When does seed limitation matter for scaling up reforestation from patches to landscapes?

T. Trevor Caughlin,[1,3] Stephen Elliott,[2] and Jeremy W. Lichstein[1]

[1]*Department of Biology, University of Florida, Gainesville, Florida 32601 USA*
[2]*Forest Restoration Research Unit, Department of Biology, Science Faculty, Chiang Mai University
Huaykaew Rd, Chiang Mai 50200 Thailand*

Abstract. Restoring forest to hundreds of millions of hectares of degraded land has become a centerpiece of international plans to sequester carbon and conserve biodiversity. Forest landscape restoration will require scaling up ecological knowledge of secondary succession from small-scale field studies to predict forest recovery rates in heterogeneous landscapes. However, ecological field studies reveal widely divergent times to forest recovery, in part due to landscape features that are difficult to replicate in empirical studies. Seed rain can determine reforestation rate and depends on landscape features that are beyond the scale of most field studies. We develop mathematical models to quantify how landscape configuration affects seed rain and forest regrowth in degraded patches. The models show how landscape features can alter the successional trajectories of otherwise identical patches, thus providing insight into why some empirical studies reveal a strong effect of seed rain on secondary succession, while others do not. We show that seed rain will strongly limit reforestation rate when patches are near a threshold for arrested succession, when positive feedbacks between tree canopy cover and seed rain occur during early succession, and when directed dispersal leads to between-patch interactions. In contrast, seed rain has weak effects on reforestation rate over a wide range of conditions, including when landscape-scale seed availability is either very high or very low. Our modeling framework incorporates growth and survival parameters that are commonly estimated in field studies of reforestation. We demonstrate how mathematical models can inform forest landscape restoration by allowing land managers to predict where natural regeneration will be sufficient to restore tree cover. Translating quantitative forecasts into spatially targeted interventions for forest landscape restoration could support target goals of restoring millions of hectares of degraded land and help mitigate global climate change.

Key words: animal seed dispersal; Bonn challenge; directed dispersal; forest dynamics model; forest landscape restoration; Lambert's W function; mathematical model; perfect plasticity approximation; secondary succession; seed addition; seed limitation; spatial model.

INTRODUCTION

Over 700 million hectares of tropical forest have been destroyed or degraded (Achard et al. 2014). Restoring forest cover to some of these areas could yield enormous benefits for carbon sequestration, human livelihoods, and biodiversity conservation (Chazdon 2014). Consequently, ambitious plans have been put forward to reforest >350 million hectares of degraded land by 2030 (Menz et al. 2013, Pistorius and Freiberg 2014). Active reforestation involves planting trees or seeds, sometimes preceded by weed removal or soil amelioration. At the landscape level, such activities are logistically difficult and very expensive (Elliot et al. 2013), but thankfully they are not always needed. Where natural regeneration occurs at an acceptable rate, passive reforestation can be sufficient to meet restoration goals. Passive restoration involves simply letting forest regeneration proceed naturally, typically

after removing barriers to regeneration, such as cattle and fire (Holl and Aide 2011). However, rates of natural forest regeneration vary greatly from <20 yr (Chazdon et al. 2007) to >1,000 yr (Cole et al. 2014), and slow forest recovery can discourage stakeholders from allocating sites to reforestation (Zahawi et al. 2014). Differences in landscape context, configuration, and history are thought to underlie these divergent results but are difficult to untangle in empirical studies, where replication at the landscape scale is limited (Norden et al. 2015).

Seed rain (the number of seeds arriving to a site per area per time) is a vital component of natural forest regeneration that depends on landscape features beyond the scale of most field studies. Recruitment of forest species in deforested patches requires external seed input, since seeds of the vast majority of tropical tree species in the soil seed bank become unviable within a year after deforestation (Elliott et al. 2006). Seed rain in deforested patches depends on multiple landscape features, including the spatial configuration of remnant seed sources, the density and species of seed-dispersing animals, and the strength and direction of wind. The impact of seed rain on tree abundance depends on the degree to which

[3]Present address: School of Forest Resources and Conservation, University of Florida, Gainesville, Florida 321611 USA.
E-mail: trevor.caughlin@gmail.com

recruitment is limited by seed input (seed limitation) vs. local conditions that affect growth and survivorship across tree life stages (establishment limitation). The degree of seed limitation is variable in space, depending on local and landscape contexts (Caughlin et al. 2013), and it can change over time, due to feedbacks between seed rain and plant demography (Kauffman and Maron 2006).

Due to these complexities, empirical studies that quantify the impact of seed rain on reforestation rate often yield contradictory results. Adding tree seeds to degraded sites sometimes increases seedling abundance (Hooper et al. 2005, Bonilla-Moheno and Holl 2010, Tunjai and Elliott 2012) and sometimes has no effect (Engel and Parrotta 2001, Doust et al. 2006, Reid et al. 2013). Similarly, some studies show that landscape features that increase seed availability (such as the amount of surrounding forest cover and nearness to forest edge) increase woody stem density and diversity in forest restoration plots (Endress and Chinea 2001, Crk et al. 2009, Griscom et al. 2009, Robiglio and Sinclair 2011), while others report no significant effects (Duncan and Duncan 2000, Zahawi et al. 2013). These contradictory results make scaling up restoration from patches to landscapes difficult, because if landscape features alter seed limitation, predictions from one patch cannot be applied to others, even if within-patch conditions are identical.

Ecological theory provides a framework for understanding feedbacks between patches and landscapes (Lichstein and Pacala 2011, Chesson 2012). A key insight from mathematical models is that differences in between-patch dispersal can result in divergence between otherwise similar communities. For example, density-dependent dispersal, between-patch movement that depends on the density of conspecific individuals, can lead to coexistence of competing species under conditions where density-independent dispersal would lead to competitive exclusion (Amarasekare 2004). A second example of dispersal variation is directional dispersal, between-patch movement in one prevailing direction, which can lead to spatial differences in plant species richness (Levine 2003). A final example is directed seed dispersal, a tendency for an increase in seed rain in high quality patches, which can increase regional tree abundance (Purves et al. 2007). Some of these theoretical insights have parallels in the empirical literature on reforestation. For example, directed seed dispersal underlies tree-planting schemes designed to attract seed-dispersing animals to reforestation sites (Elliott and Kuaraksa 2008, de la Peña-Domene et al. 2013). Quantitative models offer an opportunity to simulate between-patch interactions in a wide range of landscape configurations and extend empirical knowledge of reforestation dynamics beyond the scale of single patches (Acevedo et al. 2012, Pichancourt et al. 2014, Tambosi et al. 2014).

