Do young tropical restoration plantations exhibit a phylogenetic pattern that suggests the influence of biotic processes affecting species composition?

Daniella Schweizer, Gregory S Gilbert, Rafael Aizprua

One approach in forest restoration is to plant trees that will establish an initial canopy to promote forest recovery through natural recruitment of other species. Here we evaluate the patterns of either phylogenetic overdispersion or phylogenetic clustering on community assembly beneath seven different single-species tree plantations. We expected the presence of negative biotic interactions between closely related overstory and recruiting tree species, as well as among related recruiting species, to lead to phylogenetic overdispersion. We found no evidence for inhibition of close relatives of the overstory tree species. However, we found more understory species than expected that were very distantly related to the overstory tree when the canopy was comprised of Fabaceae species, which lead to the presence of similar species in the understory of legume species. We found weak phylogenetic patterns among species in the understory community that suggest the presence of random processes of community assembly, maybe due to the young age of the understory communities studied.

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Do young tropical restoration plantations exhibit a phylogenetic pattern that suggests the influence of biotic processes affecting species composition?

Daniella Schweizer[1*], Gregory S. Gilbert[2,3], Rafael Aizprua[4]

[1]University of Sao Paulo, School of Silviculture and Agriculture " Luiz de Queiroz", Piracicaba, Brazil, 13418-900.

[2]Environmental Studies Department, University of California, Santa Cruz, CA, 95064.

[3]Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama

[4]Flora Tropical Panama, Villa Zaita, Las Cumbres, Calle Circunvalación, Ciudad de Panamá, Panamá

Corresponding author: Daniella Schweizer. [1]University of Sao Paulo, School of Silviculture and Agriculture " Luiz de Queiroz", Piracicaba, Brazil, 13418-900. **:** daniellaschweizer@gmail.com**.** Phone: +55 19 25343392

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Introduction

One method that is often employed to restore tropical forests consists of planting tree species to establish canopies that will shade invasive grasses and create suitable conditions for the establishment of other forest species (Parrotta et al., 1997; Holl et al., 2000; Carnevale and Montagnini, 2002; Butler et al., 2008). Careful selection of which species to plant is important since some tree species induce greater recruitment and establishment (Kuusipalo et al., 1995; Parrotta, 1995; Haggar et al., 1997; Celentano et al., 2011). However, testing plantation species one-by-one to evaluate subsequent recruitment is slow and resource intensive (e.g., Guariguata et al., 1995; Powers et al., 1997; Carnevale and Montagnini, 2002; Jones et al., 2004). In this study we evaluate if tools of phylogenetic ecology applied to restoration communities can provide insights regarding processes of community assembly affecting species composition. Such an approach would be particularly valuable when system-specific empirical data are lacking.

We base our research approach on an assumption of most phylogenetic ecology research: that close relatives share ecologically important traits and thus interact with their environment in similar ways (Webb, 2000; Gomez et al., 2010; Burns and Strauss, 2011). This similarity among close relatives is a “phylogenetic signal” common among species for a wide range of morphological, physiological, behavioral, ecological and life history traits (Prinzing et al., 2001; Blomberg et al., 2003; Chazdon et al., 2003; Gilbert and Webb, 2007; Gossner et al., 2009; Cavender-Bares and Reich, 2012; Savage and Cavender-Bares, 2012).

Abiotic and biotic variables affecting community assembly can lead to two distinctive phylogenetic patterns: clustering, when there is a higher presence of close relatives than expected from chance, or overdispersion, when there is a higher presence of distant relatives. Vamosi et al., (2009) explored complexities in the interpretation of phylogenetic non-randomness. In the simplest interpretation, phylogenetic clustering results from habitat filtering acting on conserved characters. But phylogenetic evenness (overdispersion) can result from habitat filtering, competitive exclusion, or character convergence (*e.g.,* Helmus et al., 2007, see Cavender-Bares et al., 2009 for a review).

Most phylogenetic ecology studies to date have evaluated phylogenetic patterns in old growth forests, with a few recent studies looking at secondary forests under succession (Letcher, 2010, Letcher et al., 2012, Norden et al., 2012). In an enrichment experiment, we planted seedlings beneath single-species plantations of native trees in an abandoned tropical pasture, and found that seedlings planted under conspecific canopies performed much worse than seedlings planted under canopies of distant relatives due to negative biotic interactions among close relatives (Schweizer et al., 2013).

