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# Plant Functional Traits and Species Selection in Tropical Forest Restoration

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## Abstract

Restoration practitioners are faced with many decisions when restoring tropical forests in abandoned pastures. One of the most important decisions is selecting combinations of species to plant that can mitigate the many barriers seedlings face to maximize seedling establishment and growth. To aid in species selection, there is an increasing shift in using plant functional traits, yet there is still progress to be made in understanding how traits respond to barriers present during the early stages of seedling establishment. Here, I present an example of a trait–barrier relationship from our recent publication in the *Journal of Applied Ecology* and discuss how using functional traits can help develop tailored combinations of species for specific site conditions.

## Keywords

functional traits, restoration, seedling growth, succession, tropical landscapes

Restoring tropical forests in abandoned pastures is a challenging task. Not only are restoration projects typically expensive and time consuming, there is no real guarantee of success (Lamb, Erskine, & Parrotta, 2005). A principal requirement for restoration success is the ability of planted species to survive and quickly form canopies to obtain site capture. There are, however, multiple biotic and abiotic factors that can impede these establishment steps. These factors occur across multiple spatial scales, ranging from landscape scales, such as climate and topography, to local scales, including site and planting conditions and competition with resident grass and herbaceous species (Aide & Cavelier, 1994; Holl, 2017). These barriers have been identified in parallel with our growing understanding of natural forest recovery, and we have seen numerous strategies subsequently developed to mitigate these effects.

Central to most mitigation approaches is species selection. Species are often selected for restoration projects based on their varying life history strategies across a successional timeline and are planted in mixes designed to mimic natural forest recovery at an accelerated rate (Chazdon, 2014). For example, species' mixes commonly include a combination of fast-growing pioneer species and slower growing climax species. The rationale behind this is that the pioneer species are used to accelerate canopy closure to outcompete resident grass and weed species, while climax species will eventually replace pioneer species over time. However, we know that this scenario is not straightforward, due to the commonly observed growth-mortality trade-off of tropical trees, whereby fast-growing pioneer species are prone to increased levels of mortality, with the opposite being true for slow-growing climax species (Wright et al., 2010). As such, we are left with a dilemma: If we plant too many pioneer species, we may see increased growth, yet high levels of mortality may lead to delays in canopy closure or arrested succession. Conversely, if we plant too many climax species, this may improve survival rates, but will likely be to the detriment of canopy closure and speed of site capture. This situation is not new to restoration practitioners. Indeed, much research on species selection looking at combinations of pioneer and climax species

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has produced a wealth of planting strategies tailored to broad site conditions, along edaphic and climate gradients (Goosem & Tucker, 2013). However, given the heterogeneous nature of site context between restoration projects in the tropics (Holl & Kappelle, 1999), a more targeted approach to species combinations is required to deal with the specific barriers influencing seedling performance.

Functional traits, which underlie plant life history trade-offs, are increasingly used to identify and respond to site-specific barriers. Broadly, functional traits are physiological traits that can influence survival, growth, and fitness of an individual within a given environment (Violle et al., 2007). Pioneer and climax species generally have contrasting values for many traits, with some of the most notable examples being wood density, seed mass, leaf mass per area (LMA), and leaf density, with lower and higher values for each trait typical of pioneer and climax species, respectively (Chazdon, 2014; Whitmore, 1998). Increasing numbers of studies show promising evidence for the efficacy of using traits to accurately predict the performance of species in restoration contexts (Martínez-Garza, Bongers, & Poorter, 2013; Ostertag, Warman, Cordell, & Vitousek, 2015; Werden et al., 2018). Further, comprehensive frameworks of trait-based models of species assemblages have been developed to assess the importance of traits and trait values for ecological restoration success (see Laughlin, 2014). Implementing these frameworks is an emerging challenge for tropical forest restoration. There is a growing need to understand how: (a) traits vary between pioneer and climax species, (b) traits differentially effect species' responses to barriers present during the early stages of seedling establishment, and (c) trait differences can help in species' lists, tailored for success under specific site conditions. Here, I discuss these issues in light of our recent publication in the *Journal of Applied Ecology* (Charles et al., 2018), highlighting how variation in a functional trait was useful for predicted seedling survival responses to a landscape scale barrier in Australia's wet tropics. I will then expand on this result to include some seedling growth data from the same experiment (unpublished) to provide a more complete example of using a trait-based framework for species selection and finish with some important considerations of using functional traits in tropical restoration approaches.

