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# The assembly of tropical tree communities – the advances and shortcomings of phylogenetic and functional trait analyses

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Tropical tree communities present one of the most challenging systems for studying the processes underlying community assembly. Most community assembly hypotheses consider the relative importance of the ecological similarity of co-occurring species. Quantifying this similarity is a daunting and potentially impossible task in species-rich assemblages. During the past decade tropical tree ecologists have increasingly utilized phylogenetic trees and functional traits to estimate the ecological similarity of species in order to test mechanistic community assembly hypotheses. A large amount of work has resulted with many important advances having been made along the way. That said, there are still many outstanding challenges facing those utilizing phylogenetic and functional trait approaches to study community assembly. Here I review the conceptual background, major advances and major remaining challenges in phylogenetic- and trait-based approaches to community ecology with a specific focus on tropical trees. I argue that both approaches tremendously improve our understanding of tropical tree community ecology, but neither approach has fully reached its potential thus far.

Determining the processes underlying the diversity and assembly of communities is a favorite past time for ecologists. During the past century biologists have pondered and attempted to test whether non-random abiotic or biotic interactions or random events shape the composition of communities. For example, we routinely ask whether plant–soil or plant–plant and plant–herbivore interactions are the key determinants of plant distributions and patterns of co-existence or whether dispersal limitation and demographic stochasticity play a more dominant role. Solving this riddle is central to our basic understanding of biodiversity itself, but also to our ability to predict the future distribution and dynamics of that biodiversity.

The ecological and evolutionary similarity of co-occurring species is one of the key pieces of information used to test mechanisms of community assembly (Webb et al. 2002, McGill et al. 2006, Swenson et al. 2011). For example, ecologically similar species are not expected to co-occur if limits to similarity dictate community assembly and co-existence (MacArthur and Levins 1967). Conversely, ecologically similar species may be expected to co-occur if only a few ecological strategies are suitable for the abiotic environment (Keddy 1992). It is easy to design and outline such hypothesis tests, but quantifying the actual similarity of species and disentangling what the observed patterns of co-occurrence and similarity really mean is a different story.

Two different approaches can be utilized to estimate the similarity of species in order to test community assembly hypotheses. A frequently used approach in community

ecology for over a century has been to indirectly estimate similarity based on the relatedness of species (reviewed by Jarvinen 1982). An alternative is to directly measure the similarity of species by quantifying one-to-several morphological or physiological traits (i.e. functional traits) (Ricklefs and O'Rourke 1975, Ricklefs and Cox 1977, Ricklefs and Travis 1980, Weiher et al. 1998, Stubbs and Wilson 2004, Grime 2006, Swenson and Enquist 2007, 2009, Kraft et al. 2008). These indirect and direct approaches are now often referred to as community phylogenetics and functional trait-based community ecology, respectively. Both approaches are now widely utilized in community ecology and are particularly popular in investigations of tropical tree community assembly. The popularity of these approaches is due to the advantages these approaches have over analyzing the composition and abundances of Latin binomials in assemblages (Fukami et al. 2005, Swenson et al. 2011, 2012a) and due to conceptual and analytical advances that allow tropical plant ecologists to quantify the phylogenetic and functional similarity of species even in diverse assemblages (Kraft et al. 2008).

There are several good recent review articles covering phylogenetic and functional analyses in plant community ecology that are relatively comprehensive and very useful for those new to these approaches (Webb et al. 2002, McGill et al. 2006, Pennington et al. 2006, Cavender-Bares et al. 2009, Vamosi et al. 2009, Swenson et al. 2011). The goal of the present review is not to provide yet another general overview of these topics. Rather, here I will focus

Table 1. A few key advantages and disadvantages of the community phylogenetic approach to tropical tree assembly.

Advantages	Disadvantages
Allows for a rapid, albeit very imperfect, approach for quantifying the degree of similarity in an assemblage.	In most cases, the approach completely relies on phylogenetic relatedness being a strong proxy of ecological similarity.
May be used to quantify the imprint of evolutionary history on the present day distribution and dynamics of species.	The phylogenetic result is the aggregate of multiple processes operating on multiple axes of organismal function and therefore can be intractable.
May be used to indicate the importance of unmeasured traits with phylogenetic signal on community assembly.	The taxonomic sampling in a community phylogeny is generally so sparse as to prevent any meaningful evolutionary inferences.

the discussion on the advances and advantages versus the shortcomings and disadvantages of both approaches to studying tropical tree community assembly (Table 1, 2). I have chosen to focus tropical tree communities here primarily due to their complexity and diversity and due to the large debates in community ecology regarding niche and neutral processes that often focus on tropical tree datasets. The review will argue that while both phylogenetic and functional trait approaches have yielded several new and interesting insights, they both have yet to fully realize their potential and additional focus will be needed on when, where and why we should use phylogenetic and functional trait information in tropical tree community assembly research.

## Advantages and advances

Quantifying the ecological and evolutionary similarity of co-occurring species is essential to elucidate the processes driving community assembly. Ecological and evolutionary interactions and chance events govern community assembly

Table 2. A few key advantages and disadvantages of the functional trait-based approach to tropical tree assembly.

Advantages	Disadvantages
Provides information regarding the function of species in diverse communities where there is simultaneously a large degree of functional breadth and redundancy.	The traits measured are generally composite traits that are coarsely related to a physiological process of interest.
Allows for a rapid, albeit imperfect, approach for quantifying the degree of similarity in an assemblage.	Impossible to measure all traits thought to be important particularly physiological rates and defense traits and it is impossible to know all traits that are important. These traits will therefore never be measured.
Allows the researcher to disaggregate the ecological strategies of species into individual functional axes.	Traits may vary widely within and between individuals in a species and quantifying this variation is an extraordinary challenge in large tropical forest plots.

and these interactions are dictated by evolved species traits and not by Latin binomials per se. It is therefore more intuitive, informative and powerful to study the distribution of species traits and names through space and time rather than only species names through space and time (Swenson et al. 2011). For example, two communities may share no species in common (i.e. have high species beta diversity), but their functional compositions could be completely similar (i.e. have low functional beta diversity) or completely dissimilar (i.e. have high functional beta diversity). An ecologist only studying the dissimilarity of only species names between the two assemblages has far less power to detect the underlying ecological processes governing community assembly and structure than an ecologist that simultaneously studies the functional and species composition of those same communities (Fukami et al. 2005, Swenson et al. 2011).

The difficulty with the reality that species name-based approaches are far less informative when compared to those that also use functional information is that it requires ecologists to estimate functional strategies of all species in a community thereby permitting the calculation the ecological similarity of co-occurring species. The ecological similarity of species is often estimated indirectly using phylogenetic relatedness as a proxy for similarity or directly using functional traits. Both approaches, indirect and direct, are increasingly employed in tropical tree community ecology. In this section, I will briefly review the advantages of both approaches and I will provide coverage of some of the advances made using these approaches. I also summarize these advantages in Table 1 and 2.

## Phylogenetic analyses

Ecologists have utilized relatedness as a proxy for ecological similarity in their research for nearly a century (Palmgren 1921, Jaccard 1922, 1926, Elton 1946, Williams 1947, Simberloff 1970, Jarvinen 1982, Webb 2000, Webb et al. 2002). In essence the assumption underlying this research is that closely related species should be on average more similar to one another than distantly related species. Importantly this does not require closely related species to be ecologically identical, rather it just suggests that they will be more similar to one another than a distantly related species. As I will discuss below this indirect method for estimating the ecological similarity of species has its limitations, but it has been and continues to be widely used as a quick and pragmatic method for roughly estimating similarity. Specifically, the argument that is often made is that it is likely impossible to generate quantitative estimates of functional similarity for hundreds of species that may occur in the study system (Webb 2000, Webb et al. 2008). This is an argument that is particularly well-received by tropical ecologists that are accustomed to diverse systems and adverse field conditions that make detailed morphological and physiological measurements on all species in a community daunting.