In this study, we assessed the phylogenetic patterns of species colonizing naturally under those same single-species plantations. We expected that negative interactions among closely related species would lead to phylogenetic overdispersion, both between the overstory trees and the understory community (which should create greater than expected phylogenetic distances between the canopy tree and the understory immigrant community) and among the understory community (leading to overdispersed phylogenetic distances among understory immigrant species).

Materials and methods

Research site

This study was conducted in a plantation site of the PRORENA project (The Native Species Reforestation Project, http://research.yale.edu/prorena/), led by the Smithsonian Tropical Research Institute and the Yale School of Forestry and Environmental Studies. It is located in the Soberania National Park, in the watershed of the Panama Canal, Republic of Panama, and receives a mean annual rainfall of 2226 mm and 4.1 dry months annually (defined as months with <100 mm rainfall) (Wishnie et al., 2007). Soberania National Park overlies tropical ultisols that are predominantly clay or silty clays (Park et al., 2010).

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Most of Soberania National Park is covered by secondary tropical rain forest. The study site, however, had been deforested before the 1960s and then farmed for several decades. In 2003, when the PRORENA project began, the site had not been farmed for at least 10 years, and was invaded by the exotic grass *Saccharum spontaneum* L. subsp. *spontaneum* (Wishnie et al., 2007). This grass has invaded extensive deforested areas along the Panama Canal and significantly arrests forest recovery unless trees that can provide shade to the grass are planted and cared for (Hooper et al., 2002; Hooper, 2008).

Recruiting species census

The PRORENA plots consist of 9 × 12-m single-species plots with three replicates per species randomly placed across the planting area (see detailed description in Schweizer et al., 2013). Plots were established in 2003 and thinned in 2005 to a density of 10 trees each, at 6-m spacing (Wishnie et al., 2007).

For two years following planting, the understory was cleared of competing vegetation with machetes and the trees were sprayed with insecticide. We acknowledge that the application of insecticides to the planted trees until three years prior to the start of the study may have had some legacy impacts on the herbivore community (Endlweber et al., 2006; Meire et al., 2012). However, such treatments were uniformly applied across species and form part of the established reforestation management system. We thus examined phylogenetic responses in the context of practical management. We provide the results of 7 overstory species that showed good growth and were not reinvaded by *Saccharum spontaneum* in their understory (Fig. 1). These plots were removed because the strong competitive effects of *S. spontaneum* on any other understory growth may overshadow any effects of the overstory species, and *S. spontaneum* colonization varied among overstory species (Cummings et al., 2012).

During July and August 2008, three years after understory clearing ceased and the overstory trees were thinned, we surveyed all plant species that had colonized the understory of some tree

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species. We ran one 15-m long transect diagonally across each plot and at every meter counted and identified all individuals that touched a 1.5-m tall stick, held vertically, at that meter. Most species were identified in the field, but some were collected for later identification.

Data analysis

Because the overstory species is the unit of interest for analysis, and because the density of naturally recruiting plants was often quite low, we combined the data from the three replicate plots per overstory species. We did not find a significant correlation between the compositional similarity of understory immigrant species and physical distance between the selected overstory species plots (considering all replicates) (Mantel test, Z= 1629.7, P= 0.1657).

To assess the importance of common immigrant species versus uncommon species, we conducted analyses with all immigrant species and also restricted the analysis to only common species. Common species alone did not drive the overall patterns of community composition, so we show the results of analyses that included all species. Abundance data were square root transformed to reduce the weight of the most abundant species in all the analyses (Beals, 1984). Conspecific seedlings recruited beneath five species of overstory trees. Such self-recruitment - likely of their own offspring - skips the dispersal filter faced by the rest of the species and incorporates a spatial aggregation that creates bias towards finding phylogenetic clustering between overstory species and understory immigrant species. Because they do not properly form part of the overall pool of immigrants, we report the analysis without conspecific species in the data set.

