Review Article

The Functional Ecology and Diversity of Tropical Tree Assemblages through Space and Time: From Local to Regional and from Traits to Transcriptomes

Nathan G. Swenson

Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA

Correspondence should be addressed to Nathan G. Swenson, swensonn@msu.edu

Tropical tree biodiversity motivates an extremely large amount of research and some of the most passionate debates in ecology and evolution. Research into tropical tree biodiversity generally has been very biased towards one axis of biodiversity-species diversity. Less work has focused on the functional diversity of tropical trees and I argue that this has greatly limited our ability to not only understand the species diversity in tropical tree assemblages, but their distributions through space and time. Increasingly plant ecologists have turned to measuring plant functional traits to estimate functional diversity and to uncover the ecological and evolutionary mechanisms underlying the distribution and dynamics of tropical trees. Here I review much of the recent work on functional traits in tropical tree community ecology. I will highlight what I believe are the most important findings and which research directions are not likely to progress in the future. I also argue that functionally based investigations of tropical trees are likely to be revolutionized in the coming years through the incorporation of functional genomic approaches. The paper ends with a discussion of three major research areas or areas in need of focus that could lead to rapid advances in functionally based investigations of tropical trees.

1. Introduction

Tropical forests are among the most awe-inspiring ecosystems on the planet. Tropical communities and their biological diversity have presented one of the great persistent challenges to ecologists and evolutionary biologists [1–13]. How can so many species coexist? How was so much diversity generated? Is there any underlying deterministic process structuring these communities or are they an intractable and stochastic compilation? These are the fundamental questions that biologists routinely ask when confronted with tropical tree biodiversity. Critical to answering these questions is our understanding of how tropical tree species functionally interact with their abiotic and biotic environments through space and time and how tropical tree functional diversity has evolved [14].

Over the past decade functional biology has played an increasingly important role in tropical tree ecology. For years the majority of this work focused on a handful of species at a time and how they functionally interact with

the environment [15–18]. Recent research has focused more on the linkages between tree demography and organismal function and how species-level functional similarity or dissimilarity dictates the distribution and coexistence of tropical trees through space and time. In this paper, I will focus less on the generalities of how individual species functionally relate to abiotic gradients and more on the relationships between species function, demography, and community structure and dynamics. The paper will therefore at best briefly touch on some foundational work in tropical tree functional ecology and will be admittedly more biased towards recent developments in order to focus more on community-wide functional ecology and diversity. The paper will regrettably also focus little on the evolution of tropical tree function, but this omission is generally due to little research on the topic—something which I will address in Future Directions and Conclusions at the end.

We will begin by discussing the relationship between species functional traits and demographic (i.e., growth and survival) rates. We will then transition to functional trait

based investigations of community structure and dynamics and then ultimately scale up to the regional- and continental-scale to discuss tropical versus temperate tree functional diversity. I will end with a discussion of a couple of avenues of tropical tree functional biology research that should receive more attention in the future as well as a general plea for more basic tropical inventories of species and functional diversity that form the basis of all tropical plant biology studies.

2. The Linkage between Tropical Tree Demographic Rates and Functional Traits

The goal of plant functional ecology is to mechanistically link organismal function to the distribution and dynamics of individuals and species. Central to this approach is identifying the traits that underlie the abiotic and biotic interactions of individuals and species and ultimately their fitness. For the purposes of most ecological investigations, this pursuit can be effectively boiled down to identifying the traits of individuals and species that best predict growth and survival rates. Such traits, often referred to as functional traits, may be indirect measures of some physiological rate or process of interest (known as "soft functional traits") or they may be a direct measurement of that rate or process (known as "hard functional traits") [19]. Substantial effort in the past ~20 years has gone towards identifying key plant functional traits that can be easily measured across a broad array of lineages, life forms, and ecosystems [20–24]. This process has resulted in a list of a few key soft plant functional traits representing different axes of plant function that can be measured rapidly in most field settings [23]. Although this list does not include all aspects of plant function and often uses a very indirect and/or crude approximation of an actual physiological process, quantifying values for this list of functional traits generally represents the most pragmatic and repeatable approach for estimating the distribution and diversity of plant function in communities. The outcome of this work has been tremendously beneficial for plant biologists seeking to understand the functional mechanisms underlying the ecological and evolutionary patterns of interest particularly when clear linkages between a soft plant functional trait and demography have been uncovered. In this section, I will briefly discuss some of these linkages for tropical trees focusing primarily on the small list of functional traits that a field botanist is likely to measure in a tropical forest.