From 2011 to 2014, we measured the effects of a suite of abiotic and landscape factors upon seedling survival in a tropical forest restoration experiment in the Wet Tropics of Australia. Factors had all been previously reported to influence seedling performance and ranged across spatial scales including: slope, aspect, distance to nearest forest, and the identity of the person who planted individual seedlings. We also assessed whether three functional traits of the planted species (wood density, seed mass, and maximum tree height) could explain variation in seedling survival.

While we recorded a range of factors that influenced seedling survival over the 31-month period, wood density proved to be a very strong predictor of seedling survival, with species with high wood density experiencing higher rates of survival (Charles et al., 2018). While this result is consistent with past studies (Chave et al., 2009; Poorter et al., 2008), we observed an interesting relationship between wood density and the distance away from adjacent forests in which seedlings were planted. Species with low wood densities experienced decreased survival with increasing distance away from adjacent forest, while survival of species with high wood densities remained consistently high regardless of the distance from forest at which they were planted (Figure 1). This result is likely due to the underlying difference in stem mechanics and hydraulic conductivity between low and high wood density species and how this relates to increasing levels of heat exposure in pastures with increasing distance away from surrounding forest. Here, species with high wood densities may persist in exposed locations, as they have a reduced risk of xylem cavitation under water stress (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001). Conversely, while low wood density species may struggle to establish in highly exposed locations, survival of these species is greatly improved closer to adjacent forest, whereby intermittent shading throughout the day can

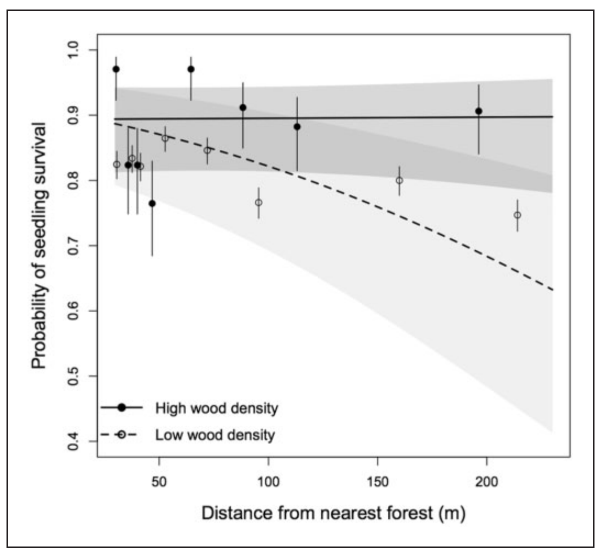


**Figure 1.** Probability of seedling survival in relation to distance to nearest forest fragment (m) with high and low species' wood density values ($g/cm^3$). Fitted line values for low and high wood density are 0.38 and 0.84 $g/cm^3$, respectively. Points for high and low wood density were calculated from the upper and lower third of wood density values, respectively. Bars are associated standard errors on the probability scale. Shaded bands represent 95% confidence intervals. Figure adapted from Charles et al. (2018).

buffer the effect of prolonged heat exposure (Duncan & Duncan, 2000).

Given that growth performance is also an important component of species selection, we then assessed how the interaction between species' wood density and distance from forest influenced seedling height relative growth rates (RGRs). Overall, seedling height RGRs decreased with increasing distance away from the nearest forest for both low and high wood density species (unpublished data), with this decrease relatively minimal for low wood density species and more pronounced for species with high wood density (Figure 2). Species with high wood densities experienced slightly increased height RGRs compared to species with low wood densities within locations very close to adjacent forests, yet this pattern reversed with increasing distance away from forest edges (Figure 2).