Community phylogenetic structure

Phylogenetic relationships among all the immigrant understory and overstory species were estimated using the Phylomatic tool implemented in the Phylocom program, version 4.2 (Webb and Donoghue, 2005 ,Webb et al. 2009, http://www.phylodiversity.net/phylocom/). We used the

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resolved angiosperm supertree, R20080417.new, which is based on APG3 phylogenies and is available online at https://github.com/camwebb/tree-of-trees/tree/master/megatrees).

We limited the species list to angiosperms to avoid biases from inclusion of very distant relatives. We estimated the ages of the interior nodes of the phylogeny using the BLADJ algorithm from Phylocom and evolutionary ages published by Wikstrom et al., (2001). We used the Wikstrom et al., (2001) ages file after correcting name-change discrepancies between this file and the R20080417 Newick file (Gastauer and Meira-Neto, 2013). To reduce polytomies in our community phylogenetic tree, we used published phylogenies of all the families with polytomies and grafted the evolutionary relationships of tribes within those families to the original newick file (Appendix S1). Following the construction of the tree, we calculated the phylogenetic distance matrix among all species pairs using the Phylomatic software implemented in Phylocom.

Overstory-to-natural recruit phylogenetic structure

We took a Monte Carlo resampling approach to evaluate whether immigrant species were more likely to be closely related (clustered) or distantly related (overdispersed) to the overstory species than expected at random. Observed phylogenetic distance distributions, per overstory species, were compared to those drawn at random from among all the immigrant species found in all the PRORENA plots, even of species that were not the seven selected for the study. This means that the null community was restricted to those species that were able to disperse to the study plots and grow under the general environmental conditions of the site. Choosing species known to be able to establish in a site should improve the power of phylogenetic tests for detecting phylogenetic structure (Swenson, 2009; Kraft and Ackerly, 2010). We chose to use the set of species that were able to disperse into the study plots for two additional reasons. First, dispersal limitation of many animal-dispersed species would likely produce an ecological filter for which species arrive to the plots, limiting which species even had the opportunity to interact with the overstory trees. It is also more conservative, because comparisons to larger species pools

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are more likely to show phylogenetic clustering than are comparisons to more local pools (Swenson et al., 2007). Second, a rigorous comparison to a regional species pool would have required extensive vegetation inventories without a clearly defined appropriate spatial scale, coupled with quantification of relative propagule production over several years. Such work would be useful, but is far beyond the scope of the present study.

We compared the observed phylogenetic distances from the overstory species to the immigrant species with those of a null community created by random sampling 1000 times from the species pool. For each resampling, we drew the same number of individuals that had been originally observed in the plot, sampling randomly from among the species encountered in all the plots with the probability of selection weighted by the overall abundance of that species. This approach has an advantage over simple means-based indices in that it examines differences across the full distribution of phylogenetic distances, which are themselves not normally distributed. Random communities were created using the R program.

For both observed and random samples, we plotted quantiles of the cumulative distribution of phylogenetic distances from immigrant understory species to the overstory tree species. To plot these quantile graphs we first organized all the individual observations (from the observed and the null communities) in order of increasing phylogenetic distance to the overstory tree beneath which they were found and determined the 1,5,10, 20, 25, 50, 75, 90, and 95% quantiles. Then we plotted the phylogenetic distance found at each quantile. We used 95% confidence intervals of the null distribution to evaluate whether close relatives to the overstory species were observed more or less frequently than expected by chance.

Phylogenetic structure among naturally recruiting species

We evaluated the phylogenetic structure among understory immigrant species under each overstory tree species using the net relatedness index (NRI) developed by Webb (2000). This index is based on the distance (in millions of years) that separates taxa in a phylogenetic tree. The index is based on the observed Mean Phylogenetic Distance (MPD) standardized to the same measure estimated from 1000 random communities (Eq. 1). MPD is the average distance between all pairs of taxa in the phylogenetic tree and is a measure of phylogenetic structure for the community as a whole. The random communities were generated using the same species pool as described above, keeping observed plot abundance of immigrant species and species selection weighted by overall abundance.

$$NRI: -[(MPD_{observedPD} - Mean\ MPD_{nullPD}) / sd_{MPDnullPD}] \qquad \text{(Eq.1)}$$

We estimated this index using the Picante package version 0.7.2 (R-Development-Core-Team, 2009; Kembel et al., 2010). A positive index value indicates phylogenetic clustering and a negative value indicates phylogenetic overdispersion (Webb 2000).

