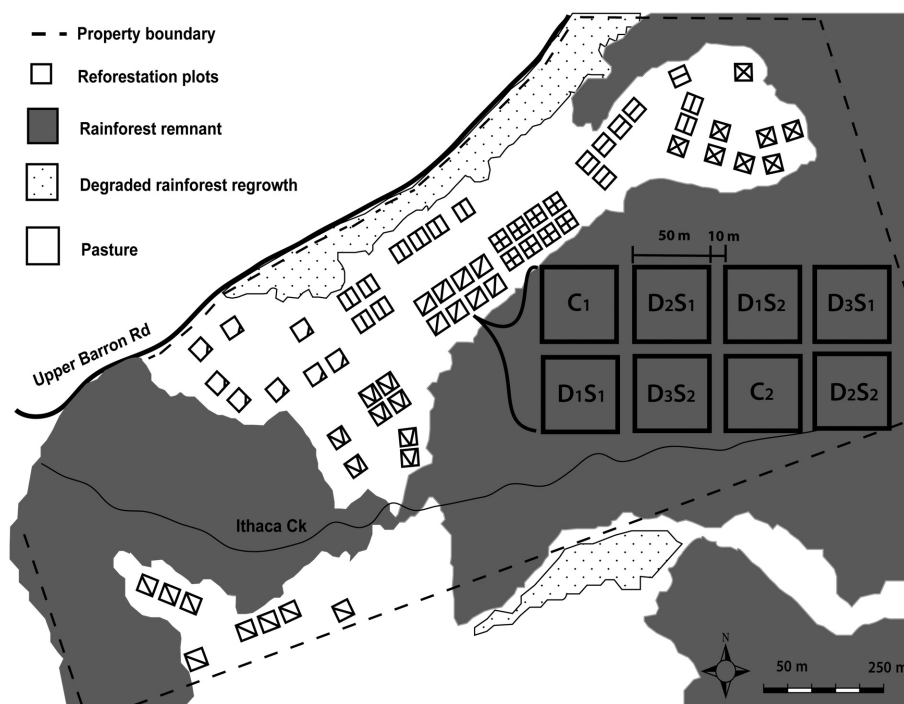


Fig. 1. Map of Thiaki Creek property. The restoration experiment consists of eight blocks, each containing eight 50 × 50 m plots. Plots within a block are labeled with individual fill patterns. The eight treatments applied within each block were C1, no planted trees; C2, no planted trees, herbicide addition; D1, 1 species; D2, 6 species; D3, 24 species; S1, 1.75 m spacing; and S2, 3.0 m spacing.

containing only *F. brayleyana*) were excluded from analyses in this study, due to a lack of variation in family, wood density, seed mass, and  $H_{\max}$ . The multispecies low-diversity treatment included one species from each of the six focal families. The high-diversity treatment included all 24 species, four from each family, and included all of those species present in the low-diversity treatment. Within each experimental block, we assigned two control treatment plots, with no planted seedlings. Plots were randomly assigned treatments within each block (Fig. 1).

Species were selected based on their abundance in local intact rainforest, availability from local nurseries, functional traits, and successional stage (Appendix S1: Table S1). When possible, we selected species in each family to span a range of wood densities, maximum adult tree heights ( $H_{\max}$ ), seed masses, and successional stages. Species from both six- and 24-species diversity treatments were randomly assigned within rows in each plot. After cattle removal and prior to planting, the pasture was dominated by the exotic grass *Urochloa decumbens*. We applied a monocot-specific herbicide (Fusillade) along designated planting rows of all treatment plots (excluding one control plot in each block), leaving alternate rows of unsprayed grass to reduce the potential for runoff and erosion. Herbicide application within rows was continued every six months until August 2012. To avoid potential desiccation of seedlings, planting was conducted during the regional wet season. However, during planting in January 2011, a tropical cyclone off the eastern coast of the study region created unseasonably dry weather during planting. No rainfall was recorded at the study site until five days after the planting was complete. Seedlings were planted without fertilizer application by professional planters using standard forestry industry techniques and were not manually watered after planting. The identity and location of planted seedlings were recorded along each row in the low- and high-diversity plots.

#### Data collection

Seedling growth was measured on plants within a central 25 × 25 m subplot within each treatment plot to minimize plot edge effects. Measures of seedling growth included seedling height (from root collar to apex) and basal stem

diameter (10 cm above root collar, hereafter termed diameter). Height and diameter growth (G) increments were calculated as:

$$G_i = (S_{i,t2} - S_{i,t1}) / (t_2 - t_1),$$

where  $S_{i,t1}$  and  $S_{i,t2}$  are the heights or diameters of stem  $i$  at time 1 and time 2, respectively, and  $(t_2 - t_1)$  is the number of days between time 1 and time 2. Seedling survival status was recorded by visual inspection, with seedlings deemed to be dead if there was pronounced stem desiccation, no leaves, and/or the seedling could not be located (Charles et al. 2018). Seedling size and survival were measured approximately every six months starting 4-months after planting in April 2011 until July 2013.

#### Explanatory variables

*Species-scale variables (functional traits).*—Wood density estimates for all planted species were obtained from Chave et al. (2009) and Zanne et al. (2009). Dry seed mass values were obtained from the literature and the Royal Botanic Gardens Kew Seed information database (Royal Botanic Gardens Kew 2017). Maximum adult height ( $H_{\max}$ ) values were obtained from Cooper and Cooper (2004). The complete list of explanatory variables examined in this study can be found in Table 1.

*Stem-scale variables.*—Tree growth is known to vary with stem size (Poorter and Carlo 1990). We therefore calculated the diameter and height of each stem at the start of each census period for use as covariates in the diameter and height growth models, respectively (Uriarte et al. 2010). Growth is also known to slow as stems die (Lambers and Poorter 1992). We therefore included a binary variable indicating if each stem was alive or dead during the next growth period. We also calculated a number of variables describing the neighborhood of each stem during each growth period. Neighborhoods were defined using a 5.2 m radius around each stem, which included all stems in the surrounding two rows (for the high-density treatment) and surrounding one row (for the low-density treatment). Because stems were only monitored within the internal 25 × 25 m subplots, individuals located within 5.2 m of the edges of subplots were excluded as focal stems, but were included in neighborhoods of focal stems. For each focal plant at each time



Table 1. Grouping variables and experimental treatments, as well as stem-, species-, plot-, and growth period-scale variables used in early-stage seedling growth analysis.

