

## Demographic costs and benefits of natural regeneration during tropical forest restoration

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### Abstract

For tropical forest restoration to result in long-term biodiversity gains, native trees must establish self-sustaining populations in degraded sites. While many have asked how seedling recruitment varies between restoration treatments, the long-term fate of these recruits remains unknown. We address this research gap by tracking natural recruits of 27 species during the first 7 years of a tropical forest restoration experiment that included both planted and naturally regenerating plots. We used an individual-based model to estimate the probability that a seedling achieves reproductive maturity after several years of growth and survival. We found an advantage for recruits in naturally regenerating plots, with up to 40% increased probability of reproduction in this treatment, relative to planted plots. The demographic advantage of natural regeneration was highest for mid-successional species, with relatively minor differences between treatments for early-successional species. Our research demonstrates the consequences of restoration decision making across the life cycle of tropical tree species.

### Keywords

Demographic model, early succession, full life-cycle analysis, individual-based model, life-history categories, natural regeneration, population-level, reforestation, successional age, tropical forest restoration.

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### INTRODUCTION

Tropical forest restoration has the potential to promote biodiversity and sequester carbon on degraded land (Aide *et al.* 2013; Poorter *et al.* 2016; Griscom *et al.* 2017). Forest recovery is the product of tree demography, as seeds arrive in disturbed sites, establish into seedlings, grow into adult trees and reproduce. Understanding tree demography is a fundamental challenge that will help achieve restoration goals (Caughlin *et al.* 2016). Variation in demographic rates (growth, survival and reproduction) can explain divergent successional trajectories, such as different rates of biomass accumulation in wet vs. dry second-growth forests (Rozendaal *et al.* 2016). Demographic variability also determines why some restoration projects succeed and others fail. The success of restoration plantings ('active restoration') depends on both the demographic rates of planted trees and on the establishment of naturally recruited trees (Ren *et al.* 2007). In turn, the success of natural regeneration ('passive restoration') depends on whether naturally-recruited trees can live long enough to become reproductive adult trees (van Breugel *et al.* 2013). Numerous demographic barriers could limit population growth rates of native plant species in restoration treatments, from low seed germination rates (Holl *et al.* 2000) to sapling dieoff (Van Breugel *et al.* 2006), to reproductive failure (Albrecht & McCue 2010). However, most studies of tree demography during restoration have focused on recruitment

rates (Ingle 2003; Zahawi & Augspurger 2006; Martínez-Garza *et al.* 2009; de la Peña-Domene *et al.* 2017) and few have tracked the fate of natural recruits beyond the seedling stage.

The knowledge gap on natural recruit demography has direct relevance for restoration decision making. A key decision for tropical forest restoration is whether natural regeneration will be sufficient to restore tree cover in a reasonable period or whether active restoration, such as tree planting, will be needed (Holl & Aide 2011; Lampert & Hastings 2014; Chazdon *et al.* 2017). An argument in favour of restoration planting is that seed rain, including seeds of native tree species from nearby forest fragments, is often higher in plantings relative to naturally regenerating areas (Reid *et al.* 2014). Increased seed rain in plantings then leads to higher density and diversity of woody seedlings in these sites (Zahawi & Augspurger 2006; Wydhayagarn *et al.* 2009), although seed arrival does not guarantee that a sufficient density of natural recruits will survive and grow large enough to re-create a diverse, native forest (Reid & Holl 2013). Therefore, if costs to subsequent life stages are greater than benefits of increased seed arrival in plantings, tree planting could have minimal benefits for long-term forest recovery. Assessing these costs and benefits requires quantifying demographic differences between planted and naturally regenerating sites across the tree life cycle.

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Successional age complicates the question of how tree planting impacts demographic rates of natural recruits. Rates of survival, growth and reproduction are likely to change during forest recovery, particularly for highly-degraded sites that begin in an herb-dominated state. For herb-dominated sites, the first decade of forest succession marks a period of dramatic environmental changes, including increased soil water potential, increased relative humidity and decreased photosynthetically active radiation (Ellsworth & Reich 1996; Lebrija-Trejos *et al.* 2011). These environmental changes affect tree community structure as the competitive advantage shifts from short-lived early successional to long-lived shade-tolerant species (Selaya *et al.* 2007; Craven *et al.* 2015). During the first 10 years of succession, average tree size also changes, as cohorts of seedlings grow into trees. Because tree demographic rates are size-dependent, with higher growth, survival and reproductive rates for larger individuals (Van Kuijk *et al.* 2008; Zuidema *et al.* 2010; van Breugel *et al.* 2011), we expect values of these rates to increase with successional age, regardless of environment or species identity. Altogether, the demographic rates of natural recruits are likely to vary depending on individual size, species identity and environmental context. To understand the demographic costs and benefits of tree planting vs. natural regeneration, we will need to disentangle the impacts of successional age on natural recruits.

Whether differences in recruit demography between planted and naturally-regenerating sites have long-term effects on the speed of forest recovery depends not just on survival, growth and reproduction, but also on how the interaction of these rates leads to population-level impacts. Achieving reproductive maturity represents a critical benchmark for restoration success that combines all three demographic rates (Elliott *et al.* 2013). Size thresholds for reproduction are the norm for woody plants and reaching them often requires multiple years of growth and survival (Wright *et al.* 2005; Wenk & Falster 2015). An assumption of restoration planting schemes designed to promote natural recruitment by attracting seed dispersers is that, over time, natural recruits will begin to reproduce, converting restoration plots from seed sinks to seed sources. While many studies have identified seed limitation as a bottleneck for seedling recruitment during forest restoration (Holl 1998; Zahawi & Augspurger 2006; Blackham *et al.* 2013), few have asked when trees in restoration plots become seed sources.