Results

We encountered 59 plant species from 26 different families recruiting in the understories of the selected overstory tree species (Table S1). The most commonly encountered families were Fabaceae (8 species) and Asteraceae (8 species). Woody species able to grow over 10-m tall were the most common growth form (34% of all species). Zoochory was the most common dispersal syndrome (57% of all species). The only species known to be dispersed by both birds and bats were restricted to the genus *Piper* (4 *Piper* species and 20% of all individuals).

We found no consistent evidence of a lower than expected presence of close relatives to the overstory species. The observed phylogenetic distances between overstory species and their understory immigrants were not significantly different from random for almost all overstory species (Fig. 2). Only *Pachira quinata* showed significant phylogenetic clustering between the first and the 40th quantile, driven by the presence of one close relative *Helicteres guazumifolia* Kunth in the understory community. Conspecific seedlings recruited beneath three overstory species (*Diphysa americana, Tectona grandis,* and *Terminalia amazonia*). Including those self-recruits in the analysis would have resulted in significant phylogenetic clustering; removal of those self-recruits from the analysis eliminated the signal of phylogenetic clustering (see Methods).

Most plots with overstory trees in the Fabaceae showed a greater than random presence of far relatives (observed in the quantile graphs as phylogenetic distances around 300 My for the 80% percentile), driven by species in the Piperaceae family, which are distant relatives to the Fabaceae (Fig. 2). The NRI showed weak and inconsistent phylogenetic patterns in the evolutionary relationships among the understory immigrant species, except beneath the overstory species *Pachira quinata* where species clustering was found (Fig. 3).

Discussion

The main objective of this study was to test whether the tree species chosen for initial restoration planting affected the phylogenetic structure of the subsequent immigrant understory community in a phylogenetic predictable way. We expected to see reduced presence of close relatives and enhanced contribution of distant relatives to the overstory species due to the negative effects of biotic interactions between overstory trees and understory immigrating species and also among understory species. We found no consistent indication of a lower presence of closely related understory species to the overstory species. Most of the overstory species belonging to the Fabaceae showed a higher than expected presence of species in the Piperaceae family; but most of the other species did not show difference from random in the distances between overstory trees and understory immigrating species. Taken together, these results suggest limited predictive power based solely on analysis of phylogenetic relationships in the restoration communities studied.

We did not test for mechanisms to explain the abundant presence of *Piper* species under Fabaceae trees. However, neotropical bats of the genus *Carollia,* which are *Piper* specialists, utilize human-modified agrarian landscapes where legumes are often employed as live fences or

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as shade for coffee and cacao (Estrada and Coates-Estrada, 2001; Estrada and Coates-Estrada, 2002). Bats use *Acacia* in Australia and Kenya as roosting sites (Law and Anderson, 2000; Webala et al., 2004). Birds, which are also *Piper* dispersers, visit more and stay longer in tropical forest restoration sites with legume trees than either scattered plantings or pasture controls (Zahawi and Augspurger, 2006; Fink et al., 2009; Cole et al., 2010;Crampton et al., 2011). The enhanced presence of *Piper* under legumes may thus be more the result of idiosyncratic use by seed dispersers.

The lack of an overarching overdispersion pattern in the phylogenetic distances between overstory and understory species and among understory species was somewhat surprising, given the existing evidence of predominantly negative biotic interactions among close relatives (e.g., Cavender-Bares et al., 2004; Webb et al., 2006; Verdu et al., 2009; Schweizer et al., 2013), and the importance that shared diseases and herbivores may have in driving the composition of natural forest communities (Gilbert and Webb, 2007; Mangan et al., 2010; Metz et al., 2010; Ness et al., 2011). However, we measured the composition of the immigrant understory community after only three years since understory clearing ceased (see Methods).

In the early stages of succession, dispersal and abiotic conditions, not biotic interactions, may be stronger determinants of community composition. Biotic interactions become more important during the later stages of succession (Guariguata and Ostertag, 2001; Chazdon, 2008). Tropical tree communities in early succession show a prevalence of closely related species moving toward overdispersion later in succession (Letcher et al., 2012; Norden et al., 2012). We might expect to see more phylogenetic overdispersion appearing in the natural recruit community after several more years.