We present a modeling framework to study reforestation in heterogeneous landscapes. We begin by developing a model for time to tree canopy closure over a dense layer of herbaceous vegetation. Because canopy closure means that trees have successfully out-competed herbs for light resources, it is a tipping point in secondary succession and a major milestone for active forest restoration (Elliot et al. 2013). We use this model to quantify the effects of seed rain on canopy closure over a wide range of tree growth and survival rates, representing within-patch differences in establishment quality. Next, we determine when positive feedbacks between seed rain and canopy cover, including directed dispersal and within-patch reproduction, can significantly accelerate canopy closure. Finally, we ask how between-patch interactions alter successional trajectories in heterogeneous landscapes. By incorporating landscape features into a model with parameters that are commonly estimated in field studies of reforestation, we address the critical need to scale up ecological knowledge for large-scale restoration projects.

Methods and Results

Model overview

Our model applies to deforested patches that are initially covered by a dense layer of shade-intolerant vegetation with little or no tree cover. This early-successional vegetation may include grasses, other herbs, vines, and/or shrubs (Hooper et al. 2002, Slocum et al. 2006, Marliana and Rühe 2014). Examples include recently abandoned cattle pasture (Zahawi and Augspurger 2006, de la Peña-Domene et al. 2013) and degraded patches dominated by invasive grasses (Hooper et al. 2005, Blackham et al. 2013). We emphasize that our model can be applied to a multitude of scenarios where tree species are recruiting beneath a layer of established vegetation, including pioneer deserts dominated by early successional trees and shrubs (Mesquita et al. 2001, Martínez-Garza and Howe 2003). For conciseness, we hereafter refer to this shade-intolerant, early-successional vegetation as the grass layer, but we emphasize that the model applies equally to nongrass early-successional vegetation that can potentially delay or prevent forest succession. Our primary objective is to predict time to canopy closure, the moment at which tree crowns completely cover the patch and the grass layer is no longer a competitive threat to tree establishment.

We model the crown area of tree cohorts over time, dividing cohorts into those beneath and those above the top of the grass layer. Tree height (at the top of the crown) determines whether a cohort is in the grass or canopy layer and is related to crown area by an allometric equation. We assume that the spatial arrangement of individual tree crowns is perfectly plastic, filling any available space in the horizontal before overlapping with other tree crowns (Strigul et al. 2008). Forest dynamics models that have employed this perfect plasticity approximation (PPA) have reproduced patterns of secondary succession in temperate forests (Zhang et al. 2014), carbon allocation of trees across gradients of water availability (Farrior et al. 2013), and forest structure in a species-rich tropical

Table 1. When will differences in seed rain change time to canopy closure?

Model	Result	Graphical result
A single patch with constant seed rain over time (Eqs. 7–9). This simple model ignores within-patch reproduction and the effects of canopy cover on seed rain (e.g., directed dispersal).	Arrested succession occurs when seed rain or establishment rates are too low to enable tree canopy closure. Equilibrium canopy cover is proportional to seed rain. If arrested succession is avoided, time to canopy closure is most strongly limited by seed rain when patch quality is just high enough to prevent arrested succession. As patch quality (e.g., tree growth and/or survival rates) increases, seed limitation sharply declines.	Fig. 1
A single patch with positive feedbacks between seed rain and canopy cover over time, due to either within-patch reproduction or directed dispersal (Eqs. 10, 11)	Feedbacks between seed rain and patch canopy cover decrease time to canopy closure when small increases in canopy cover early in succession lead to large increases in seed rain (i.e., decelerating fecundity curves in Fig. 2).	Fig. 3
Multiple reforesting patches in a landscape interact (compete for seeds) due to directed dispersal. Animals preferentially disperse seeds to patches with higher canopy cover (Eq. 12).	Directed dispersal (to patches with higher canopy cover) has the greatest effect on time to canopy closure when patch quality is heterogeneous, and when animal-dispersed seed availability (i.e., the total number of seeds available for dispersal) is at intermediate levels.	Figs. 4, 5

forest (Bohlman and Pacala 2012). Because our aim in this paper is to provide a general conceptual understanding of reforestation dynamics, we present results from a single species in the main text, and develop a more complex, multispecies version of the model in Appendix S5.

We first introduce a simple version of the model where tree recruitment in an early-successional patch depends solely on a fixed rate of seed rain from sources external to the patch. The simplicity of this model enables an exact solution for time to canopy closure that users with a wide range of quantitative expertise can explore interactively via a web app.[4] We then extend our model to include positive feedbacks between seed rain and within-patch canopy cover. Finally, we develop a multi-patch version of the model to quantify the effects of between-patch interactions on canopy closure (*model code available online*).[5] By focusing on time to canopy closure, we are able to develop tractable models for early succession, using parameters that can be estimated from data routinely collected in forest inventory plots and planting trials. In the remainder of *Methods and Results*, we derive the reforestation model and present detailed analytical and numerical results. Our main biological conclusions are summarized in Table 1. Readers who are primarily interested in the main conclusions, rather than the mathematical details, may skip the remainder of *Methods and Results* and refer to Table 1, followed by *Discussion*.

Time to canopy closure with constant seed rain

The purpose of the model presented below is to gain insights into the importance of seed rain for time to canopy closure across a range of tree establishment conditions. We begin by determining the crown area of a single tree cohort of trees of age (a), arriving with density S_0 in a grass-dominated patch. For simplicity, we assume a fixed height for the top of the grass layer (H_g; m), which is a reasonable approximation for vegetation in an arrested state of succession. We assume constant rates of height growth (G_g; m/yr) and mortality (μ_g; yr^{-1}) for trees shaded by the grass (i.e., height < H_g). These assumptions imply that the age of a tree that has grown to the top of the grass layer (a_g) is

$$a_g = \frac{H_g}{G_g} \qquad (1)$$

and that the probability that a single seed survives to reach the top of the grass layer is

$$e^{-\mu_g a_g} \qquad (2)$$

As in Strigul et al. 2008, we use a negative exponential function to represent survival. We assume that the crown area of a tree (i.e., the area of ground shaded by the tree) is proportional to its height. Thus, the crown area (m^2) of a tree above the grass layer is

$$c[H_g + G_c(a - a_g)] \qquad (3)$$

where c is a constant, relating crown area to height, G_c is the constant height growth rate (m/yr) of a tree that has emerged above the grass layer (i.e., age $a > a_g$), and the term in square brackets is the height of a tree with age $a > a_g$. Finally, we assume that trees above the grass layer die at a constant rate μ_c (yr^{-1}), so that the probability of surviving to age $a > a_g$ is

$$e^{-\mu_g a_g} e^{-\mu_c(a - a_g)} \qquad (4)$$

where the first exponential term is the probability of surviving to age a_g (or, equivalently, to height H_g; Eq. 1), and