We tracked the demography of natural recruits during the first 7 years of a restoration experiment that included both planted plots and plots undergoing natural regeneration. In our study system, tree planting increases seed rain and seedling recruitment during the first 4 years after planting (de la Peña-Domene *et al.* 2013, 2014). Here, we analyse the fate of naturally recruited seedlings, including survival, growth and reproductive status. Repeated measurements on the same individuals over 18 censuses over 7 years enabled us to disentangle the effects of species identity, size, and successional age on demographic rates. Our study addresses five questions: (1) How do growth, survival and reproduction of natural recruits differ between planted plots and plots undergoing natural regeneration? (2) How does successional age mediate the impact of planting treatments on these demographic rates?

Questions 1–2 relate to data on each demographic rate separately. Whether a new recruit can grow and survive to reach reproductive maturity is an integrative metric of demographic success that combines all three rates. We used this integrative metric to quantify the cumulative demographic costs and benefits of planting treatments: (3) Given identical starting conditions, how does the probability that a simulated recruit reaches reproductive maturity vary between planting treatments? (4) Considering that any plot-level effects on individual demography may be overwhelmed by higher seed rain in planted plots, how does the abundance of reproductive recruits vary between treatments? Finally, because we expected that answers to 1–4 depend on the successional status of natural recruits (Selaya & Anten 2010; Martínez-Garza *et al.* 2013), we grouped species into three life history categories, early-, mid- and late-successional, to ask (5) How do demographic responses to planting treatment vary depending on species successional status? Our approach provides insight into how restoration treatments impact the transition of reforesting sites from degraded seed sinks to forested seed sources.

## METHODS

We conducted our study in experimental plots embedded in cattle pasture adjacent to the Los Tuxtlas Biosphere Reserve (18°35′ 43.64″N, 95° 06′ 06.29″W). Plots span an elevational gradient from 182 to 260 m asl. Soils in the area are acidic entisols, originating from volcanic parent material. Mean annual rainfall is  $4275 \pm 404$  mm per year, with a pronounced dry season from March to May. The nearest native forest is highly fragmented lowland tropical rainforest with approximately 300 tree species (Martínez-Ramos *et al.* 2016) and the nearest forest patch is late secondary forest *c.* 100 m away from the plots (de la Peña-Domene *et al.* 2016). The cattle pasture where our experimental plots are located was cleared for agriculture approximately 45 years ago, and currently has a grazing density of *c.* two cows per ha (de la Peña-Domene *et al.* 2013).

In August 2006, researchers initiated a long-term experiment to evaluate forest restoration treatments in this pasture. The experiment was designed to compare successional dynamics in restoration plots that were planted with either animal or wind-dispersed tree species to unplanted naturally regenerating plots. Experimental plots include eight control (unplanted) plots, eight plots planted with 12 animal-dispersed tree species and eight plots planted with 12 wind-dispersed species (Martínez-Garza *et al.* 2016). Each plot is separated from neighbouring plots by 35 m of active pasture. Cattle are excluded from the entire plot, with a 1 m corridor between the interior of the plot and the cattle exclusion fence. Within the fenced area, plots are further divided into four  $13 \times 13$  m subplots.

Planted trees began with a median height of 16 cm in 2006 (Guzmán-Luna & Martínez-Garza 2016). By 2013, a majority of surviving planted trees had reached heights  $>3$  m. During the course of our 7-year study, tree canopy cover in planted plots gradually increased to *c.* 80%, whereas tree cover in naturally-regenerating plots remained at levels  $<40\%$  (de la Peña-Domene *et al.* 2016). Consequently, while the understory

of planted plots is generally dominated by woody species, naturally regenerating plots have retained patches of invasive fern (*Nephrolepis hirsutula*) and pasture grasses (*Brachiaria* and *Cynodon* spp.) throughout the study period (Howe & Davlantes 2017).

Censuses of all naturally recruited seedlings (height > 10 cm) within subplots began in June 2007 and continued approximately every four months until January 2014. During each census, individual recruits were identified to species (following Ibarra-Manríquez & Sinaca-Colín 1996), tagged and measured for basal diameter. In the subsequent analyses, we calculated seedling growth as changes in basal diameter, standardised to represent monthly growth rates in mm, and seedling survival as presence or absence in each census. We measured probability of reproduction by recording the presence or absence of reproductive structure (fruits and flowers) during each census, beginning with the tenth census, *c.* 3.41 years after the experiment began. Resprouts of trees present in plots before the experiment began were cut and not counted in censuses. Data collection resulted in a total of 18 censuses with records for 1865 individual woody recruits. The data are available in the Dryad data repository (<https://doi.org/10.5061/dryad.1c1g42k>).

### Statistical modelling

The goal of our statistical models was to quantify the effects of planting treatment (Question 1) and successional age (Question 2) on demographic rates (growth, survival and reproduction) while accounting for individual size and species identity. To accomplish this goal, we developed a hierarchical Bayesian model for each demographic rate. Below we outline the structure of our models. Additional details are presented in Appendix S1.

The foundation of our three vital rate models was generalised linear mixed effect models (GLMMs) that included effects of individual size and planting treatment. As we expected responses to successional age would vary between species, we modelled all parameters related to this term as species-level random effects. Hierarchical models are well-suited to data with uneven sampling across levels (Bolker 2015), such as tropical tree communities with a few common and many rare species (Condit *et al.* 2013). Incorporating species as a random effect enabled us to include all species present in plots in our analyses, even though not all species were represented in each treatment (Table S1). All models also included additive random effects for plot (to account for unmeasured spatial variation) and individual (to account for repeated measures of the same individuals over time). Models for survival and growth included successional age, as well as individual size and planting treatment. However, for reproduction, we did not model effects of successional age, because phenology measurements began after more than half of censuses had been completed.