For decades, taxonomic ratios such as the genus: species or family:genus ratios were used to estimate the overall similarity of co-occurring species in a community

(Jarvinen 1982). Lower values for these ratios indicate closely related, and therefore perhaps ecologically similar, species co-occurring. Higher values closer to unity indicate distantly related, and therefore perhaps ecologically dissimilar, species co-occurring. Putting aside whether or not relatedness maps onto ecological similarity, taxonomic ratios are hindered by their reliance on ranks. Specifically, not all genera or families are the same age. Thus, making the unrealistic assumption that all else is equal (e.g. rates of functional evolution were constant and equivalent between lineages through time), two species in a relatively young genus may be expected to be more similar than two species in a relatively old genus. A potential solution to this problem is to incorporate branch length information by quantifying the phylogenetic relatedness of co-occurring species. Although this potential solution was clear, the tools to implement this solution were not generally available prior to the 2000s. In other words, generating phylogenetic trees that included all species in the community under investigation, also known as community phylogenies, was not trivial in most systems and generally not possible in diverse tropical systems.

The invention of the informatics tool Phylomatic by Webb and Donoghue (2005) allowed researchers for the first time to easily, albeit crudely, estimate the phylogenetic similarity of all species in any plant community. Phylomatic works by pinning known phylogenetic topologies or taxonomy onto a 'backbone' phylogeny, generally an angiosperm phylogeny group family-level phylogeny, to produce a cladogram that can be scaled to time using estimated node dates. Thus it pastes together a 'tree of trees' and it does not generate a molecular phylogeny per se or use commonly used supertree methods (Webb and Donoghue 2005). The invention of this tool alone is responsible for reviving interest in the relatedness of co-occurring species and the tens to hundreds of papers that have followed now forming the sub-field called community phylogenetics. At this point nearly one paper per week is published that utilizes this informatics tool with many of these coming from tropical plant systems.

Phylomatic has been a particularly important development for tropical ecologists given the logistical constraints of generating molecular phylogenies containing hundreds of species. Although the Phylomatic method for producing community phylogenies will continue to be widely used and important particularly in the tropics, recent research has demonstrated the feasibility of utilizing three so-called 'DNA barcode' regions to generate molecular community phylogenies for entire tropical tree forest plots (Kress et al. 2009, 2010, Gonzalez et al. 2010, Pei et al. 2011, Swenson et al. 2012a, b). This development is important given the rapidly falling cost of DNA sequencing and given that the most detailed analysis to date comparing results from Phylomatic and molecular phylogenies has shown that Phylomatic results, particularly in species rich systems, based on phylogenies with poor terminal resolution may be strongly biased (Kress et al. 2009). In sum, over the past decade the once daunting obstacle of estimating community phylogenies for diverse tropical tree assemblages has now been removed and these methodological advances have opened the pathway to numerous investigations into the assembly of tropical tree communities.

The first wave of community phylogenetic analyses of tropical tree assemblages focused largely on local phylogenetic diversity and whether it was higher or lower than that expected given a null model. The initial analyses of phylogenetic dispersion in tropical trees were carried out by Webb and his colleagues. In his landmark study, Webb (2000) outlined the conceptual and methodological approach that is still used with minor modifications in the vast majority of community phylogenetic studies. In particular, his study defined the original net relatedness index (NRI) and nearest taxon index (NTI), that have since been slightly modified to include branch lengths and null models, to quantify whether closely or distantly related trees in Borneo tend to co-occur (Webb 2000). Subsequent research by Webb and Pitman (2002) analyzed the phylogenetic structure of relative abundance across two tropical forests and the influence of neighborhood phylogenetic diversity on seedling demographic rates (Webb et al. 2008). This work laid the foundation for recent work investigating topics such as the phylogenetic signal in commonness and rarity (Mi et al. 2012) and dynamic neighborhood models (Uriarte et al. 2010, Paine et al. 2012).

Aside from Webb's early work, the initial analyses of phylogenetic dispersion focused on the influence of spatial scaling and whether or not co-occurring species are phylogenetically overdispersed or clustered. The first studies of this type were performed by Kembel and Hubbell (2006) in Panama and Swenson et al. (2006, 2007) in Puerto Rico, Panama and Costa Rica with the general finding that the degree of phylogenetic dispersion decreases as the spatial scale increases. The tentative inferences from this work, and other temperate zone work (Cavender-Bares et al. 2006), were that biotic interactions were more important locally, giving rise to patterns of phylogenetic overdispersion, and abiotic filtering was more important at larger scales giving rise to patterns of phylogenetic clustering. Recent additional studies have yielded similar results both within forest plots and on regional scales (Kraft and Ackerly 2010, Pei et al. 2011, Eiserhardt et al. in press, Liu et al. in press). The work by Kraft and Ackerly (2010) also made the important advance of incorporating estimates of statistical power into their analyses. Specifically, Kraft and Ackerly (2010) highlight that statistical power will be inherently limited as the size of the local community approaches the size of the species pool making it increasingly difficult to reject the null expectation.

Beyond the initial interest in spatial scale and phylogenetic dispersion, alternative scaling axes such as organismal size and taxonomic scale have also been considered. Organismal size scaling has been utilized as a methodology for estimating how phylogenetic diversity is filtered through ontogeny. Specifically, the hypothesis that as ontogeny progresses biotic interactions should become increasingly important in structuring a community should result in an increase in phylogenetic overdispersion with time. It is difficult to test this directly without long-term data on individuals and their cohorts and therefore researchers have used size classes as, admittedly crude, proxies. The results have shown that generally phylogenetic overdispersion increases with the size class analyzed (Swenson et al. 2007, Gonzalez et al. 2010) therefore lending support to

the hypothesis that biotic interactions increase in importance with time so long as phylogenetic relatedness is a solid proxy for ecological similarity.

Taxonomic scaling and phylogenetic dispersion has received considerably less attention in the tropics or the temperate zone for that matter. The only tropical example that I am aware of is Swenson et al. (2006) where phylogenetic dispersion was quantified in the Puerto Rican tree assemblages. The analyses were repeated on the same assemblages, but the composition was increasingly limited taxonomically from all species in the subplot that were tracheophytes (i.e. everything from tree ferns to eudicots) to only species in the coffee family, Rubiaceae. The results showed that phylogenetic overdispersion was more common on fine taxonomic scales (i.e. within the order or family) and less common on coarse taxonomic scales. Similar results have been reported in a temperate system (Cavender-Bares et al. 2006). Interestingly, these taxonomic scaling phylogenetic results are generally consistent with those reported decades earlier in the taxonomic ratios literature (Simberloff 1978, Strong et al. 1979, Grant and Abbott 1980). In general these taxonomic scaling results are suggestive that biotic interactions are stronger on finer taxonomic scales, but this inference is complicated by the fact that phylogenetic signal in ecological strategies likely decreases as the taxonomic scale of the analysis decreases.