2.1. Wood Density. Aside from individual size, the density of wood is often the best predictor of growth and survival rates within and between species. Specifically, individuals or species with denser wood tend to have lower volumetric growth and mortality rates while individuals or species with lighter wood have higher volumetric growth and mortality rates. Wood density therefore captures a fundamental life-history tradeoff in trees and this is a reason why it is often one of the key quantitative traits used to place tropical trees on a spectrum between light-demanding pioneer species and shade tolerant species [25, 26].

The relationship between wood density and demographic rates has been consistently shown within and across forest dynamics plots from multiple continents [27–36]. As a composite trait, there are multiple facets to why wood density is a strong predictor of tropical tree demography. First, the density positively relates to mechanical strength and therefore dense trees tend to suffer a lower mortality rate due to stem breakage [27, 28]. For example, Zimmerman et al. [28] found that species with heavier wood tended to have a lower mortality rate due to hurricane disturbance in Puerto Rico than species with lighter wood. A second way in which wood density may relate to demography is that wood density is positively related to xylem resistance to cavitation [37]. Specifically, wood material itself has a density of approximately $1.5\,\mathrm{g/cm^3}$ across species [38], but the density of a stem is a composite of the wood material and the spaces (e.g., xylem conduits, latex or resin canals, etc.) within the stem such that larger xylem conduits (e.g., tracheids and vessels) reduce the stem density. Xylem conduits with larger diameters are more vulnerable to cavitation due to the negative pressure within the conduit. Therefore, all else being equal light wooded species will be more likely to experience catastrophic xylem failure and ultimately death in water stressed environments than dense wooded species. Lastly, dense woods are likely to be less susceptible to stem boring insects and are therefore less likely to experience mortality driven by stem boring insect infestation.

The downside of wood density being such a strong predictor of tropical tree demographic rates is that it is relatively difficult to measure. A commonly used technique is to core the bole of a tree, but this is labor intensive and potentially very damaging to the individual being cored. An alternative method is to quantify the wood density of a branch on an individual [39]. This is a less invasive method, but gradients in wood density within individuals make interpreting these values less straightforward. A preferred method of foresters is to quantify the density of a disk of wood taken from the bole [40], but this is obviously not a feasible, or ethical, way to conduct an ecological study in a tropical forest and therefore is only useful in concept but not practice. Thus, while wood density is potentially the best predictor we have of tropical tree demography, it remains one of the more difficult and destructive measures an ecologist can perform.

2.2. Seed Mass. After wood density, seed mass or seed size is generally the strongest predictor of demographic rates in tropical trees. The seed mass can be crudely conceptualized as the amount of food reserves available for an establishing individual. The actual composition (e.g., percent and types of lipids) of seed endosperm will vary across species, but this is generally not measured. As such ecologists will generally ignore that variation to focus solely on the total seed mass. Species with large seed masses are expected to generally have more reserves for an establishing individual in a low resource environment such as a tropical forest understory with low light levels. They are therefore expected to have lower growth and mortality rates. Species with small seed masses are expected to generally have few reserves for the establishing

individual. Thus these species typically establish and germinate best in high resource environments such as light gaps and typically have high growth and mortality rates [41–43].