Finding and measuring small seedlings introduces measurement error in growth and survival records (Alexander *et al.* 2012; Record *et al.* 2016). We addressed imperfect measurements for our growth and survival models using a state space modelling framework that assumes observed variability in

data which represents both process and observation error. Process errors result because our model (the GLMM described above) does not include all biological factors that lead to differences in growth and survival. Observation errors result because measurements of both tree basal diameter and tree presence/absence are imperfect (Eitzel *et al.* 2015; Metcalf *et al.* 2009). We estimate the observation errors and the process errors as two components of the same model.

We modelled growth using normally-distributed error for observations and gamma-distributed error for the process model. This model structure implies that while deviance in positive growth rates is biologically reasonable, shrinkage (negative growth) can only occur due to measurement error, such as slight differences in point of measurement between censuses and changes in stem thickness unrelated to growth (Clark *et al.* 2007; Eitzel *et al.* 2013). We found support for a quadratic term for the effect of successional age on growth and included both this term as well as its interaction with planting treatment in our process model for growth.

For survival, we assumed that observation error was related to imperfect detection of tagged seedlings and modelled survival using a mark and recapture model (Record *et al.* 2016). In this type of model, survival is modelled as a binomial mixture model with an occupancy and a detection layer (Royle 2008). We found that adding individual size, species identity, and successional age in the model for detection improved model fit and included these as observation-level covariates in the survival model. Our model for reproduction included the presence of flowers or fruits as a Bernoulli-distributed response variable. For this model, we assumed that measurement error in detecting flowers and fruits was minimal.

### Model-fitting

We applied a Markov Chain Monte Carlo algorithm in JAGS v. 4.2.0 (Plummer 2003) to sample from the joint posterior distribution, with six chains, each run for 100 000 iterations with a burn-in of 10 000 iterations. Except for the size parameter, prior values of parameters were constrained to biologically reasonable values and were otherwise non-informative. For the size parameter in the process model for survival and growth, we used informed priors based on regressions of survival and growth vs. size for planted trees in the same study site, monitored during the same period of early succession (Martínez-Garza *et al.* 2016). While these informed priors did not qualitatively change our results, their use improved model convergence.

### Individual-based model

The purpose of the individual-based model (IBM) was to quantify the outcome of planting treatment on the probability that a new recruit can achieve reproductive maturity (Question 3). In this dynamic simulation, natural recruits increased in size via the growth model. The survival model was linked to the growth model because survival is size-dependent. Reproduction was linked to both the survival and growth models because reproduction is conditional both on recruit size and on whether the recruit is alive. Overall, the IBM

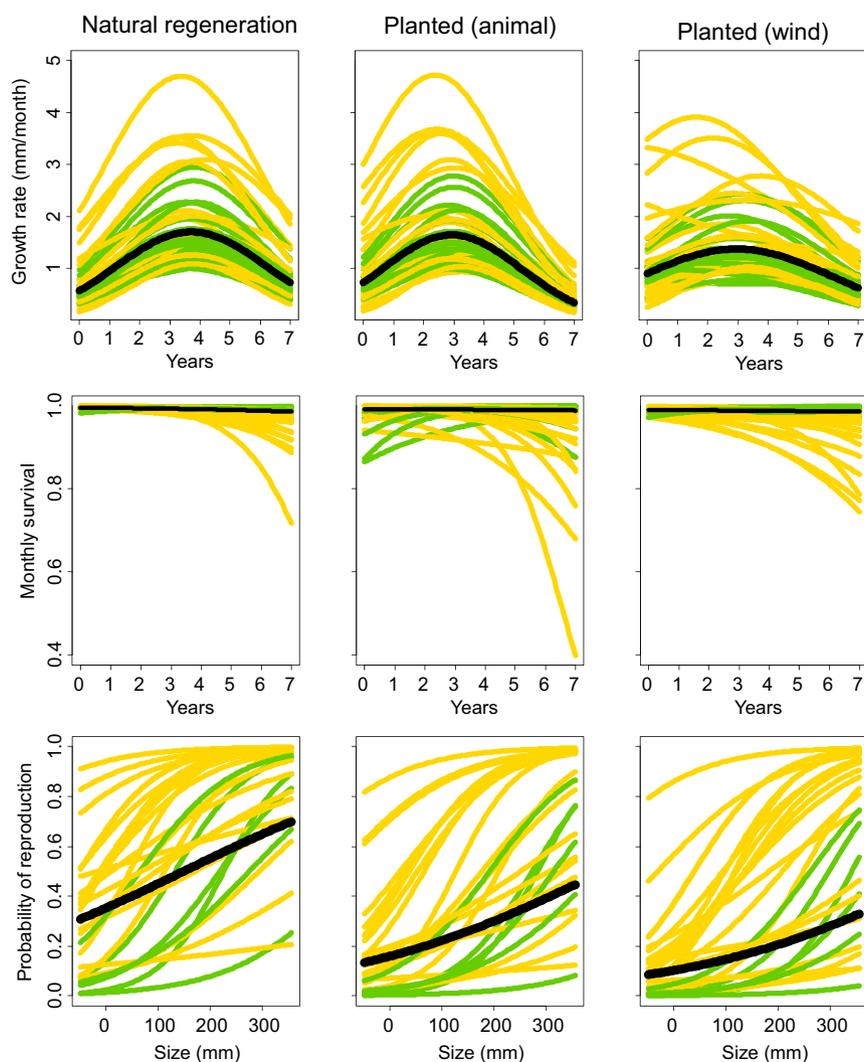
enabled us to quantify the combined effects of planting treatment, species and successional age on demographic outcomes.