Although scaling analyses are a powerful way to begin to investigate community assembly and the multiple processes that may be operating simultaneously, analyses of compositional turnover through space and time are likely to be more powerful. Given their dynamic nature and their increasing dominance in tropical landscapes, secondary forests are therefore some of the best laboratories for studying tropical tree community assembly. Accordingly several recent studies have investigated the phylogenetic dispersion of trees in these re-assembling communities (Letcher 2010, Letcher et al. 2011, Arroyo-Rodriguez et al. 2012, Ding et al. 2012, Norden et al. 2012, Whitfield et al. 2012). Despite the potential power of using disturbed tropical forests for analyzing community assembly, the interpretation of the research is muddled by the diversity of disturbance types and the reliance on chronosequences (Letcher et al. 2011). This is of course true with all research into disturbance making generalization difficult when comparing the phylogenetic structure of a secondary forest growing in an abandoned pasture versus secondary growth in response to a typhoon. The most tractable and consistent results are likely to come from studies that have little variance in the disturbance type and do not rely on chronosequences. A recent study from Norden et al. (2012) has accomplished this by analyzing the phylogenetic structure of multiple Costa Rican tree assemblages growing in abandoned pastures. Their results show that, in general, phylogenetic overdispersion between individuals increases with time since colonization, but the pattern was less clear when abundance was not incorporated into the analyses. These results lend some support to previous work focusing on size classes, but additional dynamic research such as that performed by Norden et al. (2012) is necessary to identify whether general conclusions can be reached.

The above research has focused primarily on whether phylogenetic alpha diversity is higher or lower than that expected across spatial and size scales and through time in a single area. Analyses of phylogenetic beta diversity have been less common, but the number of investigations into this topic has increased in the last two to three years. Spatial analyses of phylogenetic beta diversity in tropical tree communities has thus far primarily focused on partitioning diversity by its spatial and environmental components (Chave et al. 2007, Hardy and Senterre 2007, Parmentier and Hardy 2009, Fine and Kembel 2011, Swenson et al. 2011, Hardy et al. 2012, Zhang et al. 2012) or by conceptually linking phylogenetic alpha and beta diversity (Chave et al. 2007, Hardy and Senterre 2007, Swenson et al. 2012b). Some of this work has also sought to compare and contrast different metrics of phylogenetic beta diversity (Swenson et al. 2011) and different null modeling approaches for phylogenetic beta diversity studies (Zhang et al. 2012). These spatial analyses have generally been conducted using tree plots separated by multiple kilometers and have generally found large proportions of the variance in phylogenetic beta diversity being explained by the environment or the interaction between spatial and environmental components thereby suggesting the differential sorting of lineages across environmental gradients and a rejection of a neutral model.

Temporal analyses of phylogenetic beta diversity in tropical trees have been rare. Swenson et al. (2012a) recently analyzed the phylogenetic turnover in one Panamanian and one Puerto Rican forest dynamics plot. The results from both plots showed that the phylogenetic turnover was no different from random. This result could suggest that the dynamics of these forests are random with respect to phylogeny, but opposing non-neutral processes may be operating and ultimately produce a random phylogenetic signal (Swenson and Enquist 2009). Additional research into these possibilities and linking studies of phylogenetic beta diversity through time with dynamic analyses of demographic rates as they relate to the phylogenetic neighborhoods of individuals are needed to reconcile these results.

In general, the above inferences have been predicated on the assumption that species niches or traits had phylogenetic signal. Swenson et al. (2007) was the first to test this assumption in tropical tree assemblages using sparse and incomplete trait matrices for tropical tree communities, finding support for this assumption. As I will discuss below, recent research that has filled in the trait matrices in these forests and that has utilized more sophisticated methods for quantifying phylogenetic signal has demonstrated little phylogenetic signal in commonly measured traits (Swenson et al. 2012a, b). Additional research has sought to not measure phylogenetic signal in species traits, but to measure phylogenetic signal regarding where species land on environmental axes. A recent example of this type of analysis from Panama has demonstrated very little phylogenetic signal in where species land on a soil nutrient gradient (Schreeg et al. 2010). In particular, for the species in the Barro Colorado Island Forest Dynamics Plot, the mean soil nutrient values for all individuals of a species were generally randomly distributed across the phylogeny. The principle

exception to this was that species in the family Melastomataceae tended to be found on soils with high aluminum content, thereby supporting previous work suggesting that species in this family were aluminum accumulators (Jansen et al. 2002, Schreeg et al. 2010). While this work focusing on a single 50-ha forest plot was necessarily limited in its taxonomic sampling and spatial extent, it does throw into question whether soil niches are generally phylogenetically conserved in tropical trees and may further support the findings that soil niches may be highly labile within genera and families (Fine et al. 2004, 2006).

Contrary to the above analyses of phylogenetic signal in soil niches, large-scale analyses suggest there may be substantial phylogenetic signal in plant pathogen and pest interactions. In particular, Gilbert and colleagues (Gilbert and Webb 2007, Gilbert et al. 2012) have shown that closely related species, whether in the tropics or globally, are more likely to share similar pathogens and pests. Additional research on plant–lepidopteran interaction networks suggests that some, but not all, plant lineages have conserved lepidopteran associations where lepidoptera specialize on particular plant genera or families (Janzen 1985, Weiblen et al. 2006, Agosta and Klemens 2008). Given the potential importance of the Janzen–Connell mechanism in dictating tropical tree community assembly, these results suggest that phylogenetic analyses may continue to provide a powerful tool for tropical tree ecologists particularly since the functional traits that are currently being measured in these assemblages at best loosely relate to plant–pest interactions (Kraft et al. 2008, Swenson and Enquist 2009, Wright et al. 2010, Swenson et al. 2012a, b).

### Functional trait analyses

The study of tropical tree functional ecology has a much richer history than phylogenetically-based studies of tropical trees. The majority of this functional research has focused on a handful of species at a location and far less focus has traditionally been placed on inventories of function for all species in a community (Mulkey et al. 1996). The goal of this section is to discuss functional analyses of entire communities rather than discuss the deep literature of species-level functional analyses. The literature on the functional analysis of entire communities is much shallower primarily for two reasons. First, locating all species in rich communities, which harbor many rare species, for physiological and morphological measurements is a daunting task. Upon locating the individual or individuals necessary it is often logistically not possible to conduct detailed physiological or morphological measurements on every species in a tropical tree community over the course of a PhD dissertation or major research grant. Though, the task of taking less detailed functional trait measurements is feasible during such a time span and is easier in mapped forest dynamics plots where the spatial locations for all individuals of all species are known. However, this does not remove the second obstacle to community level inventories of function. The second major obstacle is accessibility for sampling. Often the one or few individuals of a species that are mapped and known may not have all of their organs

(e.g. leaves) easily accessible for physiological or morphological measurement. In other instances the functional trait measurement requires methods (e.g. coring bores to measure wood density) that can severely injure an individual – an undesired outcome in plots designed to quantify the natural long-term dynamics of individuals and communities. Thus complete community inventories will often require locating rare individuals outside of mapped forest plots and/or difficult to implement field sampling methodologies.

Despite these clear obstacles, community-level functional analyses are becoming more commonplace in the literature on tropical trees (Kraft et al. 2008, Swenson and Enquist 2009, Lebrija-Trejos et al. 2010, Paine et al. 2011, Swenson et al. 2011, 2012a, b, Andersen et al. 2012, Baraloto et al. 2012, Ding et al. 2012, Katabuchi et al. 2012, Liu et al. 2012). A major reason for this recent productivity is due to a synthesis in functional ecology that has focused on measuring a handful of relatively easily measured plant functional traits that have standardized measurement protocols and are indicative of several major axes of plant ecological strategies (Reich et al. 1997, Westoby 1998, Westoby et al. 2002, Cornelissen et al. 2003, Wright et al. 2004, Westoby and Wright 2006, Chave et al. 2009). The obvious advantage of this approach is that knowledge gained from measuring even these few simple traits drastically improves our mechanistic understanding of tropical tree community structure. This is particularly the case when analyzing hundreds of tree species that comprise a community that simultaneously has a larger breadth of functions than a species poor temperate community and a tighter packing of species within that functional space than a temperate community. In other words, when randomly drawing two species in a tropical tree community the degree to which they can be similar varies more widely than two species randomly selected in a temperate tree community. Thus, while it would be unwise to ignore function when analyzing any community, the negative consequences of ignoring functional information are much more severe in a tropical tree community than a temperate tree community.