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Figure 1(on next page)

Phylogenetic tree of the overstory species selected for this study

Fig 1 - Phylogenetic tree of the overstory species selected for this study

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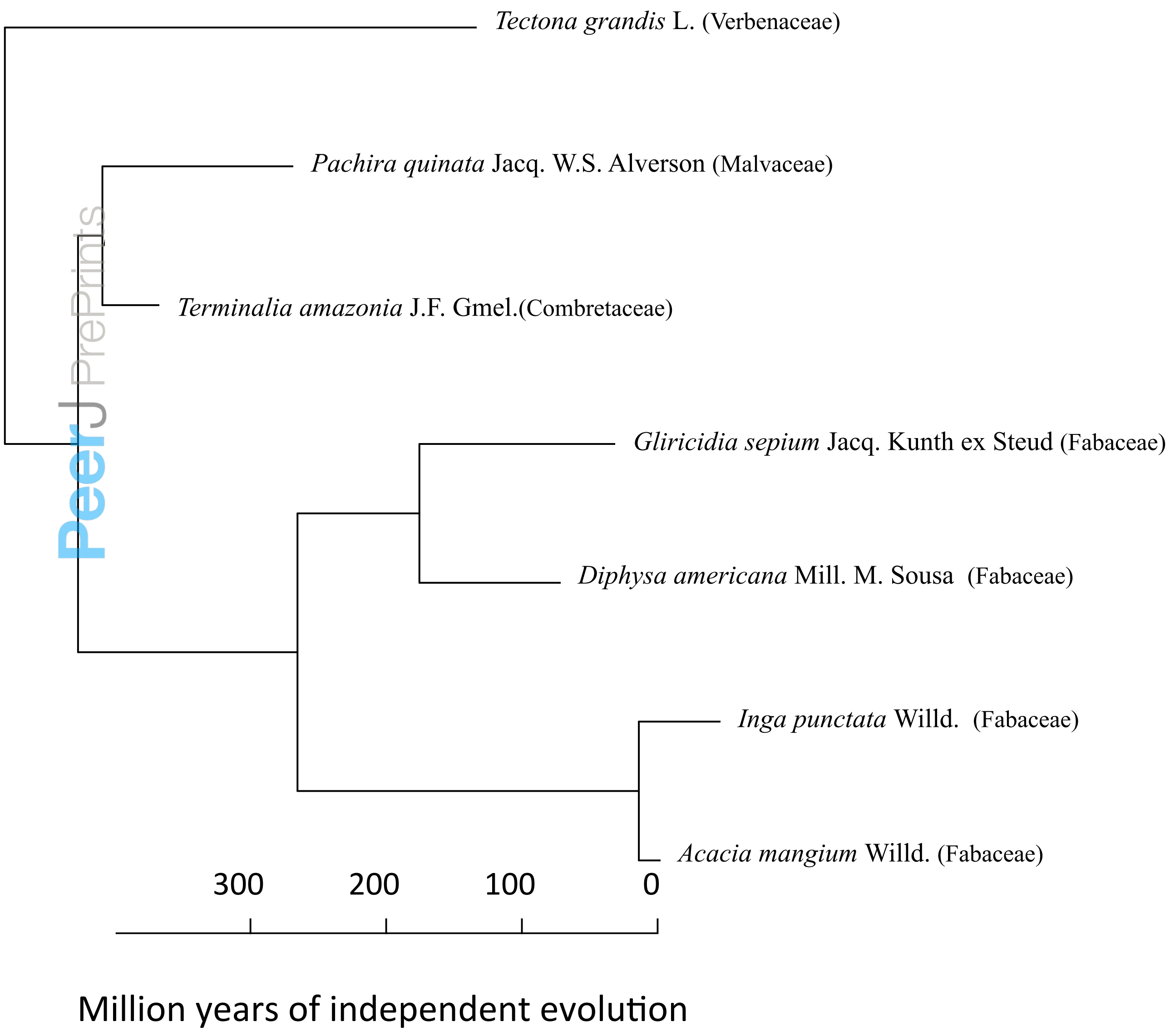

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Figure 2(on next page)

Quantiles of phylogenetic distance for each overstory tree species

Fig 2 - Quantiles of phylogenetic distance for each overstory tree species, obtained from plotting the observed vs. the random cumulative distribution of phylogenetic distances. Solid line represents observed data, dashed line represents the median quantiles expected if the recruits were a random selection of species from the species pool; thin fragmented lines are the 95% confidence intervals for the expected values