Variables	Type	Units/levels
Block	Factor, random	Eight blocks
Plot (in block)	Factor, random	Eight plots
Stem (in plot)		
Family	Factor, random	Six levels (see Appendix S1: Table S1)
Species (in family)	Factor, random	Twenty-five levels (see Appendix S1: Table S1)
Diversity treatment	Factor, fixed	Three levels (monoculture, six species, twenty-four species)
Density treatment	Factor, fixed	Two levels (1.75 m and 3.0 m spacing)
Wood density	Continuous, fixed	Measured in g/cm <sup>3</sup> (0.38–0.84 g/cm <sup>3</sup> )
Seed mass	Continuous, fixed	Measured in milligrams (0.21–11,307 mg)
Maximum adult tree height	Continuous, fixed	Measured in meters (6–50 m)
Neighborhood basal area	Continuous, fixed	Total basal diameter (mm) within 5.3 m radius of focal plant
Neighborhood height	Continuous, fixed	Average height (mm) of seedlings within 5.3 m radius of focal plant
Neighborhood richness	Continuous, fixed	Total species richness of seedlings within 5.3 m radius of focal plant
Survival status	Binary, fixed	Survival of seedlings at the start of each census period (alive or dead)
Aspect	Categorical, fixed	Two levels (north and south facing)
Slope	Continuous, fixed	Measured in degrees (13–49°)
Distance to forest	Continuous, fixed	Measured in meters (15.5–247 m)
Soil pH	Continuous, fixed	Plot level mean (4.85–5.77)
Soil inorganic nitrogen	Continuous, fixed	Plot level mean (4.08–134.91 mg/g)
Temperature	Continuous, fixed	Mean maximum daily temperature (16.5–36°C)
Precipitation	Continuous, fixed	Mean daily precipitation (1.59–5.91 mm)

point, we calculated the species richness, basal area (10 cm above ground) and mean height of surviving stems in their neighborhood.

*Plot-scale variables.*—Slope and aspect of the plots were measured using a clinometer and compass, respectively. We measured the distance from the center point of plots to the nearest surrounding forest fragments using ArcGIS (ESRI 2006). Soil samples were collected from each plot in August 2014. Samples were taken from 10 cm below soil surface at three random points around the center of each plot and were then mixed prior to analysis. Soil variables included soil pH and soil inorganic nitrogen ( $\text{NH}_4 + \text{NO}_3^-$ ). Available nitrogen was extracted by shaking soil with 2 mol/L KCl solution at a soil: solution ratio of 1:5 for one hour at 200–300 rpm. The suspension was filtered through Whatman filter paper No. 42. Ammonium was measured colorimetrically at 685 nm as described by Willis et al. (1996). Nitrate in the 2 mol/L KCl extracts was determined colorimetrically at 540 nm using a modification of Miranda et al. (2001), as described in Cavagnaro et al. (2006). All soil analysis was conducted at the University of Adelaide.

*Temporal climate variables.*—Daily rainfall and temperature data were obtained for the study

period from SILO (Jeffrey et al. 2001). For the periods between each measurement time point, we calculated the average daily rainfall (mm/day) and average daily maximum temperature (°C).

### Data analysis

In preliminary exploration of growth data from the six and 24-species plots, it was apparent that negative growth had been recorded for some stems during the study period. While negative growth has been recorded in rainforest seedlings in other studies (Kitajima 1994, Agyeman et al. 1999), both growth response variables required sqrt-transformation to meet the assumptions of linear modeling, and so all negative growth increments were converted to zeros prior to modeling. We chose to force all increments to be non-negative in this fashion instead of discarding negative increments because negative increments likely reflect negligible growth and thus include important information. Ideally, we would have estimated measurement error in both responses and used latent true growth specification within a Bayesian modeling framework (Schliep et al. 2014).

Diameter and height growth responses were modeled as a function of plot-, stem-, and species-scale variables, as well as temporally varying

climate variables (Table 1) using linear mixed-effects models. The diameter and height of stems at the start of each period were included as size covariates in the diameter and height models, respectively. These size variables were sqrt-transformed to improve linear relationships with the growth increment response variable. While ln-transformation of growth responses and size variables is the standard approach (Uriarte et al. 2010, Kunstler et al. 2016), sqrt-transformation produced much better model diagnostics for both responses examined here, likely because of our focus on very early stages of tree growth. Soil pH and soil inorganic N were strongly correlated (Pearson's product-moment correlation 0.71). Given our interest in how soil resource levels

affect growth, we only included soil inorganic N in the diameter and height growth models. Mean maximum daily temperature and mean daily precipitation were also correlated (Pearson's product-moment correlation 0.70). In this case, each climate variable was included in separate diameter and height growth models and compared using Akaike's information criterion, corrected for sample sizes values. These results indicated that diameter growth was best predicted by temperature and growth in height by precipitation. In both models, crossed random effects were included to describe spatial nesting of observations (stems within plots within blocks) and taxonomic nesting of observation (species within family).