Functional trait analyses of tropical tree communities have followed almost the identical trajectory of the phylogenetically-based analyses outlined in the previous section. In particular, the first set of analyses focused primarily on functional trait dispersion and spatial scale (Kraft et al. 2008, Swenson and Enquist 2009). Interestingly both of these initial studies found almost identical results despite one being a hyper-diverse wet forest in Ecuador and one being a much less diverse seasonal dry forest in Costa Rica. An important finding from both studies is that individual traits often have opposing patterns of dispersion at the same spatial scale. For example, seed mass values may be highly overdispersed locally while specific leaf area values may be highly clustered at this scale. This finding is important in that it highlights how opposing assembly mechanisms are likely operating simultaneously in shaping the assemblage of trees an investigator observes and that these opposing mechanisms are operating on different aspects of the organisms phenotype (Grime 2006, Kraft et al. 2008, Swenson and Enquist 2009, Paine et al. 2011). Another important implication from this work is

that opposing assembly mechanisms operating on independent axes of plant function may result in a random community phylogenetic structure (Swenson and Enquist 2009, Kraft and Ackerly 2010). Prior to this work, random community phylogenetic structure generally resulted in an inference supporting neutral processes governing community assembly. Given the functional trait results demonstrating simultaneous overdispersion and clustering of traits on a single spatial scale, the inference of neutrality from random community phylogenetic structure is no longer straightforward (Swenson and Enquist 2009). This highlights a key advantage of the functional trait approach to studying community assembly – it allows investigators to disaggregate overall species function into its constitutive parts to begin to dissect when, where and why certain assembly processes dominate over others.

The analysis of turnover in community composition through space or time using functional traits (i.e. functional beta diversity) has been exceedingly rare. The examples I am aware of come from my laboratory – two of which have concerned the spatial turnover in function (Swenson et al. 2011, 2012b) and one that concerned the temporal turnover in function (Swenson et al. 2012a). The spatial functional beta diversity research to date has been relatively simple asking whether compositional turnover is random with respect to function. The results both regionally (Swenson et al. 2011) and locally (Swenson et al. 2012b) suggest that the functional turnover is highly deterministic. The temporal analyses of functional beta diversity in tropical trees by Swenson et al. (2012a) has demonstrated lower than expected functional beta diversity in relatively undisturbed tree assemblages and higher than expected functional beta diversity in disturbed assemblages. Perhaps the most striking result from this research is that the species composition of the Barro Colorado Island 50-ha tree plot appears to drift neutrally through time, whereas the functional composition is highly constrained. Thus analyses of only the species composition would be highly misleading when making inferences regarding the assembly and dynamics of that tree community. A similar result from a series of experimental plant communities was found by Fukami et al. (2005) where the species compositional turnover remained divergent through time while the functional composition converged across plots. These two temporal analyses of functional beta diversity provide some of the most convincing evidence to date that even measuring and analyzing basic aspects of plant function can dramatically improve our understanding of the mechanisms underlying the assembly and dynamics of communities.

Nearly as soon as the first community-level analyses of functional diversity in tropical trees were conducted did researchers begin to seriously consider the degree of intra-specific variation in commonly measured functional traits. This concern materialized in two types of studies. The first type of study sought to partition the variation in functional traits within individuals of a species, between individuals of a species and between species for example (Baraloto et al. 2010, Hulshof and Swenson 2010, Messier et al. 2010). While this work demonstrated significant variation within and between individuals of a species, the majority of the variation within a particular study location

in trait values was inter-specific and not intra-specific. Though this generality may not be true when considering research sites separated by many kilometers. This possibility lead to the second type of intra-specific trait variation study that analyzed the degree to which information regarding site-specific trait values influenced the perceived functional structure of the tree community. For example, Paine et al. (2011) have demonstrated that plot-specific trait values tend to reveal stronger patterns of non-random functional structure in tree communities in French Guiana than do analyses that utilized regional-scale species-level mean trait values calculated from individuals in multiple tree plots. Similarly, Swenson et al. (2011) utilized population-level trait values to calculate functional beta diversity in tree communities along an elevational transect in Puerto Rico to uncover deterministic community assembly mechanisms that could not be detected using species level trait means calculated from all individuals sampled along the transect. Taken together the results of intra-specific trait variation investigations thus far suggest that within-tree-plots trait variation within species is generally low enough to be negligible in the analyses so long as enough individuals are sampled. Conversely, when analyzing multiple forest plots across a region, intra-specific variation is large enough between localities to necessitate trait sampling of populations in each plot rather than quantifying one trait value for a species from one plot and applying it to all other individuals in other plots.

## Disadvantages and shortcomings

The preceding sections focused on the advantages and advances made by phylogenetic and functional trait-based analyses of tropical tree community assembly. The advantage of the phylogenetic approach is that it provides a now rapid estimate of the potential overall ecological similarity of species in diverse communities. The advantage of the functional trait approach is that it takes a more direct approach to quantifying the multi-variate or uni-variate functional similarity of co-occurring species in diverse communities. Both approaches tremendously improve upon, or in some cases overturn, results generated from analyses that focus solely on composition and abundances of species names in communities and this is particularly the case for diverse tropical assemblages. These advantages have spurred the development of technological and conceptual advances resulting in a large number of investigations published over a very short period of time.

Despite these clear advantages and advances, both phylogenetic and functional trait analyses of tropical tree community assembly have been limited and have not progressed to the desired point. This lack of progress on some fronts is due to inherent limitations in the approaches that will be difficult to overcome in the near- or far-term such as the use of a phylogenetic proxy to estimate ecological similarity or the need to focus on a few easily measured functional traits. In other instances the lack of progress is due to a lack of conceptual advances that should have been made by this point, but have not and have therefore limited the collection of the data necessary to address large outstanding

questions regarding tropical tree community assembly. In particular, critical topics such as – how can we utilize phylogenetic trees for biogeographically and evolutionarily inclined analyses instead of only simple measures of dispersion or how can we effectively link function to demographic rates to explain present-day species co-occurrence and community dynamics or how can we estimate the geographic distributions of tropical tree species that make up the regional- and continental-scale pools from which our study sites draw have received surprisingly little attention. In the following I will address these disadvantages and shortcomings of the phylogenetic and functional trait approaches to studying tropical tree community assembly and I have summarized the disadvantages in Table 1 and 2. The goal is to highlight disadvantages where they lurk and suggest ways of mitigating these issues or to highlight conceptual or methodological shortcomings that must be overcome in the near term to progress the field.

### The limitations of phylogenetic proxies

There are two central approaches to using phylogenetic trees to study community assembly. One has been to utilize the phylogenetic tree as a backbone piece of information critical for uncovering how trait evolution and biogeographic history help explain the present-day co-occurrence of species (Losos et al. 1998, Gillespie 2004). The second has been to use phylogenetic genetic relatedness as a proxy for ecological similarity to uncover the degree to which similarity determines species co-occurrence (Webb et al. 2002). Despite the enormous potential of the first approach in tropical ecology (Pennington et al. 2006), phylogenetic analyses of tropical tree community assembly by-and-large have used the second approach.

The phylogenetic proxy approach to studying community assembly rests on the central assumption that closely related species are ecologically similar. This assumption can be easily accepted and dismissed by a room full of biologists (Losos 2008, Wiens 2008, Wiens et al. 2010). For example, we cannot deny that species in the palm family (Arecaceae) are generally more ecologically similar to one another than they are to species in say the Piperaceae and species in the Piperaceae are generally more similar to one another than they are to the Arecaceae. At the same time we must acknowledge that there is a large amount of important functional diversity inside of each of these families that likely is not strongly predicted by relatedness.