A number of studies have now reported support for the relationship between seed mass and demographic rates in tropical trees [31, 32, 42, 43]. Interestingly this relationship can even be uncovered in adults suggesting that this trait important for seedling demography is correlated with another trait related to adult demography. A possibility could be that it is related to wood density, but this has been shown not to be the case in general and seed mass is generally only weakly correlated with maximum height and maximum height is not a strong predictor of adult demography [31, 32]. It therefore remains a functional mystery why seed mass is a significant predictor of adult tropical tree demographic rates. Unfortunately, like wood density, seed mass is not one of the easiest functional traits to measure in tropical forests. Quantification of seed mass for all species in a community is difficult if not impossible in many forests via passive sampling (e.g., seed traps) due to the rarity of many species, masting species, difficulties in species identification, and small seeds from some lineages falling through the mesh in traps. An alternative is active seed collection, but this approach suffers from many of the same problems as passive sampling and requires the climbing of very large individuals in many cases. Thus in most cases tropical tree ecologists may have to be content with partial inventories of the seed mass for the community they are studying, but given the importance of this trait even a partial inventory can be quite informative.

2.3. Specific Leaf Area, Leaf Nitrogen, and Leaf Phosphorus. The specific leaf area (SLA: fresh leaf area divided by dry mass), leaf nitrogen content, and leaf phosphorus constitute the most commonly measured aspects of what has been termed the leaf economics spectrum [44, 45]. Species with high SLA, nitrogen, and phosphorus values generally photosynthesize at a faster rate, but have shorter leaf life spans whereas species with lower values photosynthesize at a lower rate and have longer leaf life spans. Thus, in a sense, the leaf economics spectrum represents a leaf level life history tradeoff. In individuals with a few leaves (e.g., seedlings or small herbaceous plants) it would therefore be expected that high SLA, nitrogen, and phosphorus values would be positively correlated with individual growth and mortality rates. Indeed this is the case in many herbaceous species in the temperate zone (e.g., [46]) and to some extent in tropical tree seedlings [47, 48]. That said, the relationships for tropical tree seedlings generally have low biological effect sizes and are slightly significant or non-significant [32]. Further, the leaf economics spectrum traits generally do not predict adult tropical tree demography [32]. This is perhaps not surprising because at the adult level individuals and species can vary widely in the amount of leaf area deployed and therefore their resource capture per unit time irrespective of their leaf economics trait values. Thus, as shown by Enquist et al. [49] the leaf economic spectrum traits should be expected to relate to adult demography only when placed in an allometric context where the size of the individual and the relative biomass partitioning in an individual can be taken into account. In sum, even though the leaf economics spectrum traits are perhaps the most widely and easiest measured traits in tropical plant ecology, they are some of the poorest predictors of demographic rates and future work should be aimed at integrating these measures with the leaf area deployed and allometric relationships to increase their usefulness.

3. Analyzing the Assembly of Tropical Tree Communities Using Functional Traits

3.1. The Case for Analyzing Function. The majority of the hypotheses proposed to explain the assembly of ecological communities invoke the relative importance of the ecological similarity of species. Biotic interactions such as competition, facilitation and herbivory should promote local divergence in the plant strategies [50]. Filtering by the abiotic environment, on the other hand, should promote local convergence in plant strategies [51]. Finally, neutral models do not invoke the importance of how species differ in their ecological strategies, rather they focus on the primary importance of stochastic demographic drift and dispersal limitation [10, 52]. A variety of approaches have been employed to test the relative importance of these proposed mechanisms including the examination of relative abundance distributions and patterns of species distributions and co-occurrence in space and time.

Although the analysis of species abundance, co-occurrence and dynamics patterns have been popular and have often revealed nonrandom patterns, they are fundamentally limited by the fact they are devoid of information pertaining to the ecological or functional strategies of the species under study [53]. For example, a study demonstrating nonrandom patterns of species co-occurrence or turnover cannot identify whether the species composition is functionally convergent or divergent and therefore cannot support or reject the relative importance of abiotic versus biotic interactions in structuring communities [54–57].