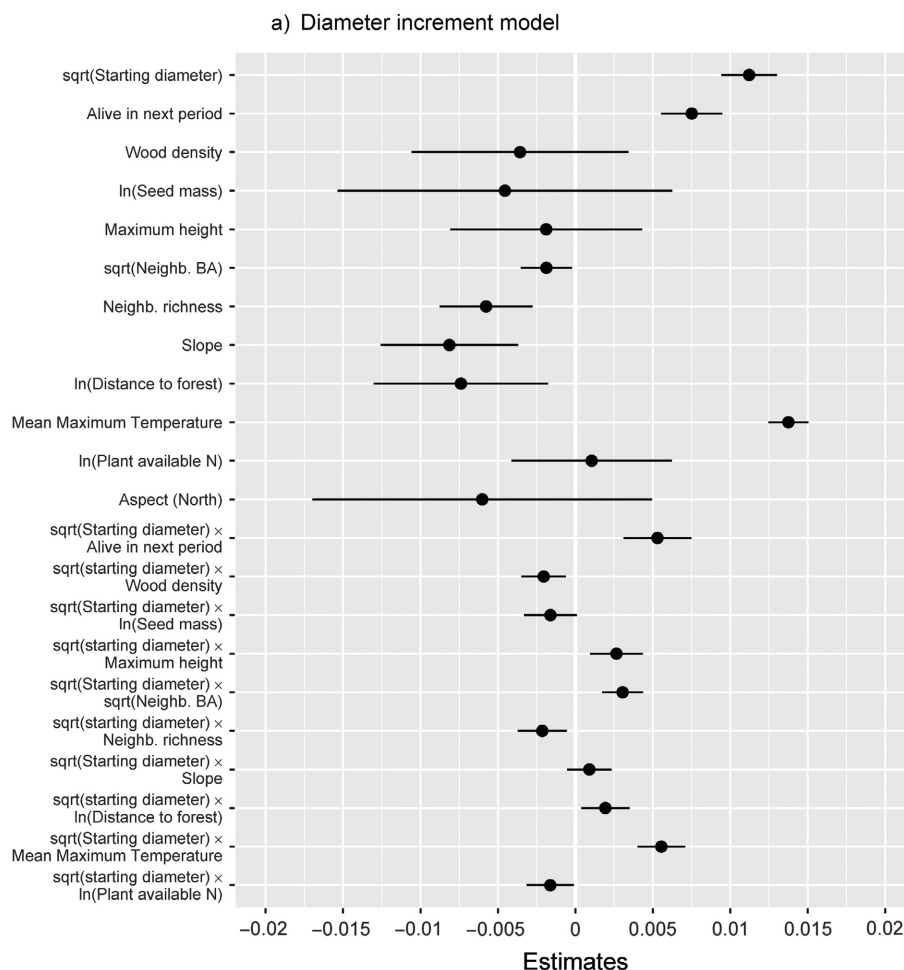
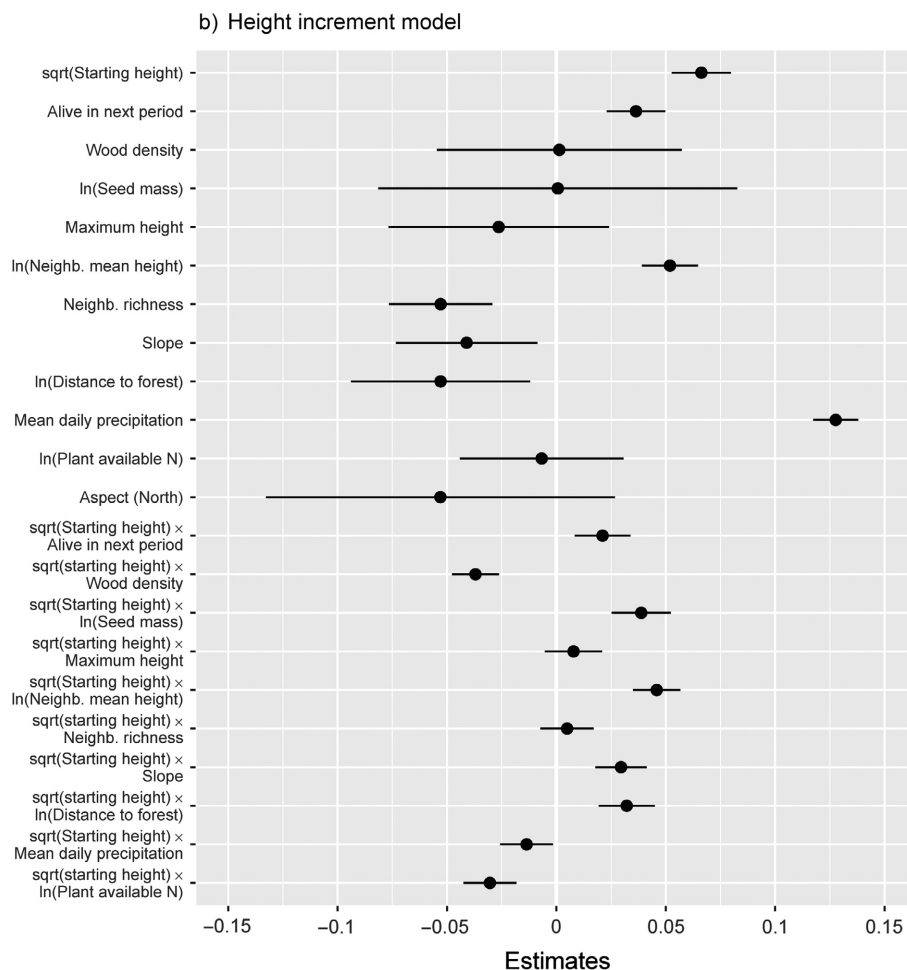


Fig. 2. Coefficient plots for the (a) diameter increment model and (b) the height increment model. Points are standardized coefficient estimate, and bars are standard errors.



(Fig. 2. Continued)

We included two-way interactions between the size covariates (sqrt-transformed starting diameter and starting height) and all other variables to assess how size-dependent growth is influenced by each of the explanatory variables. Aspect was excluded from two-way interactions due to the uneven distribution of south-facing (31%) compared to north-facing plots (69%). Despite converting all negative increments to zeros, model residuals were approximately normally distributed for both the diameter and height growth models. Data analysis was conducted using the R statistical software package version 3.3.3, using the lme4 package (R Development Core Team 2010, Bates et al. 2011). Post hoc tests of pairwise diversity treatment differences were conducted for both species height and diameter growth

using the glht function in the multcomp package (Hothorn et al. 2008).