From these results, it may be possible to formulate a planting strategy that combines low wood density pioneer species and high wood density climax species over a distance gradient that maximizes seedling survival and growth. For example, in this scenario, planting higher proportions of low wood density species closer to the forest could increase the chance of their survival, accompanying this with faster growth in seedling height. The proportion would then shift to favor high wood density species with increasing distance from the forest edge, improving seedling survival rates in these exposed locations, albeit with slower growth. However, given that the low wood density species that managed to survive in locations further away from the forest edge experienced only a slight decrease in height RGR compared to their counterparts within close proximity to adjacent forest, including some low wood density species in these exposed locations may be appropriate in conjunction with targeted management strategies; these strategies may include regular watering and weed management to improve the establishment of these species, subsequently allowing for an increased likelihood of growth and canopy closure over time.

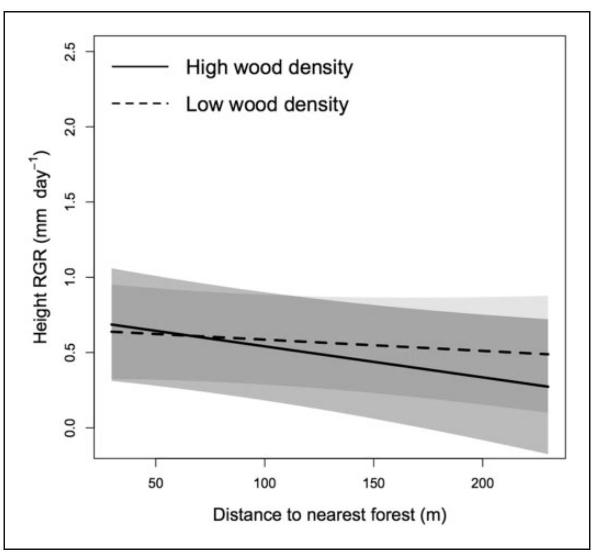


**Figure 2.** Relationships between seedling height relative growth rates (mm/day) and distance to nearest forest fragment (m) for species with different values of low and high wood density. Fitted line values for low and high wood density are 0.38 and 0.84 g/cm$^3$, respectively. Shaded bands represent 95% confidence intervals.

While this simplified example focuses on a single trait and landscape barrier, this method for species selection can be easily expanded to include other relevant traits that may mitigate specific barriers that impede seedling performance for species in restoration plantings. These could include assessing the performance of species with varying trait values of traits involved in resource acquisition, such as LMA, leaf area, and specific root length in response to light, soil nutrient and moisture gradients, or local competitive barriers such as densities of resident grasses. It is important to note, however, that many traits are correlated with one another (Díaz et al., 2016) and assessing how these trait combinations can predict species' survival and growth responses to specific barriers will be needed to provide a more robust species selection criteria than using single traits alone. In addition, when using trait-based species selection for tropical forest restoration, we should not only consider short-term outcomes but also endeavor to select combinations of traits that may be important after initial site capture. For example, it would be beneficial to select trait combinations that may alleviate competition for limiting resources between planted species while also excluding invasive species (Funk, Cleland, Suding, & Zavaleta, 2008). It will also be important that selected traits provide adequate ecosystem functioning (Laughlin, 2014), such as fruit production to attract seed dispersers and enhance natural recruitment over a larger temporal scale; this is especially important given that many restoration projects within the tropics employ a single planting regime at the beginning and have limited funding for follow-up plantings or continued site management (Chazdon, 2008).

While it is clear that there are many things to consider, adopting a trait-based approach to species selection in tropical forest restoration can provide an adaptable framework, which can be tailored to site-specific context and restoration objectives (Laughlin, 2014). Although this is far from an easy task, an abundance of past research has provided us with substantial lists of both traits and barriers relevant to tropical forest recovery and we should continue to empirically test these relationships to both augment species selection decisions and to improve planting strategies to increase the likelihood of restoration success.

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