This taxonomic-scale dependency in the relatedness – similarity relationship raises a number of important issues. First, it suggests that the utility of a phylogenetic proxy is likely maximized in studies that have a broad taxonomic scale and minimized where the taxonomic scale is fine. For example, it would be unwise to rest a study on this assumption when focusing on an assemblage of con-geners whereas the assumption is more reasonable when the taxonomic sampling in the assemblage being studied is broader. This issue may also be important when considering the forest with varying levels of species diversity. For example, forests in meso-america and Caribbean, such as Barro Colorado Island in Panama and Luquillo in Puerto Rico, have few

species per genus and those genera that do have multiple species are generally not that species rich. Contrast this with a hyper-diverse Amazonian or Malaysian forest, such as Yasuni in Ecuador or Lambir in Malaysia, where many genera may have tens of species inside the forest plot. In those cases where the overall taxonomic sampling is broad basally (e.g. the entire angiosperm phylogeny) and dense terminally (e.g. high numbers of congeners) the phylogenetic signal in trait data will likely rise. That said, this will still only represent an indirect estimation of the overall functional similarity of species (Fig. 1) and will not be able to identify dissimilarities or similarities on individual axes of function. This brings us to the second major limitation of the phylogenetic proxy.

The second major limitation of phylogenetic proxies is that under the best-case scenario phylogenetic relatedness is a strong proxy for the multivariate similarity of species. Estimating the general similarity of species is useful in some cases, but these estimates are likely averaging out important information regarding one or a few axes of species

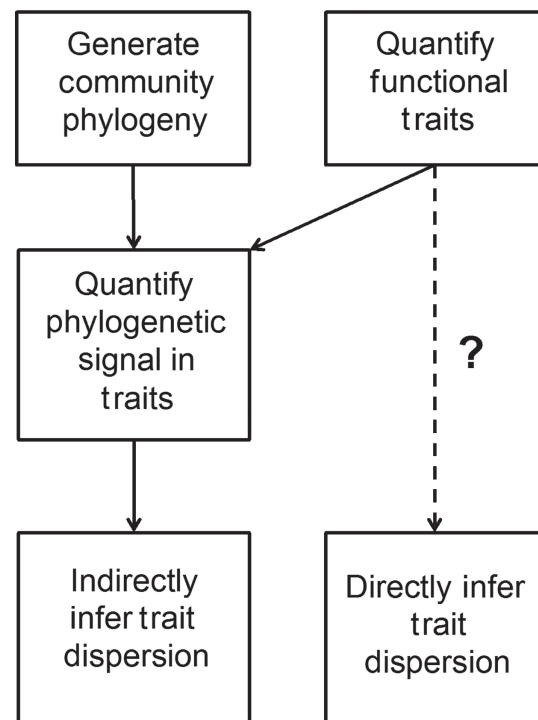


Figure 1. The phylogenetic middleman problem. Community ecologists began to utilize phylogenetic relatedness to infer the functional or ecological similarity of species. This assumption was challenged and researchers were tasked with measuring trait data and arraying it on the phylogenetic tree to demonstrate phylogenetic signal in function so that their phylogenetically-based inferences could be supported. Curiously, instead of simply measuring the trait dispersion in an assemblage and leaving the phylogeny out of the analyses, many researchers chose a very indirect approach using a phylogenetic middleman where phylogenetic dispersion and signal were measured and not trait dispersion. It is suggested here that this situation should be avoided in the future and the phylogeny should only be used, in the less optimal scenario, to indicate the importance of unmeasured traits or, in the more optimal scenario, to make meaningful evolutionary inferences.

function. For example, work by Swenson and colleagues (Swenson et al. 2006, Swenson and Enquist 2009) has shown that random phylogenetic dispersion could result from simultaneous non-random under-dispersion in some traits and over-dispersion in others. Thus, a great deal of information was lost or washed away by using a phylogenetic proxy to study assembly. An alternative problem, that is equally troubling, is that assembly and co-occurrence may be primarily dictated by a single resource axis (Tilman 1982) and potentially only one axis of function is therefore important for understanding the mechanism underlying community structure. A phylogenetic analysis, even in the best-case scenario, likely could never detect such a mechanism.

Given the irremovable limitations of a phylogenetic proxy, it has become increasingly difficult to publish work solely based on phylogenetic patterns. Thus the question becomes whether phylogenetic dispersion should still be measured particularly when traits can be measured. The answer is that yes it should still be measured for the simple reason that there is a lot of information in the phylogeny not contained in the few traits ecologists measure. This information may provide divergent or stronger results than those derived from a handful of traits (Cadotte et al. 2008). It will always be difficult to explain why the phylogenetic result differs from the trait result and authors should be careful not to over-interpret a phylogenetic pattern with no other evidence, but at the minimum it provides the research a clue as to whether or not additional unmeasured traits that may have phylogenetic signal are important. In those instances where trait data are not available and cannot be collected, phylogenetic dispersion gives a first look at whether the community is potentially non-randomly structured, though beyond that the inferences made must be hedged. Lastly, one way in which a phylogeny should no longer be used in community phylogenetics is as, what I term, a 'phylogenetic middle-man'. Specifically, researchers initially quantified the phylogenetic dispersion of the species in a community, but then were challenged to demonstrate phylogenetic signal in ecologically relevant traits. This resulted in ecologists measuring traits, quantifying phylogenetic signal and phylogenetic dispersion to infer community assembly mechanisms. This was, and is, an incredibly roundabout inference pathway when one could simply just measure the trait dispersion and leave the phylogeny out of the equation (Fig. 1). Put more simply, if the phylogeny really isn't going to be used to infer something about evolutionary processes, which is often the case in tropical forest plot studies given the sparse taxonomic sampling, and it isn't being used to estimate the importance of unmeasured traits with phylogenetic signal, then the phylogeny simply shouldn't be used.

### **So many species and traits and so little time and money**

It is rather easy to discount or discard phylogenetic analyses of tropical plant communities due to their use of phylogenetic relatedness as a proxy for similarity and to suggest that researchers simply go out and measure the 'right traits'

that determine the distribution and dynamics of species. Indeed this perspective has spurred many researchers, myself included, to attempt to inventory several functional traits for tens to hundreds of co-occurring tropical tree species (Kraft et al. 2008, Swenson and Enquist 2009, Baraloto et al. 2010, Lebrija-Trejos et al. 2010, Wright et al. 2010). Unfortunately, such studies are often criticized on two fronts – for only measuring a few easily measured traits and for ignoring intra-specific variation. These points are well taken and appreciated by the vast majority of researchers that measure these traits in the tropics and they should be considered presently.

The use of a small number of easily measured traits is certainly a concern particularly when those traits only represent one real axis of functional differentiation or one functional trait spectrum such as the leaf economics spectrum (Reich et al. 1997, Wright et al. 2004) or the wood economics spectrum (Chave et al. 2009). The problem is that completing an inventory of 'easily measured' traits in a tropical tree community is not trivial and this is under-appreciated by those working in lower diversity systems. For example, collecting values of specific leaf area, which is one of the most easily measured and criticized functional traits, for the over 1000 species in the Yasuni Forest Dynamics Plot in Ecuador required over 2400 person hours to complete (N. Kraft pers. comm.). This time estimate was for just one trait and did not include the thousands of hours necessary to quantify other traits such as wood density and leaf nutrient content and the years necessary to collect and weigh a portion of the seeds in this community (S. J. Wright pers. comm.). Thus, while it would be interesting and potentially informative to measure traits such as photosynthetic and hydraulic conductance rates for all species in large tropical forest plots, significantly more time and money will need to be invested. This investment may be possible over the course of many years, but a concern will be whether these direct measurements of physiological rates will fundamentally improve our analyses over indirect measurements of morphological and structural traits and nutrient content levels. One area where the greatest improvement is likely to occur is if more investment was made towards quantifying plant traits relating to defense. Presently a few research groups have measured traits such as leaf toughness and silica content as metrics of plant defense (Westbrook et al. 2011) with success, but analyses of chemical defense, though expensive, would nicely complement these measures of structural defense (Kursar et al. 2009). Indeed given all of the attention paid to and ink spent on writing about the Janzen–Connell mechanism in tropical tree ecology it is perhaps surprising that more community level inventories of chemical defense have not been accomplished. This is likely due to the non-trivial nature of the field and laboratory protocols, but if there is money and time to invest more information may be gained from quantifying defense compounds for which we have no functional trait proxies (Beccera 2007, Kursar et al. 2009) than quantifying photosynthetic rates for which we have at least some rough functional trait proxies such as leaf nutrient content.