Simulated recruits began the IBM with a size of 10 mm basal diameter. The standard size enabled us to more directly compare outcomes between different species in different planting treatments. We ran the IBM at a monthly time step for a total of 80 months, representing the timespan of our study. Simulations did not include plot or individual-level variation; thus results represent an average individual in an average plot. We propagated parameter uncertainty to IBM output using random draws from the posterior distributions of parameters estimated in our statistical models. We replicated each draw ten times to represent demographic stochasticity, resulting in a total of 10 000 runs for each simulation. We then ran the IBM at the community-level, as well as at the species-level, using parameters from the 27 species with observed reproduction. We evaluated IBM output by comparing size

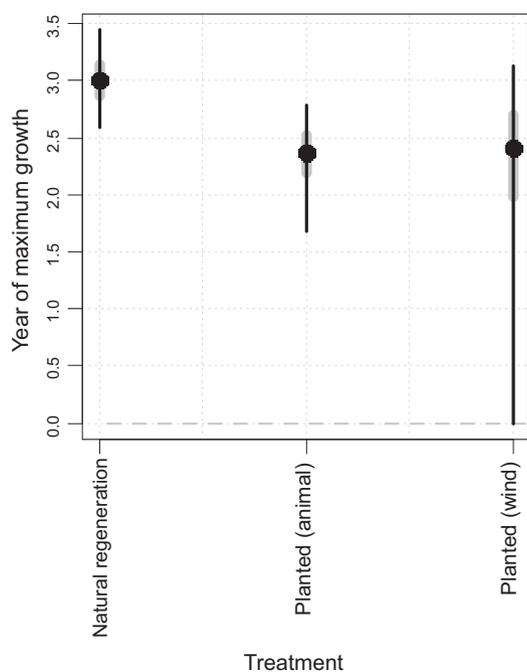
trajectories, survival probability and reproduction probability across species and planting treatments.

#### Abundance of reproductively mature recruits

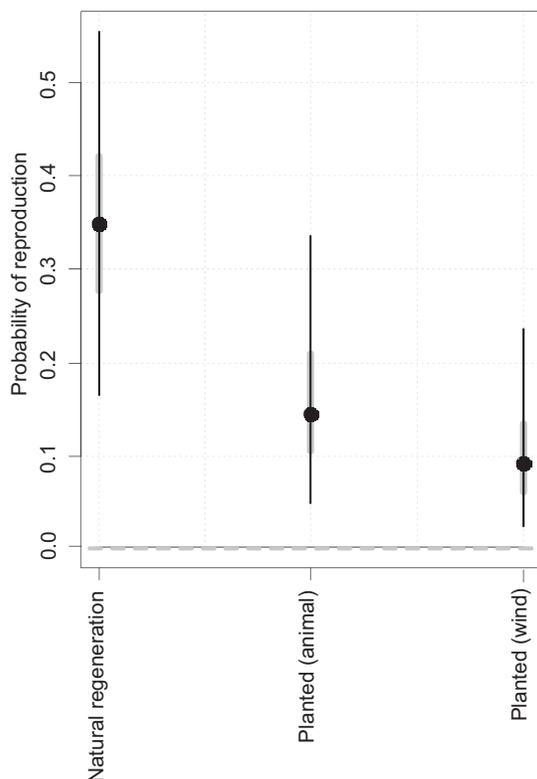
To address Question (4), we compared the total abundance of all natural recruits that emerged during the 7-year study period with the abundance of natural recruits that achieved reproductive status at least once during the same period. Previous work in our experimental plots has demonstrated that higher external seed rain in planted plots results in higher abundance of natural recruits in these plots, relative to naturally-regenerating plots (de la Peña-Domene *et al.* 2013, 2014; Li *et al.* 2017). Consequently, if the effects of planting treatment on individual demography are weak relative to the effects of planting treatment on seed arrival, we would expect a higher abundance of reproductive recruits in planted plots.



**Figure 1** Species-level effects of successional age and size on demographic rates. This figure shows predicted effects of successional age on growth (mm basal diameter per month), the probability of survival and the probability of reproduction. Each coloured line represents one species, whereas the thick-black line represents the community-level average. Green lines represent mid- and late-successional species, whereas yellow lines represent early-successional species. For growth and survival, predictions are for an individual that remains the same size over the 80-month period. For reproduction, the probability of reproduction is plotted against size.



**Figure 2** Planted treatments accelerate time of maximum tree growth rates. This figure shows the predicted time of maximum growth rate for an average individual across the three treatments. The black dot represents the median parameter estimate, thick grey lines indicate 50% CI (credibility intervals) and the solid black line represents 95% CI.



**Figure 3** Probability of reproduction is higher in unplanted plots. This figure shows the probability of reproduction for an average individual across the three treatments. Dots and lines as in Fig. 2.

To quantify the effect of planting treatment on abundance of reproductively mature natural recruits, we used a negative binomial GLMM. The response variable in this model was the abundance of recruits of each species in each subplot. The predictor variables included intercept and planting treatment as species-level random effects, along with a plot-level random intercept to account for unmeasured differences between plots.

### Species successional status

We answered Question (5), by comparing demographic outcomes between species in different successional categories, including early-, mid- and late-successional species. To classify tree species, we used demographic and associational analyses from the Los Tuxtlas region (e.g., Purata 1986; Ibarra-Manríquez & Oyama 1992). For more details on our classification of successional status see Appendix S2.