## RESULTS

### Summary of overall growth across species and families

Final seedling diameter and height varied from 1.1 to 67 mm and 80 to 4200 mm, respectively. Differences between species in their average growth of diameter and height over time were pronounced (Appendix S1: Figs. S1, S2, respectively). *Cardwellia sublimis* had the largest average diameter at the end of the study ( $23.5 \pm 9.4$  mm), and *Lomatia fraxinifolia* ( $1477 \pm 591$  mm) had the tallest average height. *Mischocarpus lacnocarpus* had the smallest average diameter at the end of

the study ( $5.51 \pm 2.6$  mm), and *Ficus destruens* ( $482 \pm 176$  mm) had the shortest average height.

Average diameter and height growth also varied considerably between families (Appendix S1: Fig. S3), with Proteaceae having both the largest final diameters ( $21.78 \pm 9.9$  mm) and tallest final heights ( $1252 \pm 577$  mm). Sapindaceae had the lowest final diameter ( $8.5 \pm 5.3$  mm), while Moraceae had the shortest heights ( $593 \pm 362$  mm). Average diameter and height-based growth rates also varied widely between species and family (Appendix S1: Table S2) and did not differ between diversity treatments (Appendix S1: Table S3).

#### *Models of diameter and height growth*

Both diameter and height growth were influenced by multiple plot-, stem-, and species-level factors, with many depending on the starting size of the stem for each census period (Fig. 2), as detailed below. However, the models explained relatively modest amounts of variation in growth (marginal  $R^2$  of 0.17 for diameter and 0.22 for height).

#### *Functional traits of focal plants*

Species-level functional traits had significant, size-dependent effects on diameter and height growth. Diameter and height growth rates of larger stems were faster for low wood density species (Fig. 3a, b). Diameter growth of larger stems was also faster for species with taller  $H_{\max}$  (Fig. 3c). A significant interaction between seed mass and starting stem size also indicated that the height growth of tall stems was much faster for species with larger seeds than those with small seeds, although large-seeded species appeared to have slower growth initially (Fig. 3d).

#### *Stem-scale factors*

Diameter and height growth were much slower for seedlings that did not survive through to the next census period than surviving stems (Fig. 2). Neighborhood basal area had minimal effects on diameter growth, but the mildly significant interaction with starting stem size (Fig. 2a) suggested that large stems grew moderately faster in high-basal area neighborhoods. A similar effect was found for height growth, with faster growth in taller neighborhoods. Significant interactions between starting stem size and

neighborhood species richness indicated faster diameter and height growth for large stems in lower diversity neighborhoods (Fig. 2).

#### *Plot-scale factors*

Diameter growth was negatively related to plot slope and distance to forest (Fig. 2a). In the height model, both of these plot-scale variables interacted with starting stem size in such a way that growth increased with plant size in steep plots further from forests, whereas in flatter plots close to forests growth varied little with stem size.

#### *Soil and climate factors*

Diameter growth was much faster during warm periods than cool periods, especially for larger stems (Appendix S1: Fig. S4a). Height growth was faster during wet periods than dry periods (Appendix S1: Fig. S4b), regardless of stem height. Diameter and height growth were also weakly influenced by soil inorganic N (Appendix S1: Fig. S4c, d), with larger stems growing faster in plots with lower N.

## DISCUSSION

After accounting for the important influence of stem size on growth rates (Poorter and Carlo 1990, Baraloto et al. 2005), the wood density of focal plants and the size and diversity of neighboring plants were the factors with the most consistent effects on diameter and height growth throughout first 31-month period of growth in this experiment. Larger seedlings consistently grew faster, demonstrating the benefits of initial stem size. Overall, species with low wood densities, larger seeds, and seedlings surrounded by larger and taller neighbors experienced the fastest growth.

#### *Effects of functional traits on seedling growth*

Wood density was negatively related to seedling diameter and growth in height, which is consistent with previous studies of restoration plantings (Erskine et al. 2005, Nguyen et al. 2014) and mature forests (Poorter et al. 2008). Relationships between stem size and growth increment (both diameter and height) were positive for low wood density species and flat for high wood density species. In particular, the slower growth in height for high wood density