[4] https://t-trevorcaughlin.shinyapps.io/ReforestationDynamics
[5] https://github.com/trevorcaughlin/ScalingUpReforestation

the second exponential term is the probability of surviving an additional $a − a_g$ years to height $H_g + G_c(a − a_g)$. Combining the above definitions and equations yields an expression for the total crown area per-unit ground area (m^2/m^2) of a single cohort i of initial density of arriving seeds S_0 (m^{-2}) as a function of the cohort's age (a_i):

$$CA_i = S_0 e^{-\mu_g a_g} e^{-\mu_c(a_i - a_g)} c[H_g + G_c(a_i - a_g)] \qquad (5)$$

Recall that a_g depends only on G_g and H_g (Eq. 1). Thus, the canopy area of a cohort in the model (Eq. 5) depends only on its age, the height of the grass layer (H_g), the initial density of arriving seeds (S_0), and the four demographic rates (G_g, G_c, μ_g, μ_c) that reflect a combination of the tree species traits and the site conditions.

Next, we derive an expression for the dynamics of the total crown area of all cohorts combined by assuming a constant flux of seed rain S (m^2/yr). S represents the number of seeds that arrive and germinate into seedlings. Adding a separate germination term would not affect our analysis of the model but would require additional data. Similar to the Lotka integral equation for age-structured populations (Lotka, 1939), we can determine the total canopy area of all cohorts combined (CA) at time $t > a_g$ by integrating over cohort age from $a = a_g$ (when a cohort first emerges from the grass layer) to $a = t$:

$$CA(t) = \int_{a_g}^{t} S e^{-\mu_g a_g} e^{-\mu_c(a-a_g)} c[H_g + G_c(a-a_g)]da \quad (6)$$

The integral simply adds up the crown areas (Eq. 5) of all cohorts taller than height H_g, while accounting for the increase in individual size and the decrease in density of each cohort as it ages. It is straightforward to solve the above integral to obtain an exact solution for canopy area at time t:

$$CA(t) =$$
$$\frac{Sce^{-\mu_g a_g}(G_c + H_g\mu_c - e^{-\mu_c(t-a_g)}[G_c + H_g\mu_c + G_c\mu_c(t-a_g)])}{\mu_c^2}$$
$$(7)$$

Given this expression for the dynamics of forest canopy area in an early-successional patch with constant seed rain S, we first determine the conditions required for canopy closure (and thus successful invasion by trees, as opposed to arrested succession), and then we determine the time to canopy closure (if the conditions for canopy closure are met). By definition, canopy closure occurs when $CA \geq 1$; i.e., when the total crown area is at least as large as the ground area (note that a second tree canopy layer forms when $CA > 1$; Strigul et al. 2008). To determine if a given set of parameters describing tree demography ($S, G_g, \mu_g, G_c,$ and μ_c) and the grass layer (H_g) will result in canopy closure, we solve for canopy area at equilibrium; i.e., as t approaches ∞. As t increases, Eq. 7 approaches the equilibrium:

$$\widehat{CA} = Se^{-\mu_g a_g} c \left(\frac{H_g}{\mu_c} + \frac{G_c}{\mu_c^2} \right)$$
$$= (Se^{-\mu_g H_g / G_g}) c \left(\frac{H_g}{\mu_c} + \frac{G_c}{\mu_c^2} \right) \qquad (8)$$

As expected, this expression reveals that $\widehat{CA}$ increases with S, G_g, and G_c, and decreases with μ_g and μ_c. Assuming biologically reasonable parameter values (e.g., $G_c > G_g$ and $\mu_c < \mu_g$), increasing H_g decreases $\widehat{CA}$. A key result from the solution in Eq. 8 is that $\widehat{CA}$ increases linearly with S: increasing seed rain (S) always increases canopy area at equilibrium ($\widehat{CA}$), regardless of other parameter values in the model.

While the equilibrium solution quantifies the demographic conditions that would result in canopy closure ($\widehat{CA} \geq 1$) vs. arrested succession ($\widehat{CA} < 1$) in the long-term, a time to canopy closure of 5 yr has very different management implications than a time to canopy closure of 100 yr (Zahawi et al. 2014). Consequently, a quantitative understanding of the model's transient dynamics is desirable. With the assumption of constant seed rain S, it is possible to find an exact solution for time to canopy closure (t_1):

$$t_1 = a_g - \frac{\left[W_{-1}\left(e^{\left(\frac{-H_g\mu_c}{G_c}-1\right)} \left[\frac{\mu_c^2 e^{\mu_g a_g}}{G_c S c_1} - \frac{H_g\mu_c}{G_c} - 1 \right] \right) + \frac{H_g\mu_c}{G_c} + 1 \right]}{\mu_c}$$
$$(9)$$

where W_{-1} is the nonprincipal branch of Lambert's W function (Corless et al. 1996, Lehtonen 2016). This closed-form expression can determine time to canopy closure, using parameters from individual-level demography, without the need for numerical simulations. As S increases, t_1 decreases to an asymptotic value of a_g; i.e., the theoretically minimum time to canopy closure is simply the time it takes for a tree to grow to the top of the grass layer (Appendix S1).

We used Eq. 9 to address our first objective and quantify the effect of seed rain on t time to canopy closure across a wide range of patch quality, represented by different growth and survival rates (Fig. 1; *application available online*).[6] Variation in demographic rates across sites could represent differences between species or differences within a single species due to changing environmental conditions. We conceptualize patch quality as variation in growth and survival rates because there is strong evidence that patch conditions (e.g., precipitation and soil fertility) impact these demographic rates during early succession (van Breugel et al. 2011) and that spatial differences in growth and survival impact forest dynamics (Vanderwel et al. 2016). A major finding of our analysis is that when patch quality is near the threshold for arrested succession ($\widehat{CA} = 1$; Eq. 8), very small increases in seed rain lead to large reductions in time to canopy closure. This

[6] https://t-trevorcaughlin.shinyapps.io/ReforestationDynamics

result holds whether low patch quality is due to low survival, low growth, or low seed rain (Fig. 1). However, time to canopy closure was sensitive to changes in seed rain only in the limited region of parameter space where t_1 is far from its asymptotic value of a_g. For example, with parameter values from Appendix S2, when seed rain is 0.22 seeds·m^{-2}·yr^{-1}, an increase of 0.01 seeds·m^{-2}·yr^{-1} led to a decrease of 7.03 yr in time to canopy closure, but when seed rain is 2.2 seeds·m^{-2}·yr^{-1}, an increase of 0.01 seeds·m^{-2}·yr^{-1} led to only a 0.03 yr decrease in time to canopy closure. These results demonstrate that changes in seed rain strongly affect canopy closure only when patch quality is high enough to prevent arrested succession (i.e., when $\widehat{CA} > 1$) and when patch quality is low enough that a small number of additional seeds can lead to substantial increases in the rate of reforestation (i.e., when $t_1 \gg a_g$).