## RESULTS

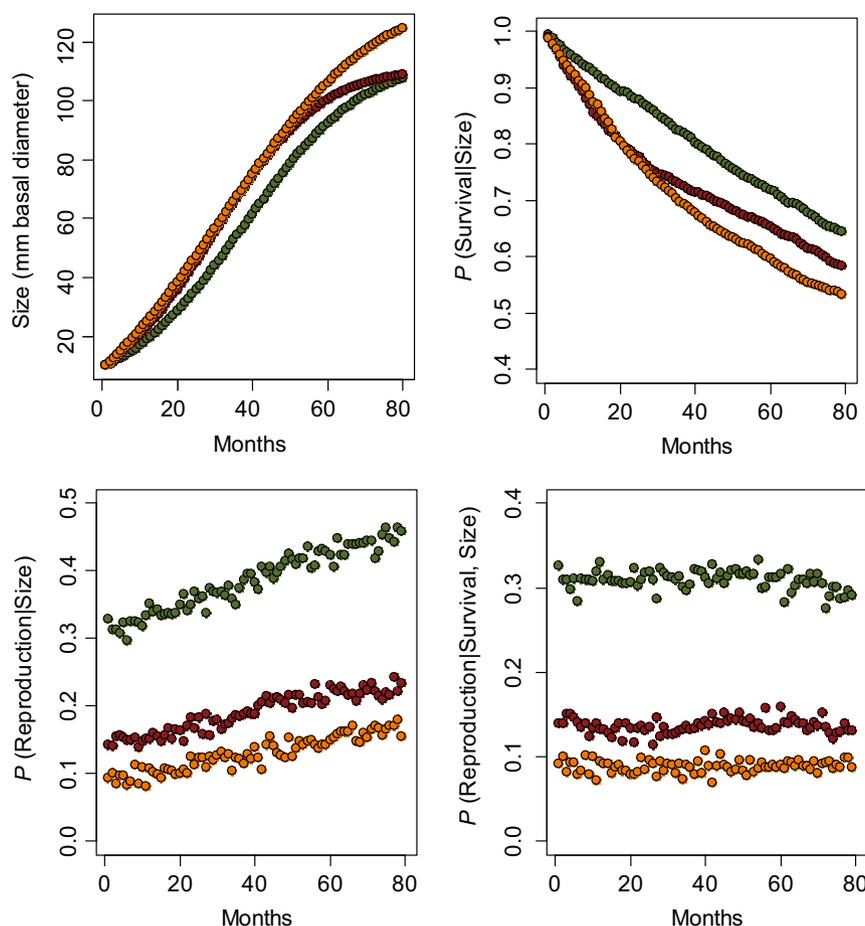
Over 18 censuses, we recorded 4871 growth measurements from 1108 individuals, 13 665 presence/absence records from 1865 individuals and 1153 reproductive phenology observations from 597 individuals. These measurements included size and survival observations from 50 species, and reproductive observations from 27 species, with a mean ( $\pm$ SD) of 37.3 ( $\pm$ 96.2) individuals per species (Fig. S1; Table S1).

### Growth

Both planting treatment and successional age had a significant impact on community-level growth rates. The strongest community-level effect was for the quadratic term for successional age, with a negative value indicating that the modelled relationship between successional age and growth was non-monotonic (hump-shaped) with a concave-down shape (Fig. 1). Growth rates in the wind-dispersed planting treatment were both lower overall and exhibited less of an effect of successional age, relative to the naturally regenerating or animal-dispersed treatments.

At the community-level, the interaction between planting treatments and successional age resulted in different timing of peak growth rates during the 80-month study period. For both planting treatments, peak growth occurred a median of 7.60 (animal-dispersed treatment) and 7.17 (wind-dispersed treatment) months earlier than in the natural regeneration treatment (Fig. 2). There was more uncertainty in estimates of peak time for growth in wind-dispersed plots than animal-dispersed plots, including a > 7% chance that peak growth rate occurred within the first 12 months of succession in this treatment.

We found the biggest impacts of species-level variation on growth for the intercept term, with a range of baseline growth rates from 0.98 mm to 4.51 mm per month. Five early-successional species had significantly higher growth rates than the average species: *Trema micrantha*, *Cecropia obtusifolia*, *Heliocarpus donnell-smithii*, *Eupatorium galeotii*, and *Heliocarpus appendiculatus*.



**Figure 4** Demographic tradeoffs of natural regeneration for simulated seedlings. These panels represent outcomes of the individual-based model (IBM) for new recruit demography. Each color dot represents the average of 10,000 runs of the IBM at a particular time point. The dark green dots represent natural regeneration, red dots represent the animal-dispersed planted treatment and orange dots represent the wind-dispersed planted treatment. In clockwise order, the panels represent predictions for size alone, predictions for survival conditional on size, predictions for reproduction conditional on size, and predictions for reproduction conditional on both size and survival.

## Survival

In contrast to growth, effects of successional age and planting treatment on survival were generally weak and uncertain (Fig. 1). The strongest community-level effect was for the impact of successional age on survival, with a median value of  $-0.64$  (95% CI:  $-1.36$  to  $0.07$ ), suggesting a negative relationship between survival and successional age. Detection rates were also negatively impacted by successional age, with a significant decline in the probability of re-finding a recruit over the course of the study.

Species-level survival was more variable than species-level growth. While the effects of successional age and planting treatment were minor for most species, a handful of early-successional species showed dramatic declines in survival over time, including *Piper umbellatum*, *Witheringia nelsonii*, and *Eupatorium galeotii*, with decreases in monthly survival over time of up to *c.* 25% for these species.