A last obvious weakness of the functional trait approach is intra-specific trait variation. While intra-specific variation



is no doubt important, it is impractical to quantify trait values for each individual in a forest. In one case researchers have sampled all individuals in multiple plots with an enormous amount of effort spent (Baraloto et al. 2010). Even this herculean effort was restricted to only sampling individuals larger than 10 cm in diameter and leaves were sampled in one position in the canopy. Thus, the large numbers of individuals and species less than this size cutoff that likely do influence community dynamics could not be measured and even the large variation known to exist within a canopy of a single tree was not measured. No one can fault Baraloto et al. (2010) for these shortcomings as they have surely done the best job of quantifying intra-specific variation to date. I use this example to simply highlight that individual-level sampling is generally highly impractical. This type of sampling may also become an endless task with very little return for the effort. In particular, intra-specific variation in traits may be negligible within a forest plot and may not influence the types of statistical analyses most ecologists perform. This is not to say this variation isn't important, but the enormous cost involved in quantifying this variation may not justify the returns.

### Where did the evolution and biogeography go?

As noted elsewhere in this review relatedness was originally integrated into community ecology as a way to estimate the ecological similarity of co-occurring species. An entirely different approach to integrating phylogenetic information into community ecology has been to use the phylogeny as a backbone for tracing the biogeography of lineages and the evolution of key traits in order to understand the historical assembly and evolution of communities (Losos et al. 1998, Gillespie 2004). One of the great promises of incorporating phylogenies into community ecology was to address these exact questions, but few botanical studies have taken this approach thereby leaving the synthesis of phylogenetics and plant community ecology incomplete. In other words, we are still not answering the interesting and important evolutionary and biogeographic questions regarding community assembly that phylogenetic trees could help answer.

Key barriers to taking this alternative phylogenetic approach to plant community ecology is that it requires complete or nearly complete taxonomic sampling. In zoological examples such as *Anolis* where a single trophic level is defined by a single genus this problem becomes more tractable (Losos et al. 1998). On the other hand tropical tree communities are composed generally of tens of co-occurring genera that are broadly distributed geographically with many con-geners not found in the assemblage being studied. This makes tracing trait evolution on a plant community phylogeny of little evolutionary interest. The alternative for a plant ecologist is to broadly study the evolution of one or a few lineages, but this comes with the cost of ignoring the numerous other un-studied lineages that are co-occurring and interacting with those being studied (Fine et al. 2004, Pennington et al. 2004, Kursar et al. 2009, Sedio et al. 2012). This is, of course, a substantial problem given that we would need a complete

understanding of the geographic and phylogenetic distribution of all lineages in our study systems and a complete understanding of their functional ecology. That said, the only clear way to start fulfilling the promise of integrating evolution and biogeography into community ecology via phylogenies is to increase the number of investigations that focus on the historical biogeography and trait evolution of large and important lineages across scales. It will be always difficult to link such work to present day local-scale ecological interactions, but it will greatly help us understand the broader scale processes that brought those species to that local scale setting in the first place.

### Linking traits to demographic rates and static versus dynamic analyses

As functional trait and phylogenetically based analyses of community assembly have increased so to has the awareness that mapping process to the observed patterns of trait and phylogenetic dispersion is non-trivial (Swenson and Enquist 2009, Mayfield and Levine 2010). This is particularly the case when the study focuses on 'static' analyses. Static analyses focus on the phylogenetic or trait dispersion of an assemblage at a single point in time and constitute the vast majority of the studies published to date (Webb 2000, Swenson et al. 2006, 2007, Hardy and Senterre 2007, Kraft et al. 2008, Kress et al. 2009, Gonzalez et al. 2010). Less common have been 'dynamic' analyses that have explicitly investigated the linkage between species demography, phylogeny and function (Uriarte et al. 2010, Paine et al. 2012).

As local-scale co-occurrence on ecological time scales can be boiled down to individual demographic rates, phylogenetic and functional similarity should ideally be linked to demographic rates. Thus this has been mainly accomplished in one of two ways. The first way has been through correlative analyses of traits and demographic rates (Poorter et al. 2008, Kraft et al. 2010, Wright et al. 2010). These analyses have often shown significant relationships between traits, specifically wood density and seed mass, with growth and mortality rates, but in most cases these relationships have been weak. Given that, by definition, functional traits are supposed to be linked to species performance these weak relationships raise the question of whether functional ecologists are truly measuring the 'right traits'. While this is certainly one possibility other possibilities remain. For example it is possible that individual trait axes are important during different ontogenetic stages such that seed mass is likely not important for an adult, but is likely very important in the seedling stage, while other trait axes such as wood density may be important throughout ontogeny. Another possibility is that linkages between demography and plant functional traits are best made by integrating several functional axes at once and by scaling these traits to plant size (Enquist et al. 2007). For example, the specific leaf area of species A may be lower than species B suggesting species A has a lower rate of resource uptake, but species A may deploy relatively more leaf area per unit body mass thereby giving it a higher rate of resource uptake when integrated across the entire

individual. Such relationships cannot be recovered when examining a single trait and they are likely important when considering large individual organisms like trees.

A second way in which researchers have attempted to link demographic rates to phylogeny and traits has been to utilize neighborhood models. This work has focused on whether the phylogenetic or functional ‘neighborhood’ surrounding a focal individual influence its growth or survival rate compared to that expected for that species (Uriarte et al. 2010, Paine et al. 2012). Only these two studies have been accomplished thus far in the tropics with many more likely soon to appear. The results thus far have been inconsistent with respect to the influence of phylogenetic relatedness and individual traits. In some cases, the phylogenetic relatedness of neighboring individuals matters little, but this may be unsurprising in forests that have few congeneric species. Whereas in more diverse forests that have many genera with multiple species co-occurring, we might expect a stronger influence of neighborhood relatedness on individual performance. Similar to correlative studies traits and demographic rates, future neighborhood studies will need to consider integrative phenotypes. Further they will need to consider the logistical and conceptual problem of individual-level variation in traits and genetic diversity and the degree to which this unmeasured variation masks the ecological processes of interest.

### Scaling out and mapping the distribution of tropical trees

A key limitation to any future investigations into the assembly of tropical tree communities is our rather poor knowledge regarding the continental-scale or even regional-scale distribution of species. Tropical forest dynamics plots have been valuable for understanding local-scale phenomena, but community assembly is not solely driven by these local-scale processes and regional-scale phenomena are likely more important. Studying community assembly therefore requires us to scale from the regional- or continental-scale down to the local-scale and this can only be achieved by having access to the distribution and diversity of species across scales.