Feedbacks between canopy cover and seed rain

The analytical tractability of this model relies on several simplifying assumptions, including the assumption of constant seed rain, which is unlikely in a changing landscape. Seed rain reaching a reforesting patch is likely to increase as canopy cover in the patch increases due to within-patch reproduction, as trees mature and begin fruiting, and directed dispersal, as tree canopy cover attracts seed-dispersing animals. Although within-patch reproduction can provide fruiting resources that attract animals and increase directed dispersal, directed dispersal can occur regardless of fruit availability (de la Peña-Domene et al. 2013). For example, adding bird perches to pasture can significantly increase seed rain (Holl 1998). We modified our model to include these positive
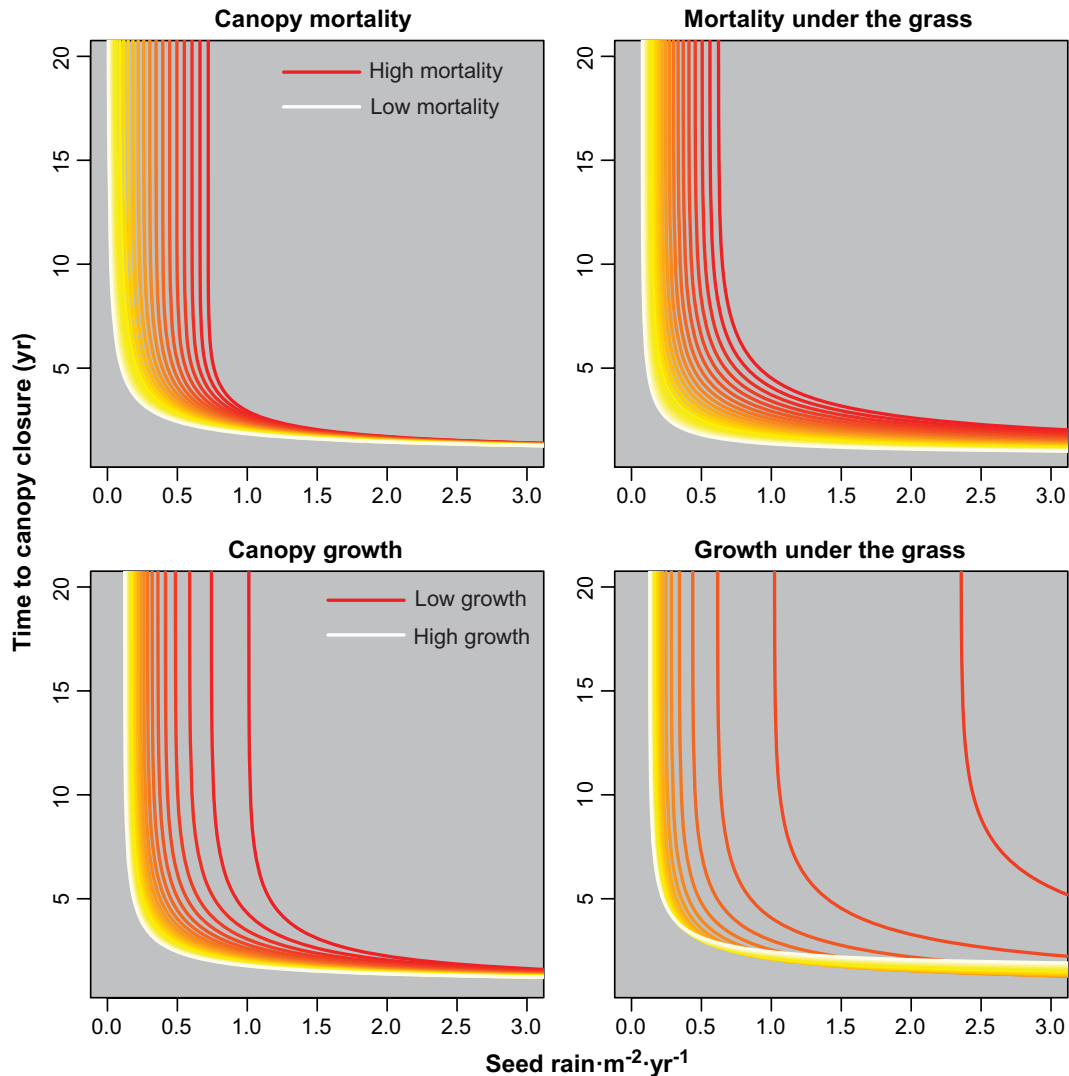

Fig. 1. Sharp thresholds in sensitivity of canopy closure to seed rain. Each panel represents a vital rate in the reforestation model, perturbed by a proportional factor from −0.99 to 0.99. Each line represents a single perturbed value of each vital rate. The red line represents the lowest growth or highest mortality rate, while lighter yellow colors represent high growth or low mortality.

feedbacks between canopy cover and seed rain as well as an additive term for baseline global seed rain (i.e., seed rain that is distributed randomly across the landscape independent of the patch state). Because adding feedbacks between canopy cover and seed rain complicates an analytical solution for time to canopy closure, we used numerical simulations of a discrete-time version of the model to evaluate how within-patch reproduction and directed dispersal affect reforestation dynamics.

Within-patch reproduction at time t in the simulation model is the sum of the reproduction of the n tree cohorts in a patch, which we assume follows a power law function of crown area. Combining this within-patch reproduction with constant global seed rain yields the total seed rain in a patch at time t:

$$S_t = \text{global} + \sum_{i=1}^{n_t} [f_1 CA_{i,t}^{f_2}] \tag{10}$$

where $CA_{i,t}$ is the crown area of cohort i at time t, n_t is the number of cohorts in the patch at time t; and f_1 and f_2 are parameters relating reproduction to crown area.

