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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.

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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(Farrell, 2001; Blomberg et al., 2003; Chazdon et al., 2003). Conservation of ecologically important traits can mean that closely related species are able to occupy similar habitats (Kozak and Wiens, 2006; Donoghue, 2008; Wiens et al., 2010), but also that they are more likely to compete strongly for resources (Elton, 1946; Dayan and Simberloff, 2005; Wilson and Stubbs, 2012) and share pests and pathogens (Novotny et al., 2002a, 2002b; Gilbert and Webb, 2007). Indeed, biotic interactions of all types are phylogenetically conserved across the entire tree of life (Gomez et al., 2010), and evolutionary distance between plant species can be useful as an index of the likelihood that species share important ecological traits. For instance, phylogenetic distance is a good and easily determined predictor of whether a pathogen or pest of one plant species will cause disease on another (Gilbert and Webb, 2007; Ness et al., 2011; Gilbert et al., 2012). This phylogenetic signal in host range of pests and pathogens may provide an integrative index of the likely performance of seedlings growing under established canopies of different tree species.

We know from numerous empirical tests of the Janzen–Connell Hypothesis (Janzen, 1970; Connell, 1971) that tropical tree seedlings and saplings growing closer to conspecific adults often perform worse and suffer greater attack from natural enemies than do seedlings growing under a canopy of heterospecific trees (e.g. Clark and Clark, 1984; Hubbell et al., 1990; Gilbert et al., 1994; Metz et al., 2010; Bagchi et al., 2011; Paine et al., 2012). One recent experimental test of the Janzen–Connell Hypothesis found that seedlings survive significantly less in soil from below conspecific trees than in heterospecific soil due to the presence of soil pathogens (Liu et al., 2012). What is less clear is whether there is a continuous increase in performance with phylogenetic distance of heterospecifics; or instead, are all heterospecific canopies broadly equivalent for increased seedling performance regardless of their phylogenetic distance to the seedlings?

We tested whether phylogenetic distance between overstory trees and seedlings planted beneath them is a useful predictor of seedling growth and survival, as well as of damage to leaves by pests and pathogens shared with the overstory trees. In addition, we conducted a cross-inoculation experiment to test whether the likelihood of developing foliar disease symptoms decreased continuously with phylogenetic distance between seedling and overstory species. We expected that seedlings closely related to the overstory tree species would have lower performance and higher foliar damage than those more distantly related. This study aims to evaluate whether this phylogenetic approach could provide a useful tool for restoration practitioners to select which species may be planted together most successfully when species-specific empirical data are lacking. Evolutionary relationships may reduce the need for extensive multi-species field-testing and guide more efficient empirical testing. The incorporation of phylogenetic diversity in ecosystems restoration may promote ecosystem stability through increased trait and functional diversity (Forest et al., 2007; Cadotte et al., 2012; Tan et al., 2012; Verdu et al., 2012).

2. Materials and methods

2.1. Study sites

We conducted this study in "The Native Species Reforestation Project" (PRORENA), located in Soberania National Park in the Panama Canal Watershed, Republic of Panama. PRORENA was established by the Center for Tropical Forest Science at the Smithsonian Tropical Research Institute (STRI) and by the Yale Tropical Resources Institute to assess the forestry potential of native tree species and promote their use in forestry and reforestation (Wishnie et al., 2007).

Soberania National Park has a strongly seasonal climate with a mean annual rainfall of 2226 mm and 4.1 dry months annually between December and May (dry months have < 100 mm rainfall). Soberania National Park overlies tropical ultisols that are predominantly clay or silty clay (Park et al., 2010). Most of the park is covered by secondary tropical rain forest. The PRORENA study site was deforested prior to the 1960s and then farmed for several decades until it was incorporated into the park in the 1980s. Prior to the PRORENA project, the plot was fallow for at least 10 years and was invaded by dense stands of the exotic grass *Saccharum spontaneum* L. (Wishnie et al., 2007).

2.2. Enrichment planting design and methods

Overstory tree species at PRORENA were planted in 2003 in 9-m × 12-m monospecific plots with each overstory tree species planted in three randomly-selected, replicate plots (Fig. A1). Trees were planted at an initial density of 20 trees per plot. Understory vegetation was kept clear with machetes and string trimmers for 2 years following planting, and the planted trees were sprayed with insecticide. After 2 years, the plots were thinned to leave ten trees spaced at 6 m, and understory clearing and pesticide treatment stopped (Wishnie et al., 2007). Of the 24 native tree species originally planted, we chose 11 overstory species that had good growth and that produced a closed canopy at least during the rainy season (i.e., some species are dry-season deciduous) (Table 1).

We planted a total of 2512 seedlings from 20 species and 14 families beneath the canopies of the 11 chosen overstory species (Fig. A1). We chose seedling species that would cover the widest breadth possible of phylogenetic distances (time of independent evolution) from the overstory species from those available as nursery seedlings, which resulted in planting between four and six different seedling species beneath each overstory tree species (Table 2 and Appendix A2). Some seedling species, such as *Copaifera aromatica*, *Swietenia macrophylla* and *Tabebuia rosea*, were planted more than other species since they represented a similar evolutionary distance beneath most overstory species. In this experimental design we replicated the phylogenetic distances not the seedlings species identity. The number of initially planted seedlings beneath each overstory species varied from 12 to 17 per seedling species. We included the number of initially planted individuals as a variable in the growth and survival models to test its effect.

The phylogenetic distances were calculated using the Phylomatic tool in Phylocom, version 4.1 (Webb et al., 2008). We used the most recent, maximally resolved Angiosperm tree (R20080417.new) as backbone to our phylogenetic tree, which is based on the APG3 classification and we dated it using Wikstrom ages (Wikstrom et al., 2001; Stevens, 2008). The phylogenetic distance between the seedling and the overstory species ranged from 0 to 233.1 My of independent evolution. Time of independent evolution is twice the time to most recent common ancestor. For the species in this study, 0 My corresponds to conspecifics, 57.2–87.8 My to confamilials, 90.5 My corresponds to the single conordinal pair in the study (*T. rosea* beneath *Tectona grandis*), and 91+ My to extraordinals. Congeneric species were not available for this study.

The design of this study is such that the independent variable of interest is the phylogenetic distance between the seedlings and the tree species beneath which they were planted, rather than the species identity of the seedlings or of the overstory species. Due to this experimental design only three species – *Colubrina glandulosa*, *Pachira quinata*, and *Terminalia amazonia* – were planted under canopies of both conspecifics and heterospecifics (Table 2). These three species provide a means to evaluate effects of phylogenetic distance to the overstory species with a standard reference