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# Phylogenetic ecology applied to enrichment planting of tropical native tree species

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## ABSTRACT

Enrichment planting within established plantations or secondary forests is a common strategy to enhance forest recovery, given that later successional forest species tend to have low dispersal and limited recruitment into these sites. It is difficult, however, to predict how species of seedlings will perform when planted under different overstory species. The field of phylogenetic ecology offers tools to help guide the selection of seedlings, drawing on the evolutionary conservatism of important functional traits. We evaluated the survival, growth, foliar disease, and herbivory of various native tropical tree seedlings at different evolutionary distances from monospecific stands of trees beneath which they were planted. We expected that seedlings planted under conspecific overstory trees would have low survival and growth and high percent foliar damage (as predicted by the Janzen–Connell Hypothesis), and that seedling performance would improve steadily with phylogenetic distance between seedling and overstory species. We found that seedlings planted under conspecific canopies had lower survivorship, reduced growth, and greater foliar damage than seedlings planted under canopies of different tree species. An overall increase in seedling performance with greater phylogenetic distance between seedling and overstory species was dominated by the contrast in performance between conspecific pairs and seedlings planted beneath extra-familial overstory species; but lack of available congeneric pairing limited inference about interactions among close relatives. Most pathogenic fungi isolated from enrichment-planted seedlings also caused disease when inoculated on the overstory tree species where the seedlings had been planted; this is consistent with overstory trees being an important reservoir of pathogens that affect seedlings. We conclude that enrichment planting with species more distantly related to those that dominate the canopy should enhance seedling's performance. Closer analysis at the congeneric level is warranted because of expected strong biotic interactions at close phylogenetic distances.

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## 1. Introduction

Restoring tropical forests on abandoned agricultural lands often requires human intervention. Lack of seed dispersal, competition from exotic grasses, and stressful biotic conditions combine to slow or prevent natural succession to pre-deforestation communities (Holl, 1999; Aide et al., 2000; Cole et al., 2010). One promising restoration strategy is to establish early successional species tolerant of open conditions, followed by enrichment planting of desired woody species under an established canopy (Lamb, 1998, 2011; Paquette et al., 2006). This approach can accelerate succession, increase biodiversity, and enhance carbon sequestration (Ashton et al., 1998; Schulze, 2008; Keefe et al., 2009; Paquette et al., 2009). However, choosing combinations of overstory and enrichment species that are likely to be successful is largely a process of trial and error.

Empirical studies that inform choices of enrichment species have mainly focused on the effect of light (i.e. how canopy species vary in the depth of shade they create and how seedlings vary in their shade tolerance) and on competition among species (Ashton et al., 1998; Menalled et al., 1998; Pena-Claros et al., 2002; Schuler and Robison, 2010). Fewer studies have looked at other interactions that affect species performance. Some studies have found high pest incidence on seedlings planted under monospecific stands of common forestry species in *Eucalyptus*, *Pinus*, and Dipterocarpaceae (Kirton and Cheng, 2007; Lombardero et al., 2008; Zhou et al., 2008; Chungu et al., 2010). The predictive power of how particular seedling species will perform under a given overstory species is limited by the small number of species that have been evaluated. Here we combine a large experimental test of the performance of enrichment-planted tree species under established overstory trees with the analytical tools of phylogenetic ecology to evaluate whether phylogenetic relationships provide a predictive framework for choosing species for successful enrichment planting.

Ecologically important traits are often phylogenetically conserved (e.g., drought tolerance is conserved within the cacti)

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