To explore the effects of directed dispersal, we modified Eq. 10 so that the power law function applies to the total crown area in a patch, assuming that visitation by animal seed dispersers depends on patch canopy cover. In this case, the total seed rain in a patch at time t is

$$S_t = \text{global} + f_1 \left[\sum_{i=1}^{n_t} CA_{i,t} \right]^{f_2} \tag{11}$$

The shapes of the above power laws depend on the exponent f_2. When f_2 is >1, seed rain increases with canopy cover at an accelerating rate, with an initially small response that increases as canopy cover increases. In contrast, when f_2 is <1, seed rain increases with canopy cover at a decelerating rate, with an initially large response that decreases as canopy cover increases (Fig. 2). For both within-patch reproduction and directed dispersal, accelerating ($f_2 > 1$) and decelerating ($f_2 < 1$) functions correspond to different biological scenarios. Within-patch reproduction is likely accelerating for most tree species that only reproduce when they are large (Caughlin et al. 2013) and decelerating for fast-growing shrubs that reach maturity when still relatively young and small (e.g., Deering and Vankat 1999). Directed dispersal is likely accelerating for disturbance-sensitive primary seed dispersers, such as primates that only visit patches with high canopy cover (Kirika et al. 2008), and decelerating for disturbance-resistant animals, such as small birds that increase visitation rates in response to small increases in perching habitat (e.g., Holl 1998, Zahawi and Augspurger 2006). Simulation experiments enabled us to disentangle the effects of both types of seed rain feedback for time to canopy closure. However, we note that in reality, within-patch reproduction and directed dispersal are likely to covary (trees that with large seeds dispersed by
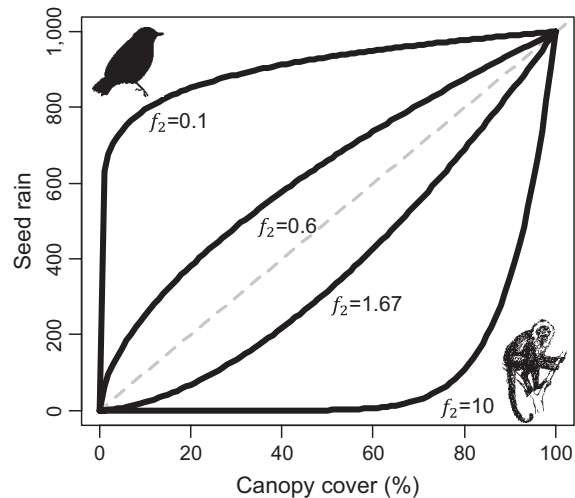

Fig. 2. Accelerating and decelerating feedbacks in canopy cover and seed rain. Each line represents a different shape of the power law that defines the relationship between canopy cover and seed rain. Numbers below each line represent the exponent term of the power law (f_2). Values of $f_2 > 1$ indicate accelerating functions, while values of $f_2 < 1$ indicate decelerating functions. For directed dispersal, disturbance-resistant birds are expected to respond to canopy cover with a decelerating curve, while primates are expected to respond with an accelerating curve.

disturbance-sensitive frugivore are also likely to have large size thresholds for reproductive maturity; Martínez-Garza and Howe 2003).

We illustrate our results using parameter values for a representative species (Appendix S2), but we note that our results are qualitatively robust across a wide range of growth, mortality, and seed rain parameters (Appendix S3). In the absence of within-patch reproduction or directed dispersal, a constant global seed rain of 0.005 seeds·m^{-2}·yr^{-1} leads to an equilibrium canopy cover of 2%; i.e., reforestation fails, and the early-successional state persists. Using this example of arrested succession as a baseline scenario, we evaluated the effects of directed dispersal and within-patch reproduction with both accelerating and decelerating seed rain feedbacks over a 25-yr period.

The key result from our simulations is that feedbacks between canopy cover and seed rain are most likely to decrease time to canopy closure when the shape of the feedback is decelerating ($f_2 < 1$). For example, canopy closure occurs within 5 yr for simulations with $f_2 = 0.1$, and within 9 yr with $f_2 = 0.6$, for both within-patch reproduction and directed dispersal scenarios (Fig. 3). In contrast, after 25 yr, accelerating feedbacks ($f_2 = 10$ and $f_2 = 1.67$) result in canopy cover only slightly different from the arrested-succession equilibrium predicted by the constant seed rain (no feedbacks) model. Relative to overall differences between accelerating and decelerating functions, differences between directed dispersal and within-patch reproduction were minor.
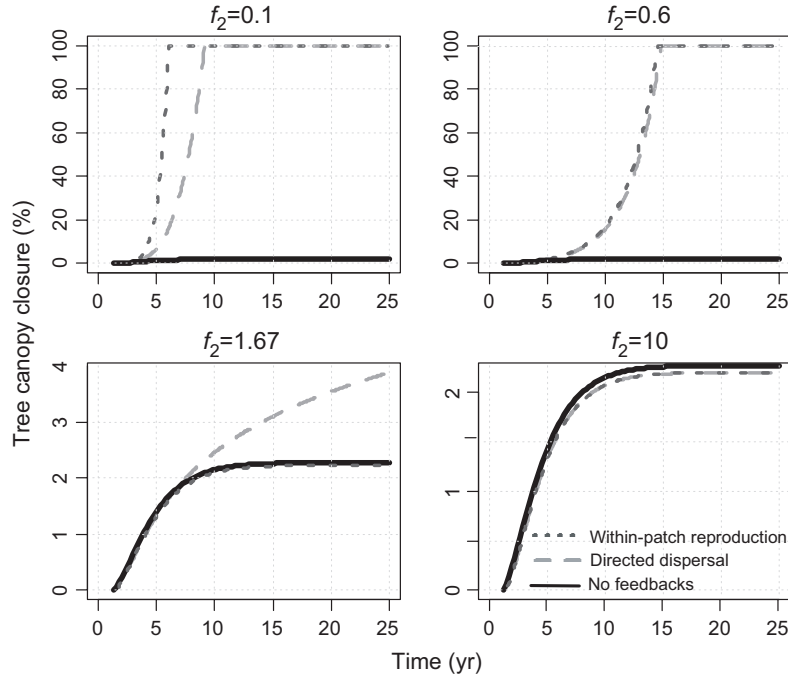
FIG. 3. Feedbacks between canopy cover and seed rain strongly affect time to canopy closure if the seed-rain vs. canopy-cover curve is decelerating. Each panel shows canopy cover during a 25-yr simulation. The dotted gray line represents within-patch reproduction, the dashed gray line represents directed dispersal, and the solid black line represents no feedbacks with seed rain only from a global seed rain term. While canopy cover in simulations with accelerating feedbacks ($f_2 > 1$; Fig. 2) is very similar to the model with no feedbacks, simulations with decelerating feedbacks ($f_2 < 1$; Fig. 2) reach higher levels of canopy cover faster.