## Reproduction

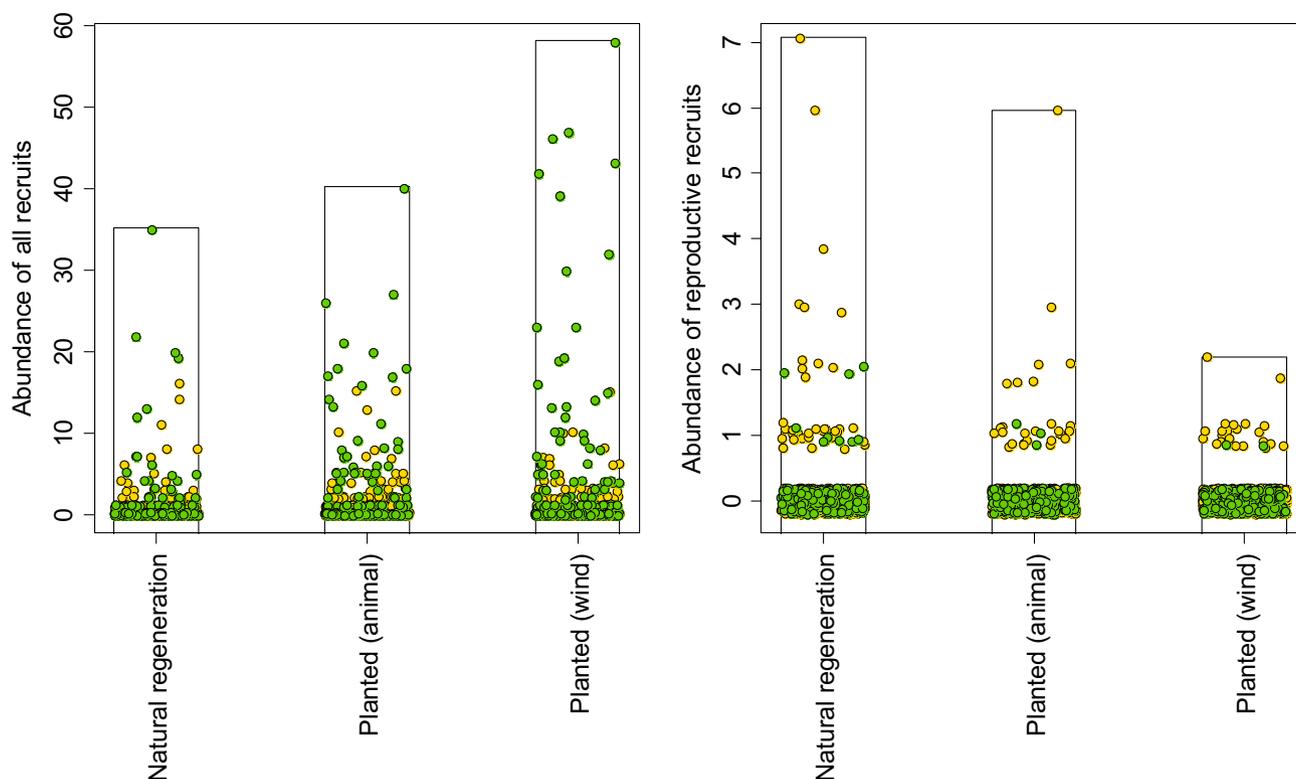
Community-level reproduction was strongly influenced by planting treatment, with a significantly lower probability of

reproduction in both planting treatments relative to natural regeneration (Fig. 3). For an average-sized individual, the probability of reproducing in the naturally-regenerating treatment was higher by a median of 19.0% (95% CI: 0.8 to 37.3%), relative to the animal-dispersed treatment, and higher by a median of 24.6% (95% CI: 8.8 to 43.6%), relative to the wind-dispersed treatment.

Species-level effects for reproduction showed far higher variance than either growth or survival (Fig. 1). Baseline reproduction probability ranged from a median of 1.6 to 93.9% for an average-sized individual. Three early-successional species had significantly higher baseline reproduction compared to an average species: *Piper* sp., *Witheringia nelsonii*, and *Conostegia xalapensis*, whereas two mid-successional species had significantly lower baseline reproduction: *Bursera simaruba* and *Cordia alliodora*. The species-level effect of size on reproduction ranged over an order of magnitude, with a tendency for greater size-dependence in mid-successional species.

## Individual-based model

At the community-level, the combined effect of successional age and size on growth led to sigmoidal size trajectories (Fig. 4).



**Figure 5** Abundance of all natural recruits vs. reproductive natural recruits This figure compares the observed abundance, across all censuses, of all recruits (left) and only those recruits that reproduced at least once (right). Each point represents one species by subplot combination. The colour of each point corresponds to successional status (yellow=early-successional and green=mid-successional). Data points were jittered to assist visual interpretation.

On average, our IBM predicted that new recruits in the naturally regenerating treatment remain slightly smaller than new recruits in the animal and wind-dispersed planted treatments. Median survival was consistently higher in naturally-regenerating treatments, although this effect was also relatively minor, with a maximum difference of *c.* 13% probability of survival between the naturally regenerating and wind-dispersed treatments. Relative to growth and survival, median differences in probability of reproduction over time were much larger between treatments, with a maximum difference of 24.3% probability between the naturally regenerating and wind-dispersed treatments. Without accounting for survival, the probability of reproduction tended to increase over time, as recruit size increased. However, when survival was factored in, the probability of reproduction remained nearly constant over the 80-month simulation (Fig. 4).