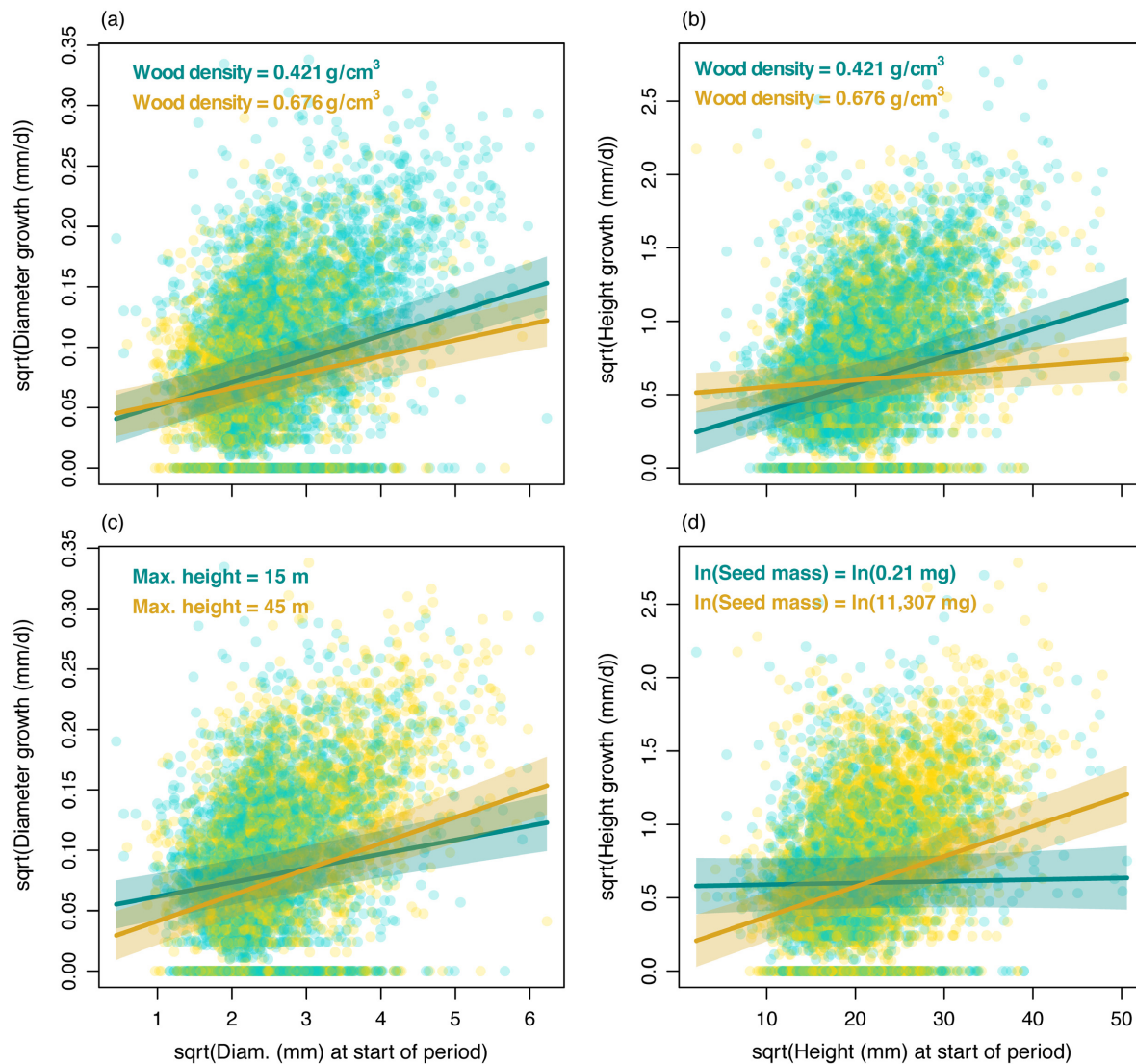


Fig. 3. Relationships between seedling growth increments and initial size for species with different functional trait values: (a) diameter growth for species with low and high wood density, (b) height growth for species with low and high wood density, (c) diameter growth for species with low and high  $H_{\max}$ , and (d) height growth for species with light and heavy seeds. Colored points represent the values below (green) and above (gold) the mean of the trait variable included in the interaction with initial stem size. The fitted lines show relationships for the 10th and 90th percentile of trait values. Other explanatory variables not included in the plotted interactions were held at their means during line fitting. Shaded bands represent 95% confidence intervals.

species is likely due to greater allocation of biomass to stem volume for structural support than shoot growth for height (Niklas 1994). Despite typically being shorter-lived, low wood density species are commonly used in restoration plantings to accelerate canopy closure and suppress competition from grasses (Lamb et al. 2005)

especially where resident grasses are dense and funds are lacking for ongoing grass management (Goosem and Tucker 1995, Florentine and Westbrook 2004). However, species with low wood densities are known from this system and others to have low establishment rates in restoration plantings (Lamb 2011, Charles et al. 2018). Given

that restoration success results from a combination of tree survival and tree growth, it is important to consider growth rate results in light of survival rates in the system over the same time period, which were very low in our experiment (Charles et al. 2018). In combination, our results (along with others; Kanowski et al. 2003, Chazdon 2008, Rodrigues et al. 2011) suggest that planting species with both low and high wood densities may maximize both early-stage seedling survival and growth. However, separate strategies depending on the planting site should be considered when selecting proportions of low and high wood density species. For example, planting species with high wood densities at greater abundances with fewer low wood dense species maximize survival in plantation sites where there are limited funds for follow-up plantings. Conversely, if follow-up funds are available, planting a higher proportion of low wood dense species may accelerate canopy closure and suppress competition from grasses, followed by supplementary plantings of slower growing shade-tolerant species to allow for species replacement over time. Our results also show that if low wood density species managed to survive, their growth rates were much faster than species with high wood density. Therefore, developing strategies to improve the survival of species with low wood density is crucial to ensure plantings can more rapidly achieve canopy closure. We also observed that regardless of wood density values, seedlings that were larger had faster diameter and height growth, suggesting that planting larger seedlings may improve overall growth (Jobidon et al. 1998, South et al. 2001).

Stem size at the start of each growth period also interacted with  $H_{\max}$  and seed mass in the diameter and height models, respectively. In particular, height growth rates increased as stems grew taller for species with larger seeds than those with small seeds, although large-seeded species appeared to have slower growth initially. This result was unexpected given the commonly observed negative relationship between seed mass and growth in both restoration plantings (Baraloto et al. 2005, Martínez-Garza et al. 2013a) and in mature forests (Osunkoya et al. 1993, Poorter and Rose 2005, Poorter et al. 2008). Our result may be a product of a seed resource legacy effect, whereby species

with high seed mass can produce larger seedlings (Paz and Martínez-Ramos 2003), driven by the slow release of resources from the seed over longer time periods (Kitajima 1996). This legacy effect may also be enhanced by the positive relationship between seed mass and specific root length (SRL; Westoby et al. 1992), which can reduce post-planting seedling stress (Grossnickle 2005) and increase seedling growth (Wright and Westoby 1999). While larger seeded species commonly display higher survival rates (Baraloto et al. 2005, Poorter et al. 2008), with greater establishment success promoting further growth (Schupp 1995), our recent study of survival in the same experiment revealed a negative relationship between seed mass and seedling survival, though this was not significant (Charles et al. 2018). To a lesser extent, species with taller  $H_{\max}$  experienced faster diameter growth as they increased in size compared to species with shorter  $H_{\max}$ . While this pattern has been observed within saplings in mature forests (Wright et al. 2010), the relationship between  $H_{\max}$  and juvenile growth is considered weak and may be dependent on co-varying traits (Poorter et al. 2006, Wright et al. 2010) and is not considered a robust indicator of seedling growth in restoration plantings (Martínez-Garza et al. 2013a).