Effect of between-patch interactions on canopy closure

The directed dispersal model in the previous section assumes that seed dispersal to a patch depends only on canopy cover in the patch. However, visitation by seed-dispersing animals, the mechanism behind directed dispersal, is affected by landscape processes, including between-patch interactions. For example, birds in fragmented landscapes preferentially visit patches with higher canopy cover (Zahawi and Augspurger 2006), potentially leading to decreased visitation to early-successional patches that are near late-successional patches (Reid et al. 2014). In this section, we extend our model for directed dispersal from a single patch to a landscape with multiple patches, where seed rain is directed towards patches with higher canopy cover.

Our multi-patch model represents a landscape with five patches, each with the same initial conditions. Seed rain into a patch depends on a constant global seed rain term and a directed dispersal term that allocates seeds to a patch based on its canopy cover relative to the canopy cover in surrounding patches at a given time:

$$S_{j,t} =$$

$$\text{global} + f_1 \left(\sum_{i=1}^{n_{j,t}} \text{CA}_{i,j,t} \right)^{f_2} \frac{\left(\sum_{i=1}^{n_{j,t}} \text{CA}_{i,j,t} \right)^{f_2}}{\frac{1}{5} \sum_{k=1}^{5} \left[\left(\sum_{i=1}^{n_{k,t}} \text{CA}_{i,k,t} \right)^{f_2} \right]} \quad (12)$$

where $S_{j,t}$ is the seed rain (m^2/yr) in patch j at time t; f_1 represents animal-dispersed seed availability (in addition to the baseline global seed rain); $\text{CA}_{i,j,t}$ is the crown area of cohort i in patch j at time t; and $n_{j,t}$ is the number of cohorts in patch j at time t. Without the quotient on the far right, Eq. 12 is identical to Eq. 11, which describes seed rain for an isolated patch, assuming directed dispersal depends on the patch's canopy cover. The quotient on the right represents the between-patch interactions in the multi-patch model as the ratio of the attractiveness of a patch to animal seed dispersers to the mean attractiveness of the five interacting patches in the multi-patch model. Our multi-patch model assumes that animal seed dispersers will be more or less attracted to a given patch depending on its canopy cover relative to other nearby patches, which is consistent with observations (Reid et al. 2014).

We quantified the importance of between-patch interactions for canopy closure by comparing canopy cover of an isolated patch to that of an initially identical connected patch in the multi-patch model. If between-patch interactions are important for canopy closure, we would expect the isolated and connected patches to differ in their time to canopy closure. In our model, the strength of between-patch interactions depends on three factors: availability of animal-dispersed seeds (f_1), landscape heterogeneity (variation in tree growth and mortality rates among patches in the multi-patch model), and the shape of the directed dispersal function (f_2). We designed a
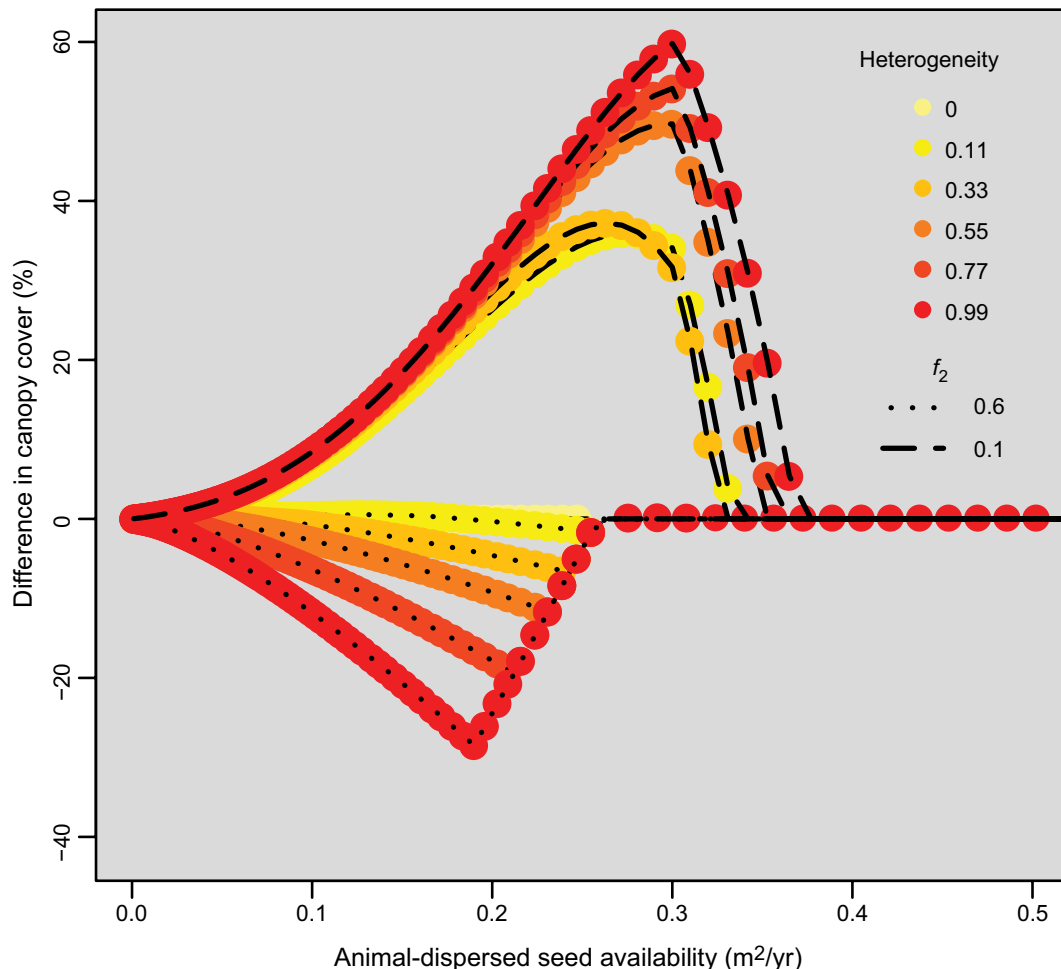
Fig. 4. Effect of landscape heterogeneity on between-patch interactions. This figure shows differences in percentage of canopy cover between an isolated and a connected patch after 30 yr, representing the effect of between-patch interactions on reforestation dynamics. *Y*-axis values of 0%, −50%, and 100%, respectively, represent cases where canopy cover in the isolated patch was the same, half as much, or twice as much as in the connected patch. Each point represents a different run of the simulation experiment with a given level of animal-dispersed seed availability and a level of landscape heterogeneity from 0 (all patches are identical, lightest colored dot) to 0.99 (99% difference between the best and worst patch in the landscape, darkest colored dot). Dotted lines represent runs of the simulation with $f_2 = 0.1$ and dashed lines represent runs where $f_2 = 0.6$