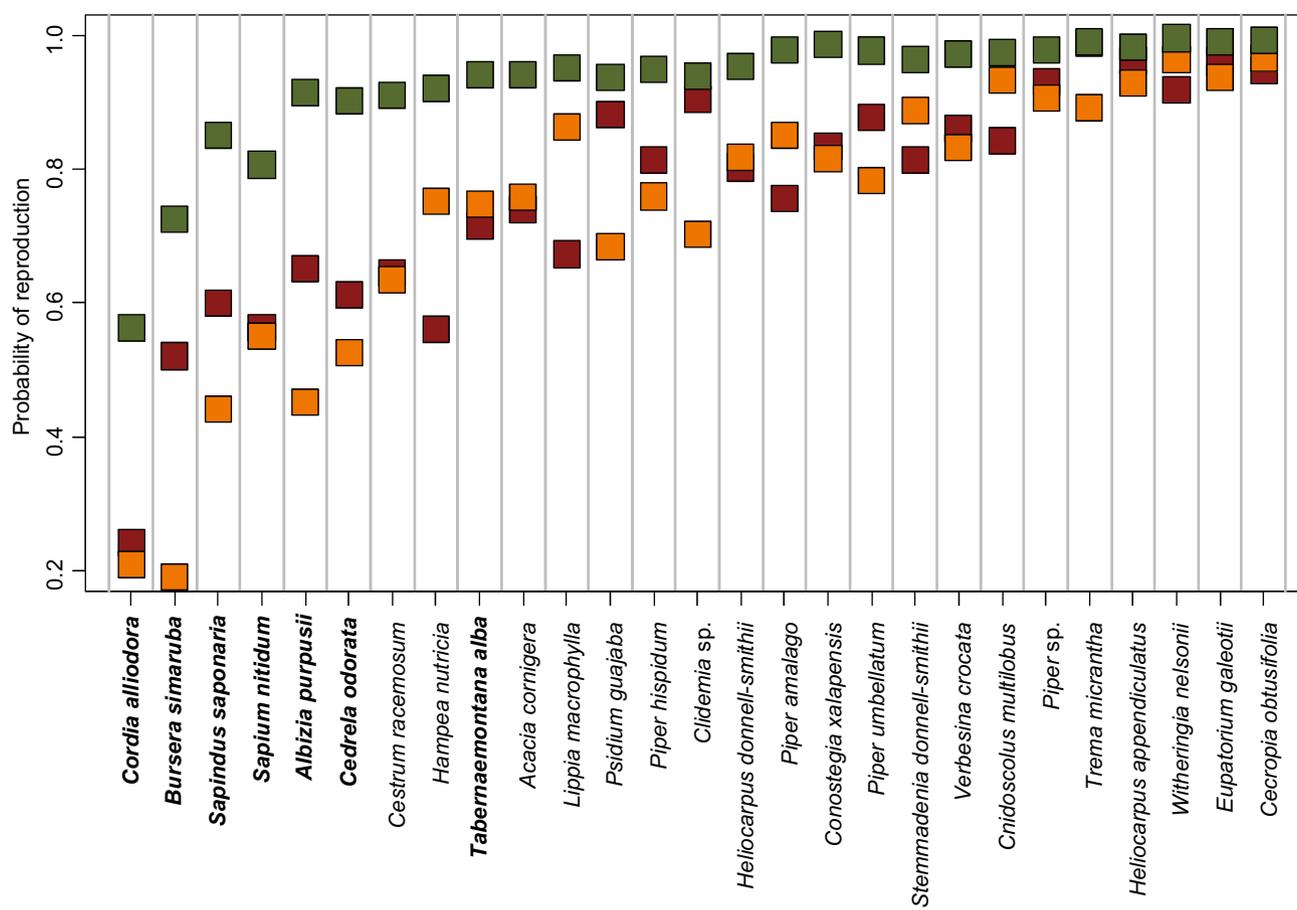
#### Abundance of reproductively mature recruits

Natural recruit abundance was lower in naturally-regenerating plots, with a total of 400 recruitment events in these plots compared to 676 and 912 recruitment events in animal-dispersed and wind-dispersed planted plots. However, the abundance of natural recruits that had achieved reproductive maturity was higher in naturally regenerating plots, with a total of 75 reproductive individuals in these plots, compared to 42 and 26 individuals in animal and wind-dispersed plots (Fig. 5). The negative binomial GLMM revealed that planting

treatments had significantly negative effects on reproductive recruit abundance, relative to natural regeneration, with a predicted decrease in abundance of 47% (95% CI: 22–95%) for animal-dispersed plots and a predicted decrease in abundance of 40.2% (95% CI: 19–78%) for wind-dispersed plots. This result indicates that the cumulative demographic benefits of natural regeneration for recruits outweigh higher rates of seed arrival in planted treatments.

#### Impacts of successional status on demographic outcomes

The best and worst treatments for achieving reproductive maturity during the 80-month period were similar across the 27 species in the IBM, with the best performance in naturally regenerating plots, followed by animal-dispersed planted plots, with wind-dispersed planted plots last (Fig. 6). The demographic benefits of natural regeneration were strongest for mid-successional species, with a maximum increase of *c.* 40% probability of achieving reproductive maturity for *Cordia alliodora* in natural regeneration vs. plantings. While none of the six species classified as late-successional reproduced during the course of the study, species with higher wood density (a functional trait related to successional status; Lasky *et al.* 2014; Boukili & Chazdon 2017) tended to perform worse in planted plots (Fig. S2). Overall, the species with the highest differences in demographic performance between natural regeneration and planted plots included six out of seven of the species classified as mid-successional.



**Figure 6** Effect of tree planting is greatest for non-pioneer tree species. This figure represents the outcome of the species-level IBM for the 27 species with observed reproduction during the study period. Species are ordered by average probability of achieving reproduction. Each square represents the probability an individual reproduced during the course of the 80-month simulation. Green squares represent natural regeneration, red squares represent animal-dispersed planted treatment and orange squares represent the wind-dispersed planted treatment. Mid-successional species are represented by bold text.

## DISCUSSION

The long-term success of forest restoration depends on whether native tree species can grow, survive and reproduce at sufficient rates to form self-sustaining populations. We monitored the demographic rates of naturally-recruited tree seedlings during the first 7 years of a tropical forest restoration experiment that included both plantings and plots undergoing natural regeneration. We found that the costs and benefits of tree planting for natural recruits varied across demographic rates. Demographic benefits of tree planting include higher recruitment rates early in succession and accelerated onset of peak growth rates. The primary demographic cost of tree planting was suppressed reproduction. We evaluated the cumulative impacts of these demographic costs and benefits by quantifying the probability that a new recruit achieves reproductive maturity. We found that for an average species, the probability of achieving reproductive maturity was nearly three times higher in naturally regenerating plots than planted plots. Despite higher overall recruitment in planted plots, abundance of reproductive recruits was higher in naturally regenerating plots, indicating that the demographic benefits of natural regeneration outweighed initial

differences in recruitment. The beneficial effect of natural regeneration on achieving reproductive maturity was highest for mid-successional species and minimal for early-successional species. Altogether, our study provides insight into the demographic mechanisms that underlie tropical forest restoration across the tree life cycle, from seedling to reproductive adult.