#### *Effects of neighborhood composition on seedling growth*

Neighborhood basal area and average height interacted with starting stem size such that larger and taller stems grew faster when surrounded by larger, taller neighbors. Our results are consistent with Setiawan et al. (2017) who observed that saplings surrounded by larger neighbors displayed increased height and diameter growth in a seven-year-old plantation in Belgium. This suggests that competition among seedlings is weak, which is unsurprising given the small size of many plants during our monitoring period. Instead, the positive relationships with surrounding basal area and surrounding average heights most likely indicate shared growth responses to unmeasured environmental conditions at the stem and neighborhood scales, rather than positive density dependence (e.g., facilitation). That said, there might have been instances where groups of faster-growing plants collectively shaded out grasses, which may have

further accelerated seedling growth due to reduced competition with grasses.

Neighborhood species richness had weak negative effects on both diameter and height growth. This appears to be, in part, due to a selection effect caused by the increased presence of one particular fast-growing species (*Cardwellia sublimis*) in the low-diversity treatment. The effect of *C. sublimis* on neighboring seedling growth was likely diluted in the high-diversity treatment where this species was far less abundant. It is important to note, however, that given the relatively young age of these seedlings, it is likely that these neighborhood effects will change over time with evidence linking differences of neighborhood composition and reduced plant growth with canopy closure (Li et al. 2014) and increased crowding (Uriarte et al. 2004).

#### *Effects of landscape and climate on seedling growth*

Growth was moderately faster on shallow slopes and closer to forests, which matches well with the high seedling mortality we observed on steeper slopes and further from forests (Charles et al. 2018). Within the same experimental plots used in this study, Cheesman et al. (2018) recorded an increase in soil organic matter with decreasing slope angle, resulting in an increase in available soil phosphorus on shallower slopes. Cheesman et al. (2018) further demonstrated that variation in soil P was an important predictor for growth of *Flindersia brayleyana* and *Cardwellia sublimis*, suggesting that some of the planted species may be P limited. Unfortunately, we do not have measures of soil P, which limits our ability to assess the effect of slope and soil P on the growth rates of all 24 species. Seedling growth was not influenced by aspect, which was somewhat surprising given the commonly observed relationships between plant photosynthetic rates, light availability, and slope orientation (Holland and Steyn 1975, Parker 1982). However, within our experimental landscape, we did not have east- or west-facing plots, which reduced our ability to assess aspect effects fully.

As expected, diameter growth was faster during warmer periods, especially for larger stems. Warmer optimal temperatures can result in increased photosynthesis rates in the tropics (Lloyd and Farquhar 2008), further promoting

growth (Bloor and Grubb 2003). Height growth was also faster during wetter than dry periods, consistent with Wishnie et al. (2007) and Bristow et al. (2005). Seedlings planted in pastures commonly experience high evapotranspiration and low plant available water compared to mature forests (Jipp et al. 1998). In these situations, they may allocate resources to root growth to maximize moisture uptake (Gerhardt 1993), at the expense of shoot growth. Growth was also weakly influenced by soil inorganic N, with tall stems growing slightly faster in plots with lower N. Because soils were collected approximately three years after planting, the observed N levels more likely represent N uptake, that is, what is left following uptake by actively growing plants (Buschbacher et al. 1988, Chapin et al. 1990). In addition, the few samples taken in each plot, which were then averaged to provide a single value per plot, may not adequately represent N availability in each plot.

#### CONCLUSION

Central to the success of restoration plantings within abandoned pastures is the ability of seedlings to establish and grow rapidly to form canopies to suppress grasses. Species selection can be difficult, because growth rates are affected by combinations of biotic and abiotic factors operating across multiple spatial scales. Our study highlights that seedling growth is influenced by stem-, species-, plot-, and climate-level factors, with the strength of these effects strongly dependent on the size of the seedling. Specifically, we show that species wood density is an important predictor for both seedling growth and survival (Charles et al. 2018) and clearly demonstrates the mortality–growth tradeoff strategies commonly employed by tropical trees. Restoration approaches that plant species with both high and low wood densities may maximize early-stage seedling growth and survival, yet selecting proportions of low and high wood density species will depend on the site context and availability of funds. In addition, producing large-sized seedling stock prior to planting may also improve seedling growth and survival rates during the critical early period of seedling establishment and although this may increase initial costs, the increased likelihood of canopy closure may reduce the need for future expenditure



on follow-up plantings and prolonged grass and weed control.