simulation experiment to quantify how all three factors affect between-patch interaction strength, by varying f_2 from 0.1 to 1.7, f_1 from 0.002 to 100 seeds·m^{-2}·yr^{-1} and manipulating landscape heterogeneity in the four patches surrounding the connected patch from 0 (all patches are the same) to 0.99 (worst patch has growth and survival 99% lower and best patch has growth and survival 99% higher than the connected patch). Varying animal-dispersed seed availability (f_1) in our simulations implicitly represents landscape features that alter seed rain, such as distance to primary forest (Griscom et al. 2009, Robiglio and Sinclair 2011). Spatially explicit models can directly include such distance metrics (e.g., Middendorp et al. 2016), but the complexity of these models limits general conceptual understanding, which was our main goal. Landscape heterogeneity can refer to

a wide range of environmental variables, including edaphic/topographic conditions, different forms of land use, and the degree of habitat fragmentation (Arroyo-Rodríguez et al. 2015). In the context of our simulations, landscape heterogeneity specifically refers to variability in patch quality (i.e., survival and growth rates) within a group of patches. In all simulations, the isolated and connected patches had identical growth and survival conditions, and all patches had a constant (global) seed rain of 0.005 seeds·m^{-2}·yr^{-1}.

As expected, isolated and connected patches only differed in their dynamics if the connected patches were embedded in a heterogeneous landscape (Fig. 4). In many cases, only a small amount of heterogeneity was required for strong between-patch interactions (Appendix S4). When landscape heterogeneity was present, the strength of
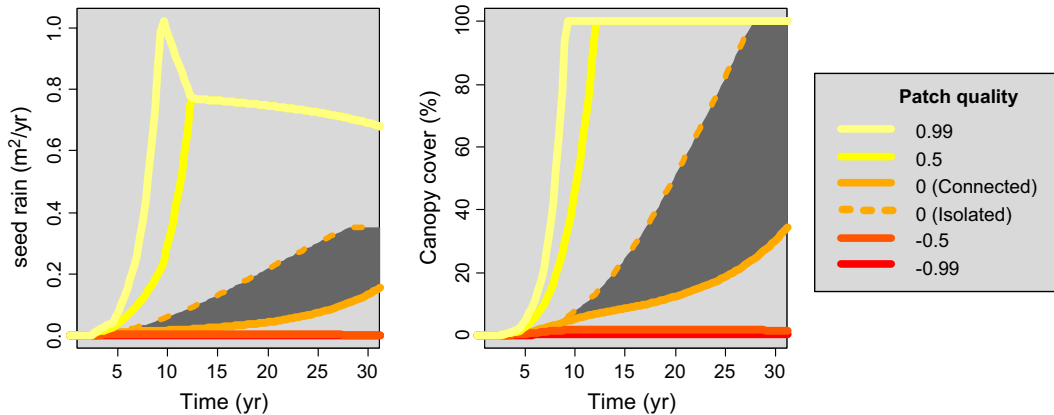
Fig. 5. Between-patch interactions lead to divergent canopy cover in two initially identical patches. This figure shows seed rain (m²/yr) and canopy cover (%) from a single run of the simulation experiment. Each line represents a single patch. Patch quality represents growth and survival, perturbed from 99% lower to 99% higher than a mean patch that is either connected to the other patches or isolated. The red line represents the lowest quality patch, while the lighter yellow represents the highest quality patch. The isolated patch is represented by a dashed line, while the connected patch is represented by a solid line. The dark gray shaded polygon indicates the difference between isolated and connected patch types. In this simulation, the connected patch receives lower seed rain than the isolated patch, a consequence of between-patch interactions. As a result, canopy cover in the isolated patch is higher than in the connected patch during the 30 yr of simulation.

between-patch interactions varied widely, depending on the two parameters in the directed dispersal function (f_1: availability of animal-dispersed seeds and f_2: shape of the directed dispersal function). Between-patch interactions were strongest at intermediate levels of animal-dispersed seed availability. Specifically, when there were enough animal-dispersed seeds available for their addition to impact canopy dynamics, yet few enough that not every patch could receive sufficient animal-dispersed seeds, between-patch interactions could result in a near 100% difference between isolated and connected patches (Fig. 5). The amount of animal-dispersed seed availability required for strong between-patch interactions depends on the shape of the directed dispersal function, determined by f_2. When f_2 was low ($f_2 < 1$; decelerating relationship between canopy cover and seed rain), between-patch interactions only occurred at low values of animal-dispersed seed availability (<3 seeds·m²·yr^{-1}). In contrast, when the directed dispersal function was accelerating ($f_2 > 1$), between-patch interactions only occurred at high levels of animal-dispersed seed availability (Appendix S4). Overall, our simulation results demonstrate how between-patch interactions can alter the successional trajectories of otherwise identical patches (Fig. 5).

DISCUSSION

We show how patch quality, directed dispersal, and between-patch interactions can determine whether reforestation dynamics are strongly or weakly limited by seed rain, thus reconciling seemingly contradictory observations in the literature. In a single patch receiving constant seed rain over time, time to canopy closure was very sensitive to seed rain when patch quality was just above the threshold for arrested succession and

insensitive to changes in seed rain when patch quality was more favorable. In models incorporating positive feedbacks between canopy cover and seed rain, feedbacks led to large decreases in time to canopy closure when seed rain responded to initial, small increases in canopy cover. Finally, preferential visitation of seed-dispersing animals to patches with higher canopy cover, a between-patch interaction, strongly affected canopy closure only at intermediate levels of animal-dispersed seed availability. These results explain why field studies in sites with different landscape configurations may find different effects of seed limitation on reforestation rate.

We found steep thresholds in the relationship between seed rain and time to canopy closure. Small changes in seed rain had large effects on canopy dynamics when patch quality was slightly above a threshold for arrested succession, but these effects diminished as patch quality increased (Fig. 1). Empirical comparisons of tree recruitment among patches with different levels of seed rain sometimes reveal an effect of seed limitation and sometimes do not (Hooper et al. 2005, Tunjai and Elliott 2012, Reid et al. 2014). Our model reproduces results of field studies that have shown that seed addition has a minimal effect on canopy closure when establishment conditions are very poor (Holl 1998, Reid et al. 2013) but also predicts diminishing returns of seed addition in patches where tree recruitment is already high. While the analytically tractable version of our model clearly oversimplifies the complex dynamics of secondary succession, in cases where restoration decisions are made primarily from tree growth and survival rates (e.g., field planting trials), our simple model could aid decision-making by integrating multiple vital rates into a single metric (time to canopy closure). Elsewhere, we demonstrate an app that uses the analytically tractable model to predict canopy cover from user-supplied

parameters (*data available online*).[7] We anticipate that publicly available tools, such as our app, could enable a broad audience of land managers and stakeholders to use mathematical models for restoration decision support.