The differences in natural recruit demography between naturally regenerating vs. plantings found in our study have implications for the long-term consequences of these restoration treatments. Evidence on the ecological outcomes of active restoration compared to natural regeneration is mixed with vigorous debate on the relative merits of both treatments (Zahawi *et al.* 2014; Prach & del Moral 2015). In some cases, tree planting results in significantly faster recovery of canopy cover and tree species diversity (Shoo *et al.* 2016). Nevertheless, a recent meta-analysis found higher success rates of natural regeneration than restoration plantings for several biodiversity and forest structural attributes (Crouzeilles *et al.* 2017; but see Reid *et al.* 2018). In our study site, planted treatments increase the abundance of recruits early in succession, demonstrating potential benefits of planting for carbon sequestration and biodiversity (Li *et al.* 2017). Our results

show that these benefits of planted plots may come at a demographic cost to natural recruits.

Previous studies at our site and others have shown that tree planting accelerates early succession by increasing seed rain in planted plots (Zahawi *et al.* 2013; de la Peña-Domene *et al.* 2014, 2017). In this study, we found that natural regeneration improved the demographic performance of established recruits to the degree that abundance of reproductive recruits was higher in naturally regenerating plots, despite lower overall abundance of recruits in these plots. One implication of this result is that, over time, increased seed production by natural recruits within naturally regenerating plots could counterbalance the initial advantage of increased seed dispersal in planted plots. Indeed, one of the few studies to compare seed rain over time between plantings and naturally regenerating treatments during tropical forest restoration found that, despite significantly higher tree seed abundance in plantings during the first few years of succession, tree seed abundance became similar across all plots after 6–9 years (Reid *et al.* 2014). Increased reproduction in naturally regenerating plots could provide one explanation for the equivocal performance of restoration plantings and natural regeneration over long time periods. An essential qualification is that any demographic benefits of natural regeneration for recruits are conditional upon seed arrival. In landscapes where seed rain is extremely limited (Duncan & Chapman 1999; Blackham *et al.* 2013), the initial benefits of tree planting may overwhelm any disadvantages to natural recruits later on.

We found that mid-successional species benefited more from natural regeneration than early-successional species. Out of a total of 27 species, the 6 out of 7 species classified as mid-successional trees exhibited the greatest between-treatment differences in probability of achieving reproductive maturity. Because early-successional species generally have faster growth rates (Martínez-Garza *et al.* 2013) and reproduce at smaller sizes relative to other species (Wright *et al.* 2005), they may be able to achieve reproductive maturity early in succession, regardless of tree planting (Guzmán-Luna & Martínez-Garza 2016). A demographic advantage of natural regeneration for later successional tree species contrasts with studies that have found a lower abundance of these tree species in naturally regenerating plots, (Reid *et al.* 2014; Shoo *et al.* 2016). The apparent contradiction between benefits of tree planting for seed dispersal and costs of tree planting for reproductive potential at later life stages emphasises the importance of evaluating demography across the tree life cycle.

Our results highlight interactions between successional age and restoration treatments during the first 7 years of secondary succession. These interactions include peak growth rates for recruits in plantings, die-offs of some early successional species after *c.* 4 years, and higher reproduction in naturally regenerating plots. Accelerated growth early in succession in plantings could result from alleviation of barriers to tree growth, including competition with grass, high herbivory and water stress, by plantings in plots dominated by herbaceous vegetation (Holl *et al.* 2000; Hooper *et al.* 2005; Griscom *et al.* 2009). However, once tree canopy closure occurs, competition with other trees for light and below-ground resources is likely to become a major demographic bottleneck (Lasky *et al.* 2014), potentially

resulting in suppressed tree reproduction (Blake & Loiselle 1991) and lower growth rates. An important next step will be to explicitly quantify impacts of environmental covariates, such as tree canopy cover, root competition and conspecific density, on the demographic rates of natural recruits. Understanding these environmental factors could promote the design of restoration projects, such as applied nucleation, that optimise the density of planted trees (Zahawi *et al.* 2013).

While the first 7 years of data from our site reveal demographic differences between treatments, continued monitoring will be necessary to understand how these differences impact long-term forest recovery. Our metric of demographic success was the reproductive maturity of natural recruits, many of which are likely to represent the first generation of established trees in these restored plots. The presence of reproductive structures may not guarantee continued population growth rate if pollination failure (Wilcock & Neiland 2002) seed predation (Holl *et al.* 2000), or low germination rates (Doust *et al.* 2006) restrict establishment of the next generation of recruits. To forecast population growth rates, demographic monitoring that links seed production of individual trees to seedling recruitment will be required. In addition, environmental conditions in plots are likely to continue to change beyond the 7-year period of our study. These changes, including conspecific density, light environment and soil composition, could alter the demographic costs and benefits of each treatment over time. For example, negative density dependence in plots with high recruit abundance could suppress tree growth and survival later in succession (Uriarte *et al.* 2005). Finally, our results represent a small subset of tree species diversity at our site, limited to species with observed reproduction during the study period, including only seven mid-successional tree species and no late-successional species. As more trees recruit into our restored plots, we anticipate extending our analyses to a broader range of species. Overall, our work speaks to the critical importance of long-term monitoring for understanding the dynamics of tropical forest restoration (Rozenaal *et al.* 2016).

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#### AUTHORSHIP

CMG designed the experimental plots and MDP created the field sampling scheme for the natural recruits. TTC analysed the data. All authors contributed to writing the manuscript.

## DATA ACCESSIBILITY

Data are available in the Dryad data repository (<https://doi.org/10.5061/dryad.1c1g42k>).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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