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## LITERATURE CITED

- Agyeman, V. K., M. D. Swaine, and J. Thompson. 1999. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology* 87:815–827.
- Baraloto, C., P.-M. Forget, and D. E. Goldberg. 2005. Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology* 93:1156–1166.
- Bare, M. C., and M. S. Ashton. 2016. Growth of native tree species planted in montane reforestation projects in the Colombian and Ecuadorian Andes differs among site and species. *New Forests* 47:333–355.
- Bates, D., M. Maechler, and B. Bolker. 2011. lmer4: linear mixed-effects models using S4 classes.
- Bechara, F. C., S. J. Dickens, E. C. Farrer, L. Larios, E. N. Spotswood, P. Mariotte, and K. N. Suding. 2016. Neotropical rainforest restoration: comparing passive, plantation and nucleation approaches. *Biodiversity and Conservation* 25:2021–2034.
- Bell, F. C., J. W. Winter, L. I. Pahl, and R. G. Atherton. 1987. Distribution, area and tenure of rainforest in northeastern Australia. *Proceedings of the Royal Society of Queensland* 98:27–40.
- Bloor, J. M. G., and P. J. Grubb. 2003. Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology* 91:77–85.
- Bristow, M., P. D. Erskine, S. McNamara, and M. Annandale. 2005. Species performance and site relationships for rainforest timber species in plantations in the humid tropics of Queensland. Pages 84–100 in P. D. Erskine, D. Lamb, and M. Bristow, editors. *Reforestation in the Tropics and Subtropics of Australia: Using rainforest tree species*. Rural Industries Research and Development Corporation, Canberra, Australian Capital Territory, Australia.
- Burdett, A. N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Canadian Journal of Forest Research* 20:415–427.
- Buschbacher, R., C. Uhl, and E. A. S. Serrao. 1988. Abandoned pastures in Eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology* 76:682–699.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Camargo, J. L. C., I. D. K. Ferraz, and A. M. Imakawa. 2002. Rehabilitation of degraded areas of central Amazonia using direct sowing of forest tree seeds. *Restoration Ecology* 10:636–644.
- Catterall, C. P., and D. A. Harrison. 2006. Rainforest restoration activities in Australia's tropics and subtropics. Cooperative Research Centre for Tropical Rainforest Ecology and Management, Rainforest CRC, Cairns, Queensland, Australia.
- Catterall, C. P., J. Kanowski, and G. W. Wardell-Johnson. 2008. Biodiversity and new forests: interacting processes, prospects and pitfalls of rainforest restoration. Pages 510–525 in N. E. Stork and S. M. Turton, editors. *Living in a dynamic tropical forest landscape*. Blackwell Publishing, Malden, Massachusetts, USA.
- Cavagnaro, T. R., L. E. Jackson, J. Six, H. Ferris, S. Goyal, D. Asami, and K. M. Scow. 2006. Arbuscular mycorrhizas, microbial communities, nutrient availability, and soil aggregates in organic tomato production. *Plant and Soil* 282:209–225.
- Celis, G., and S. Jose. 2011. Restoring abandoned pasture land with native tree species in Costa Rica: effects of exotic grass competition and light. *Forest Ecology and Management* 261:1598–1604.
- Chapin, F. S., E.-D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21:423–447.
- Charles, L. S., J. M. Dwyer, T. J. Smith, S. Connors, P. Marschner, and M. M. Mayfield. 2018. Species wood density and the location of planted seedlings drive early-stage seedling survival during tropical forest restoration. *Journal of Applied Ecology* 55:1009–1018.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a

- worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320:1458–1460.
- Cheesman, A. W., N. D. Preece, P. van Oosterzee, P. D. Erskine, and L. A. Cernusak. 2018. The role of topography and plant functional traits in determining tropical reforestation success. *Journal of Applied Ecology* 55:1029–1039.
- Cooper, W. T., and W. Cooper. 2004. *Fruits of the Australian tropical rainforest*. Nokomis Editions, Melbourne, Victoria, Australia.
- Erskine, P., D. Lamb, and G. Borschmann. 2005. Growth performance and management of a mixed rainforest tree plantation. *New Forests* 29:117–134.
- Erskine, P. D., D. Lamb, and M. Bristow. 2006. Tree species diversity and ecosystem function: Can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management* 233:205–210.
- ESRI. 2006. ArcGIS. ESRI, Redlands, California, USA.
- Florentine, S. K., and M. E. Westbrooke. 2004. Restoration on abandoned tropical pasturelands: Do we know enough? *Journal for Nature Conservation* 12:85–94.
- Gerhardt, K. 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science* 4:95–102.
- Goosem, S. P., and N. I. J. Tucker. 1995. *Repairing the rainforest: theory and practice of rainforest re-establishment in North Queensland's Wet Tropics*. Wet Tropics Management Authority, Cairns, Australia.
- Grant, J. C., J. D. Nichols, M.-C. Pelletier, K. Glencross, and R. Bell. 2006. Five year results from a mixed-species spacing trial with six subtropical rainforest tree species. *Forest Ecology and Management* 233:309–314.
- Grime, J. P., and A. V. Curtis. 1976. The interaction of drought and mineral nutrient stress in calcareous grassland. *Journal of Ecology* 64:975–988.
- Grossnickle, S. C. 2005. Importance of root growth in overcoming planting stress. *New Forests* 30:273–294.
- Holl, K. D., and T. M. Aide. 2011. When and where to actively restore ecosystems? *Forest Ecology and Management* 261:1558–1563.
- Holl, K. D., R. A. Zahawi, R. J. Cole, R. Ostertag, and S. Cordell. 2011. Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology* 19:470–479.
- Holland, P. G., and D. G. Steyn. 1975. Vegetational responses to latitudinal variations in slope angle and Aspect. *Journal of Biogeography* 2:179–183.
- Hooper, E., R. Condit, and P. Legendre. 2002. Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecological Applications* 12:1626–1641.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363.
- Jeffrey, S. J., J. O. Carter, K. B. Moodie, and A. R. Beswick. 2001. Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling & Software* 16:309–330.
- Jipp, P. H., D. C. Nepstad, D. K. Cassel, and C. R. de Carvalho. 1998. Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia. Pages 255–272 in A. Markham, editor. *Potential impacts of climate change on tropical forest ecosystems*. Springer Netherlands, Dordrecht, The Netherlands.
- Jobidon, R., L. Charette, and P. Y. Bernier. 1998. Initial size and competing vegetation effects on water stress and growth of *Picea mariana* (Mill.) BSP seedlings planted in three different environments. *Forest Ecology and Management* 103:293–305.
- Kanowski, J., C. P. Catterall, G. W. Wardell-Johnson, H. Proctor, and T. Reis. 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management* 183:265–280.
- Khurana, E., and J. S. Singh. 2002. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest : a review. *Environmental Conservation* 28:39–52.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Kitajima, K. 1996. *Ecophysiology of Tropical Tree Seedlings*. Pages 559–596 in S. S. Mulkey, R. L. Chazdon, and A. P. Smith, editors. *Tropical forest plant ecophysiology*. Springer US, Boston, Massachusetts, USA.
- Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- Kunstler, G., et al. 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529:204.
- Lamb, D. 2011. *Regreening the bare hills: tropical forest restoration in the Asia-Pacific region*. Springer, Dordrecht, The Netherlands.
- Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. *Science* 310:1628–1632.



- Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* 23:187–261.
- Ley-López, J. M., G. Avalos, and E. Chacón-Madriral. 2016. Seedling growth and survival of five tree species in secondary forests and adjacent pastures in the montane rain forests of Southern Costa Rica. *Revista de Biología Tropical* 64:1565–1583.
- Li, Y., W. Härdtle, H. Bruelheide, K. Nadrowski, T. Scholten, H. von Wehrden, and G. von Oheimb. 2014. Site and neighborhood effects on growth of tree saplings in subtropical plantations (China). *Forest Ecology and Management* 327:118–127.
- Lloyd, J., and G. D. Farquhar. 2008. Effects of rising temperatures and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:1811–1817.
- Lugo, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99:9–19.
- Martínez-Garza, C., F. Bongers, and L. Poorter. 2013a. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management* 303:35–45.
- Martínez-Garza, C., V. Peña, M. Ricker, A. Campos, and H. F. Howe. 2005. Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management* 217:365–379.
- Martínez-Garza, C., W. Tobon, J. Campo, and H. F. Howe. 2013b. Drought mortality of tree seedlings in an eroded tropical pasture. *Land Degradation & Development* 24:287–295.
- Miranda, K. M., M. G. Espey, and D. A. Wink. 2001. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. *Nitric Oxide* 5:62–71.
- Montagnini, F., E. Gonzalez, C. Porras, and R. Rheingans. 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* 74:306–314.
- Muñoz-Castro, M. A., G. Williams-Linera, and J. M. R. Benayas. 2006. Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. *Journal of Tropical Ecology* 22:431–440.
- Nagamatsu, D., K. Seiwa, and A. Sakai. 2002. Seedling establishment of deciduous trees in various topographic positions. *Journal of Vegetation Science* 13:35–44.
- Nguyen, H., J. Firn, D. Lamb, and J. Herbohn. 2014. Wood density: a tool to find complementary species for the design of mixed species plantations. *Forest Ecology and Management* 334:106–113.
- Niklas, K. J. 1994. *Plant allometry: the scaling of form and process*. University of Chicago Press, Chicago, Illinois, USA.
- Ostertag, R., L. Warman, S. Cordell, and P. M. Vitousek. 2015. Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology* 52:805–809.
- Osunkoya, O. O., J. E. Ash, A. W. Graham, and M. S. Hopkins. 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *Journal of Tropical Ecology* 9:1–18.
- Parker, A. J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Physical Geography* 3:160–168.
- Paz, H., and M. Martínez-Ramos. 2003. Seed mass and seedling performance within eight species of *Psychotria* (Rubiaceae). *Ecology* 84:439–450.
- Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management* 255:781–786.
- Piotto, D., F. Montagnini, L. Ugalde, and M. Kanninen. 2003. Growth and effects of thinning of mixed and pure plantations with native trees in humid tropical Costa Rica. *Forest Ecology and Management* 177:427–439.
- Plath, M., K. Mody, C. Potvin, and S. Dorn. 2011. Establishment of native tropical timber trees in monoculture and mixed-species plantations: small-scale effects on tree performance and insect herbivory. *Forest Ecology and Management* 261:741–750.
- Poorter, L., L. Bongers, and F. Bongers. 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* 87:1289–1301.
- Poorter, H., and R. Carlo. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83:553–559.
- Poorter, L., and S. A. Rose. 2005. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. *Oecologia* 142:378–387.
- Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89:1908–1920.
- Potvin, C., and P. Dutilleul. 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. *Ecology* 90:321–327.
- R Development Core Team. 2010. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Rodrigues, R. R., S. Gandolfi, A. G. Nave, J. Aronson, T. E. Barreto, C. Y. Vidal, and P. H. S. Brancalion. 2011. Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management* 261:1605–1613.
- Royal Botanic Gardens Kew. 2017. Seed Information Database (SID), Version 7.1. <http://data.kew.org/sid/>
- Schliep, E. M., T. Q. Dong, A. E. Gelfand, and F. Li. 2014. Modeling individual tree growth by fusing diameter tape and increment core data. *Environmetrics* 25:610–620.
- Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* 82:399–409.
- Setiawan, N. N., M. Vanhellemont, L. Baeten, T. Van de Peer, E. Ampoorter, Q. Ponette, and K. Verheyen. 2017. Local neighbourhood effects on sapling growth in a young experimental forest. *Forest Ecology and Management* 384:424–443.
- South, D. B., J. L. Rakestraw, and G. A. Lowerts. 2001. Early gains from planting large-diameter seedlings and intensive management are additive for loblolly pine. *New Forests* 22:97–110.
- Tracey, J. G. 1982. The vegetation of the humid tropical region of north Queensland. CSIRO, Melbourne, Victoria, Australia.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- Uriarte, M., N. G. Swenson, R. L. Chazdon, L. S. Comita, W. J. Kress, D. Erickson, J. Forero-Montaña, J. K. Zimmerman, and J. Thompson. 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters* 13:1503–1514.
- Valladares, F., E. Gianoli, and J. M. Gómez. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* 176:749–763.
- Webb, M. J., M. Bristow, P. Reddell, and N. Sam. 2005. Nutritional limitations to the early growth of rainforest timber trees in north Queensland. Pages 69–82 in P. Erskine, D. Lamb, and M. Bristow, editors. *Reforestation in the tropics and subtropics of Australia: using rainforest tree species*. Rural Industries Research and Development Corporation, Canberra, Australian Capital Territory, Australia.
- Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* 7:368–372.
- Willis, R. B., M. E. Montgomery, and P. R. Allen. 1996. Improved method for manual, colorimetric determination of total Kjeldahl Nitrogen using Salicylate. *Journal of Agricultural and Food Chemistry* 44:1804–1807.
- Wishnie, M. H., D. H. Dent, E. Mariscal, J. Deago, N. Cedeño, D. Ibarra, R. Condit, and P. M. S. Ashton. 2007. Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. *Forest Ecology and Management* 243:39–49.
- Wright, I. J., and M. Westoby. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* 87:85–97.
- Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann, and J. Chave. 2009. Data from: towards a worldwide wood economics spectrum. Dryad Digital Repository.

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