Adding feedbacks between canopy cover and seed rain complicates the model but adds realism by representing within-patch reproduction and directed dispersal. On short time scales relevant for reforestation, the effect of these feedbacks depends on their shape. In our simulations, decelerating feedbacks, with an initially large response of seed rain to small increases in canopy cover, led to more rapid canopy closure than accelerating feedbacks (Fig. 2). In reality, directed dispersal and within-patch reproduction are likely to covary (Martínez-Garza and Howe 2003); however, our results suggest that how seed rain changes in response to initially small increases in tree canopy cover may be more important for time to canopy closure than the mechanism underlying the feedback between tree canopy cover and seed rain (Fig. 3). Directed dispersal during early succession is likely to exhibit decelerating feedbacks, because small birds (a primary agent for seed dispersal in degraded habitats) increase visitation to degraded sites with the addition of only a few perches (Holl 1998, Zahawi et al. 2013). Seeds of tree species that are dispersed between-patches by disturbance-sensitive frugivores (e.g., large-seeded tree species dispersed by primates) are more likely to exhibit accelerating feedbacks and may contribute little to canopy closure without active restoration techniques. Because large-seeded species are often slow to return to naturally regenerating secondary forests (Martínez-Garza and Howe 2003, Shoo et al. 2016), the overall shape of the directed dispersal function for a given patch is likely to change during secondary succession. Most empirical studies in reforestation plots have evaluated effects of directed dispersal in discrete treatments, for example, comparing tree seedling recruitment in tree plantations vs. pasture (de la Peña-Domene et al. 2013, Zahawi et al. 2013). Because the shape of the curve relating canopy cover to seed rain appears critical, empirical studies that measure how continuous differences in canopy cover affect seed rain are likely to have large payoffs for our understanding of successional dynamics.

A central question for forest landscape restoration is whether ecological field data, collected at the patch-level, can be scaled up to heterogeneous landscapes (Tambosi et al. 2014). If within-patch factors determine successional dynamics, a landscape can be represented as a collection of independent patches, and scaling-up merely requires an understanding of patch-scale processes. However, if between-patch interactions play an important role, predicting landscape-scale reforestation rates from patch-scale processes may be impossible. Empirical research has revealed conflicting results as to the importance of landscape features for within-patch reforestation (Endress and Chinea 2001, Zahawi et al. 2013). We found that even in a

relatively simple model with a single between-patch interaction, preference of seed-dispersing animals for patches with higher canopy cover, a multitude of outcomes are possible. Our results suggest that patch-scale processes determine reforestation rates in landscapes with very high animal-dispersed seed availability (such as patches close to primary forest) or very low animal-dispersed seed availability (such as *Imperata* mega-grasslands; Blackham et al. 2013). However, in landscapes where animal-dispersed seed availability is sufficiently high to have an impact on successional dynamics, yet low enough to present a barrier to tree population growth, we predict that between-patch interactions can critically impact reforestation rate. In our model, landscape heterogeneity (due to variable growth conditions among patches) magnifies the consequences of directed dispersal for between-patch interactions (Fig. 4). We expect other forms of landscape heterogeneity (e.g., differences in patch age) that affect animal seed-disperser visitation rates would have similar effects to those documented here.

In addition to tree canopy closure, tree biodiversity is also an important metric of forest restoration success (Chazdon et al. 2007). For example, in degraded pastures of Amazonia, a single genus of early successional trees (*Vismia*) can dominate regenerating stands for decades (Mesquita et al. 2015). Although tree canopy closure has occurred in these *Vismia* stands, their ability to restore biodiversity and provide ecosystem services is limited. Our model can be modified to represent cases where a few species of relatively short-statured early successional trees or shrubs form a persistent, low-diversity pioneer desert (sensu Martínez-Garza and Howe 2003) by increasing the height threshold to the height of the pioneer layer rather than the height of the initial herbaceous vegetation (e.g., grass). In this case, the model's end point of tree canopy closure represents the time at which recruiting trees have outcompeted the pioneer stage. Another complication related to species diversity is that tree functional diversity can determine the rate of reforestation (Lasky et al. 2014). While we present results for a single species, the perfect plasticity approximation used here can accommodate multiple species, including diverse tropical forest communities (Strigul et al. 2008, Bohlman and Pacala 2012), and adapting our model to include multiple species with varying demographic rates is possible (Appendix S5). Assuming that interactions between tree species are minimal before tree canopy closure, many of our general insights are likely to apply to multiple species communities (Appendix S5: Fig. S1). However, interactions among tree species, including competition and facilitation, are likely to affect early successional dynamics in many cases, and developing models to quantify these effects remains a formidable challenge (Gómez-Aparicio 2009).

Our model provides conceptual insights into how seed rain and patch quality affect if, and how fast, reforestation will occur. However, several simplifying features of our model will require more realistic treatments to guide specific landscape restoration projects. We assumed a constant

environment without taking into account stochastic disturbances, such as fire (Hooper et al. 2005) and forest clearance (Robiglio and Sinclair 2011), that generate spatial variability and alter successional dynamics (Lichstein and Pacala 2011). We assume that all patches begin with zero trees, however, the presence of isolated trees, live tree stumps, and tree seedbanks, can greatly speed up reforestation rate within patches (Elliot et al. 2013). The costs of incorporating these realistic but complicating factors into models of successional dynamics include increased data requirements and increased model complexity. Our minimally complex model provides a tractable case that can be understood in detail, and which can guide the development and interpretation of application-specific models.

Meeting the demand for large-scale forest restoration, in regions that lack extensive field data, will require synthesizing site-specific data across a range of empirical studies. Our model could provide a useful supplement to qualitative guidelines for reforestation, where seed availability has been identified as an important landscape threshold for determining restoration techniques (Holl and Aide 2011, Elliott et al. 2013). Translating quantitative forecasts into spatially targeted interventions for forest landscape restoration could support the UN's target of restoring hundreds of millions of hectares of degraded land within the next 15 years and help mitigate global climate change (Menz et al. 2013, Pistorius and Freiberg 2014).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1410/full

DATA AVAILABILITY

R code for the models and simulations in this paper is available online at http://dx.doi.org/10.5281/zenodo.57097.