While continental-scale tree distribution data is available in most of the temperate zone this information is generally lacking from the tropics. Even generating smoothed maps of vascular plant species richness in tropical latitudes has been considered a great achievement (Clinebell et al. 1995, Ter Steege et al. 2003, 2006, Kier et al. 2005, Kreft and Jetz 2007). Thus, in order to enable integrative ecological and evolutionary research into the assembly and diversity of tropical tree communities more emphasis must be placed on empowering research efforts designed to document or estimate the geographic distribution of tropical trees. There are initiatives now underway to map the estimated distribution of plant species in the tropics. These efforts will rely heavily on a wealth of geo-referenced specimen data and geographic range prediction models (Loiselle et al. 2008, Mateo et al. 2012). The resulting maps will be a great step forward and will enable more regional-scale research into the distribution and diversity of

tropical trees. That said, this data will always be limited by collector bias, imperfect sampling of biodiversity, and the numerous and often unavoidable biases inherent in range modeling. Proactively dealing with these biases and not letting them retard our advancement and refinement of our knowledge of the geographic distribution of tropical trees will be critical whether that is by the development of novel biodiversity informatics tools and approaches or by simply highlighting the geographic and phylogenetic regions that have been severely under-collected to spur future directed sampling.

### Conclusions

The number of phylogenetic and functional trait analyses of species assemblages has exploded in the past decade. This explosion has been spurred by key technological innovations permitting the rapid estimation of community phylogenies (Webb and Donoghue 2005, Kress et al. 2009) and key conceptual syntheses regarding how to rapidly estimate the plant ecological strategies of tens to hundreds of species using functional traits (Westoby 1998, Westoby et al. 2002). While this initial growth phase has been impressive and informative, several important research objectives have conspicuously not been met (Table 1, 2). These shortcomings are due to inherent weaknesses in community phylogenetic and functional trait analyses or a failure to conceptually and analytically push these fields and approaches in new directions. It is my hope that this review will spur serious discussion about what the next decade of phylogenetic and functional trait research in tropical tree ecology should look like and how we can achieve our major research objective of identifying the mechanisms underlying the assembly and dynamics of tropical tree communities across scales.

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### References

- Agosta, S. J. and Klemens, J. A. 2008. Ecological fitting of phenotypically flexible genotypes: implications for species associations, community assembly and evolution. – *Ecol. Lett.* 11: 1123–1134.
- Andersen, K. M. et al. 2012. Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest. – *Oecologia* 168: 519–531.
- Arroyo-Rodriguez, V. et al. 2012. Maintenance of tree phylogenetic diversity in a highly fragmented rainforest. – *J. Ecol.* 100: 702–711.
- Baraloto, C. et al. 2010. Functional trait variation and sampling strategies in species-rich plant communities. – *Funct. Ecol.* 24: 208–216.
- Baraloto, C. et al. 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. – *J. Ecol.* 100: 690–701.

- Beccera, J. X. 2007. The impact of herbivore–plant coevolution on plant community structure. – *Proc. Natl Acad. Sci. USA* 104: 7483–7488.
- Cadotte, M. W. et al. 2008. Evolutionary history and the effect of biodiversity on plant productivity. – *Proc. Natl Acad. Sci. USA* 105: 17012–17017.
- Cavender-Bares, J. et al. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. – *Ecology* 87: S109–S122.
- Cavender-Bares, J. C. et al. 2009. The merging of community ecology and phylogenetic biology. – *Ecol. Lett.* 12: 693–715.
- Chave, J. et al. 2007. The importance of phylogenetic structure in biodiversity studies. – In: Storch, D. et al. (eds), *Scaling biodiversity*. Santa Fe Inst. Editions, pp. 151–167.
- Chave, J. et al. 2009. Towards a worldwide wood economics spectrum. – *Ecol. Lett.* 12: 351–366.
- Clinebell, R. R. et al. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. – *Biodivers. Conserv.* 4: 56–90.
- Cornelissen, J. H. C. et al. 2003. A handbook of protocols for standardisation and easy measurement of plant functional traits worldwide. – *Aust. J. Bot.* 51: 335–380.
- Ding, Y. et al. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. – *Oikos* 121: 1263–1270.
- Eiserhardt, W. L. et al. in press. Separating environmental and geographical determinants of phylogenetic community structure in Amazonian palms (Arecaceae). – *Bot. J. Linn. Soc.*
- Elton, C. 1946. Competition and the structure of ecological communities. – *J. Anim. Ecol.* 15: 54–68.
- Enquist, B. J. et al. 2007. A general integrative model for scaling plant growth and functional trait spectra. – *Nature* 449: 218–222.
- Fine, P. V. A. and Kembel, S. W. 2011. Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. – *Ecography* 34: 552–565.
- Fine, P. V. A. et al. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. – *Science* 305: 663.
- Fine, P. V. A. et al. 2006. The growth–defense trade-off and habitat specialization by plants in Amazonian forests. – *Ecology* 87: S150–S162.
- Fukami, T. et al. 2005. Species divergence and trait convergence in experimental plant community assembly. – *Ecol. Lett.* 8: 1283–1290.
- Gilbert, G. S. and Webb, C. O. 2007. Phylogenetic signal in plant pathogen–host range. – *Proc. Natl Acad. Sci. USA* 104: 4979–4983.
- Gilbert, G. S. et al. 2012. Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. – *Evol. Appl.* in press.
- Gillespie, R. G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. – *Science* 303: 356–359.
- Gonzalez, M. A. et al. 2010. Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. – *J. Ecol.* 98: 137–146.
- Grant, P. R. and Abbott, I. 1980. Interspecific competition, island biogeography and null hypotheses. – *Evolution* 34: 332–341.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. – *J. Veg. Sci.* 17: 255–260.
- Hardy, O. J. and Senterre, B. 2007. Characterizing of phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. – *J. Ecol.* 95: 493–506.
- Hardy, O. J. et al. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. – *Global Ecol. Biogeogr.* 21: 1007–1016.
- Hulshof, C. M. and Swenson, N. G. 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. – *Funct. Ecol.* 24: 217–223.
- Jaccard, P. 1922. La chorologie selective et sa signification pour la sociologie vegetale. – *Mem. Soc. Vaudoise Sc. Nat.* 2: 81–107.
- Jaccard, P. 1926. Le coefficient generique et le coefficient de communautaire dans la flore maro-caine. – *Mem. Soc. Vaudoise Sc. Nat.* 2: 385–403.
- Jansen, S. et al. 2002. Aluminum accumulation in leaves of 127 species in Melastomataceae, with comments on the order Myrtales. – *Ann. Bot.* 90: 53–64.
- Janzen, D. H. 1985. On ecological fitting. – *Oikos* 45: 308–310.
- Jarvinen, O. 1982. Species-to-genus ratios in biogeography: a historical note. – *J. Biogeogr.* 9: 363–370.
- Katabuchi, M. et al. 2012. Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. – *J. Ecol.* 100: 643–651.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. – *J. Veg. Sci.* 3: 157–164.
- Kembel, S. W. and Hubbell, S. P. 2006. The phylogenetic structure of a neotropical forest tree community. – *Ecology (Suppl.)* 87: S86–S99.
- Kier, G. J. et al. 2005. Global patterns of plant diversity and floristic knowledge. – *J. Biogeogr.* 32: 1–10.
- Kraft, N. J. B. and Ackerly, D. D. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. – *Ecol. Monogr.* 80: 401–422.
- Kraft, N. J. B. et al. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. – *Science* 322: 580–582.
- Kraft, N. J. B. et al. 2010. The relationship between wood density and mortality in a global tropical forest dataset. – *New Phytol.* 188: 1124–1136.
- Kreft, H. and Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. – *Proc. Natl Acad. Sci. USA* 104: 5925–5930.
- Kress, W. J. et al. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. – *Proc. Natl Acad. Sci. USA* 106: 18621–18626.
- Kress, W. J. et al. 2010. Advances in the use of DNA barcodes in building a community phylogeny for tropical trees in a Puerto Rican forest dynamics plot. – *PLoS One* 5: e15409.
- Kursar, T. A. et al. 2009. The evolution of antiherbivore defenses and their contribution coexistence in the tropical tree genus *Inga*. – *Proc. Natl Acad. Sci. USA* 106: 18073–18078.
- Lebrija-Trejos, E. et al. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. – *Ecology* 91: 386–398.
- Letcher, S. G. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. – *Proc. R. Soc. B* 277: 97–104.
- Letcher, S. G. et al. 2011. Phylogenetic community structure during succession: evidence from three Neotropical forest sites. – *Perspect. Plant Ecol. Evol. Syst.* 14: 79–87.
- Liu, X. et al. 2012. Covariation in plant functional traits and soil fertility within two species-rich forests. – *PLoS One* 7: e34767.
- Liu, X. et al. in press. The environment and space, not phylogeny, determine trait dispersion in a subtropical forest. – *Funct. Ecol.*
- Loiselle, B. A. et al. 2008. Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? – *J. Biogeogr.* 35: 105–116.
- Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. – *Ecol. Lett.* 11: 995–1007.