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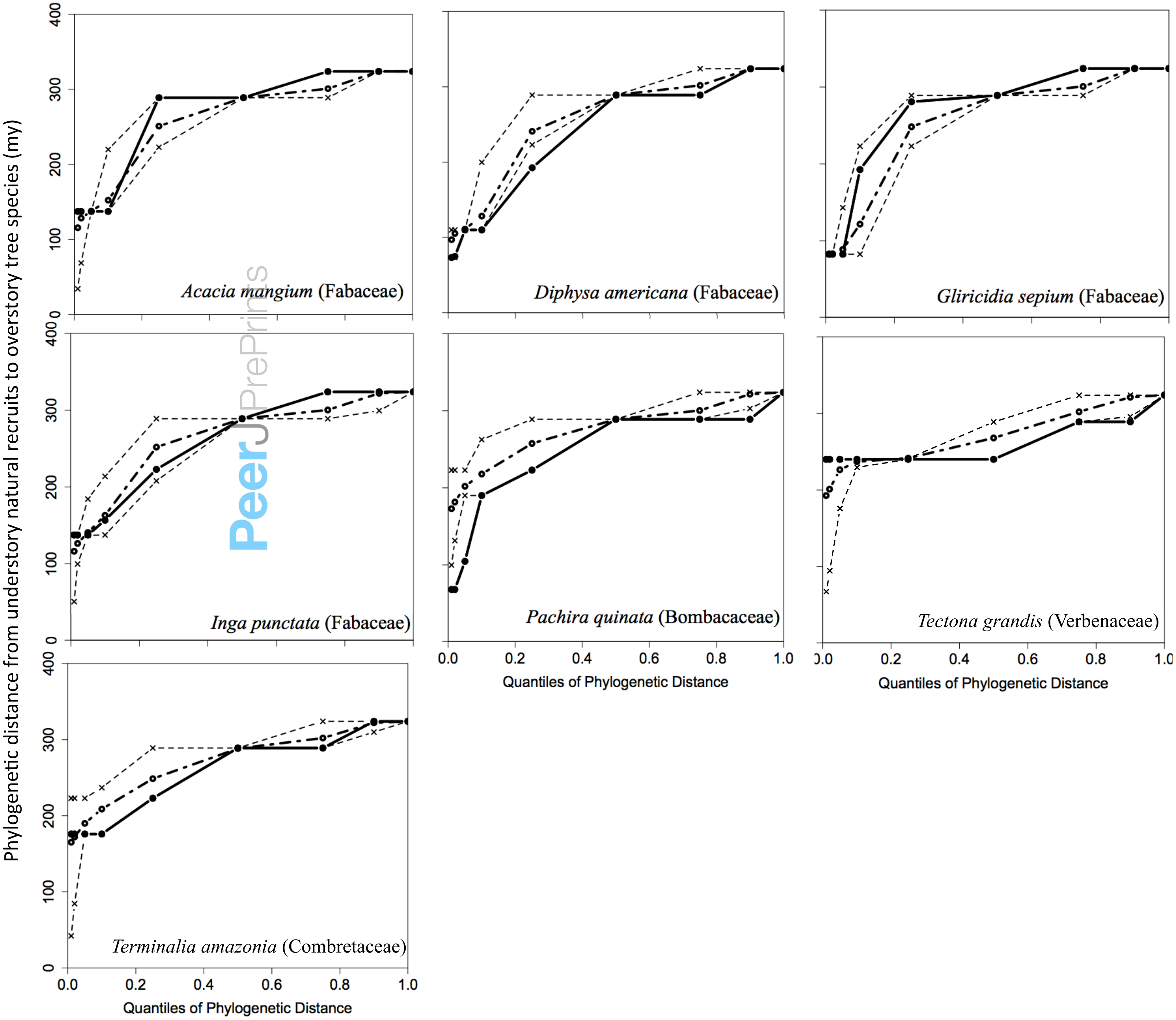

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Figure 3(on next page)

Net Relatedness Index of the recruitment community (NRI).

Fig 3 - Net Relatedness Index of the recruitment community (NRI).

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