- Losos, J. B. et al. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. – *Science* 279: 2115–2118.
- MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. – *Am. Nat.* 101: 377–385.
- Mateo, R. G. et al. 2012. Do stacked species distribution models reflect altitudinal diversity patterns? – *PLoS One* 7: e32586.
- Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – *Ecol. Lett.* 13: 1085–1093.
- McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- Messier, J. et al. 2010. How do traits vary across ecological scales? A case for trait-based ecology. – *Ecol. Lett.* 13: 838–848.
- Mi, X. et al. 2012. The contribution of rare species to community phylogenetic diversity across a global network of forest plots. – *Am. Nat.* 180: E17–E30.
- Mulkey, S. S. et al. 1996. Tropical forest plant ecophysiology. – Springer.
- Norden, N. et al. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in tropical plant communities. – *Ecology* 93: S70–S82.
- Paine, C. E. T. et al. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. – *Oikos* 120: 720–727.
- Paine, C. E. T. et al. 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. – *Ecol. Lett.* 15: 34–41.
- Palmgren, A. 1921. Die Entfernung als pflanzen-geographischer Faktor. – *Acta Soc. Fauna Flora Fenn.* 49: 1–113.
- Parmentier, I. and Hardy, O. J. 2009. The impact of ecological differentiation and dispersal limitation on species turnover and phylogenetic structure of inselberg's plant communities. – *Ecography* 32: 613–622.
- Pei, N. C. et al. 2011. Exploring tree-habitat associations in a Chinese subtropical forest plot using a molecular phylogeny generated from DNA barcode loci. – *PLoS One* 6: 21273.
- Pennington, R. T. et al. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. – *Phil. Trans. R. Soc. B* 359: 515–538.
- Pennington, R. T. et al. 2006. Insights into the historical reconstruction of species-rich biomes from dated plant phylogenies, phylogenetic community structure and neutral ecological theory. – *New Phytol.* 172: 605–616.
- Poorter, L. et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. – *Ecology* 89: 1908–1920.
- Reich, P. B. et al. 1997. From tropics to tundra: global convergence in plant functioning. – *Proc. Natl Acad. Sci. USA* 94: 13730–13734.
- Ricklefs, R. E. and O'Rourke, K. O. 1975. Aspect diversity in moths: a temperate-tropical comparison. – *Evolution* 29: 313–324.
- Ricklefs, R. E. and Cox, G. W. 1977. Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. – *Oikos* 29: 60–66.
- Ricklefs, R. E. and Travis, J. 1980. A morphological approach to the study of avian community organization. – *Auk* 97: 321–338.
- Schreeg, L. A. et al. 2010. Phylogenetic analysis of local-scale tree soil associations in a lowland moist tropical forest. – *PLoS One* 5: e13685.
- Sedio, B. E. et al. 2012. Trait evolution and the coexistence of a species swarm in the tropical forest understory. – *J. Ecol.* 100: 1183–1193.
- Simberloff, D. 1970. Taxonomic diversity of island biotas. – *Evolution* 24: 23–47.
- Simberloff, D. 1978. Using island biogeographic distributions to determine if colonization is stochastic. – *Am. Nat.* 112: 713–726.
- Strong, D. R. et al. 1979. Tests of community-wide character displacement against null hypotheses. – *Evolution* 33: 897–913.
- Stubbs, W. J. and Wilson, J. B. 2004. Evidence for limiting similarity in a sand dune community. – *J. Ecol.* 92: 557–567.
- Swenson, N. G. and Enquist, B. J. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. – *Am. J. Bot.* 91: 451–459.
- Swenson, N. G. and Enquist, B. J. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. – *Ecology* 90: 2161–2170.
- Swenson, N. G. et al. 2006. The problem and promise of scale dependency in community phylogenetics. – *Ecology* 87: 2418–2424.
- Swenson, N. G. et al. 2007. The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. – *Ecology* 88: 1770–1780.
- Swenson, N. G. et al. 2011. Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. – *Proc. R. Soc. B* 278: 877–884.
- Swenson, N. G. et al. 2012a. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. – *Ecology* 93: 490–499.
- Swenson, N. G. et al. 2012b. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. – *Ecology* 93: S112–S125.
- Ter Steege, H. et al. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. – *Biodivers. Conserv.* 12: 2255–2277.
- Ter Steege, H. et al. 2006. Continental-scale patterns of tree composition and functional across Amazonia. – *Nature* 443: 444–447.
- Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.
- Uriarte, M. et al. 2010. Trait similarity, shared ancestry, and the structure of neighborhood interactions in a subtropical wet forest: implications for community assembly. – *Ecol. Lett.* 13: 1503–1514.
- Vamosi, S. M. et al. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. – *Mol. Ecol.* 18: 572–592.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. – *Am. Nat.* 156: 145–155.
- Webb, C. O. and Pitman, N. C. A. 2002. Phylogenetic balance and ecological evenness. – *Syst. Biol.* 51: 898–907.
- Webb, C. O. and Donoghue, M. J. 2005. Phylomatic: tree assembly for applied phylogenetics. – *Mol. Ecol. Not.* 5: 181–183.
- Webb, C. O. et al. 2002. Phylogenies and community ecology. – *Annu. Rev. Ecol. Syst.* 33: 475–505.
- Webb, C. O. et al. 2008. Ecological organization, biogeography, and the phylogenetic structure of tropical forest tree communities. – In: Carson, W. and Schnitzer, S. (eds), *Tropical forest community ecology*. Blackwell, pp. 79–97.
- Weiblen, G. D. et al. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. – *Ecology* 87: S62–S75.
- Weiher, E. et al. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. – *Oikos* 81: 309–322.
- Westbrook, J. W. et al. 2011. What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant woody species in a Neotropical forest. – *Am. Nat.* 177: 800–811.

- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology scheme. – *Plant Soil* 199: 213–227.
- Westoby, M. and Wright, I. J. 2006. Land-plant ecology on the basis of functional traits. – *Trends Ecol. Evol.* 21: 261–268.
- Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. – *Annu. Rev. Ecol. Syst.* 33: 125–159.
- Whitfield, T. J. S. et al. 2012. Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. – *Ecography* 35: 821–830.
- Wiens, J. J. 2008. Commentary: niche conservatism *deja vu*. – *Ecol. Lett.* 11: 1004–1105.
- Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – *Ecol. Lett.* 13: 1310–1324.
- Williams, C. B. 1947. The generic relations of species in small ecological communities. – *J. Anim. Ecol.* 16: 11–18.
- Wright, I. J. et al. 2004. The world-wide leaf economics spectrum. – *Nature* 428: 821–827.
- Wright, S. J. et al. 2010. Functional traits and the growth-mortality tradeoff in tropical trees. – *Ecology* 91: 3664–3674.
- Zhang, J. et al. 2012. Phylogenetic beta diversity in tropical forests: implications for the roles of geographical and environmental distance. – *J. Syst. Evol.* in press.