In the temperate zone a lack of functional information in tree community assembly investigations somewhat reduces the power of the investigation, but this problem is mitigated because relatively few species have similar functional strategies. In other words there are fewer species per functional group. In tropical forests, on the other hand, a lack of functional information in assembly investigations greatly reduces the power of the investigation. This is due to the high degree of functional similarity or overlap between species and the large number of species in what may be called functional groups or guilds [58]. A clear example of this can be seen in the study of beta diversity or compositional turnover through space and time [59]. Tropical communities are often renowned for their high degree of compositional turnover through space (but see [60]) and investigations into these patterns have played a key role in testing niche versus neutral models in tree community assembly. For example, the rapid turnover of species composition through space can be attributed to dispersal limitation. The problem is that one realization of species beta diversity could have

numerous scenarios of functional beta diversity underlying the pattern ranging from complete species functional turnover as one might expect with niche partitioning along a spatially structured environmental gradient to complete species turnover with no functional turnover as one might expect where both niche-based processes and dispersal limitation are important. In other words, examination of the species turnover alone is insufficient to determine the relative importance of niche versus neutral processes.

Given the limitations of examining tropical tree species abundance distributions and patterns of co-occurrence and turnover through space and time without information regarding the ecological strategies of species, tropical tree community ecologists are increasingly estimating the ecological strategies of all tree species in their study systems by measuring quantitative plant functional traits. The perceived advantage of this approach is that it allows for a rapid inventory estimating the ecological similarity of the species under study thereby allowing for stronger inferences regarding the assembly and dynamics of tropical tree communities. This interest has resulted in a number of recent studies that investigate static community patterns (i.e., patterns of co-occurrence or compositional turnover in space from a single forest census) and dynamic community patterns (i.e., individual demography and community compositional turnover through time from repeated forest censuses). In the following two subsections I will describe this recent static and dynamic research.

3.2. Static Analyses of Functional Similarity in Tropical Tree Communities. A fundamental question in ecological research is to what degree does the ecological similarity of species dictate their co-occurrence and interactions. Niche-based theory posits two potential outcomes. First, abiotically challenging environments are expected to select for a subset of ecological strategies that can tolerate that environment [51]. This process of abiotic filtering is therefore expected to promote the co-occurrence of species that are more ecologically similar than expected from a random sample of the species that could colonize the study site. Second, in less abiotically challenging environments biotic interactions are posited to become more important and ecological differentiation is expected to facilitate co-occurrence [50]. Thus, co-occurring species are expected to be more ecologically diverse than expected given a random sample of the potential species that could colonize the study site. These niche-based theories are typically contrasted with a neutral model that does not invoke the importance of species-level ecological differentiation. Rather neutral models invoke the importance of dispersal limitation and stochastic birth and death rates [10, 52]. Therefore, neutral models are expected to produce random patterns of ecological similarity between co-occurring species particularly when spatial autocorrelation (i.e., dispersal limitation) is incorporated into the analysis.

The above basic niche and neutral predictions regarding the ecological similarity of co-occurring species have been tested for approximately a century. The initial studies of this type utilized the relatedness of co-occurring species as an indicator of their ecological similarity. In particular, the assumption was that closely related species are expected to be, on average, more ecologically similar to one another than they are to distantly related species due sharing a more recent common ancestor [61–63]. Early studies therefore analyzed taxonomic ratios such as the genus-to-species ratio where a low genus-to-species value, for example, indicated closely related species co-occurring and the importance of abiotic filtering and a high genus-to-species ratio indicated distantly related species co-occurring and the importance of biotic interactions. Such analyses persisted in plant ecology even into this millennium and have recently been replaced by analyses that scale the relatedness of co-occurring species based on their phylogenetic relatedness rather than taxonomic ratios [64, 65]. This community phylogenetic approach is widely used in ecology and in tropical plant ecology in particular (e.g., [66–73]). This popularity in tropical ecology can partly be explained by the reality that it is often difficult, if not impossible, to quantify the functional strategy of all species in a tropical community and phylogenetic information may be used to rapidly, if crudely, assess the ecological similarity of co-occurring species [74]. The obvious problem, though, with this explicitly phylogenetic approach is that it assumes that relatedness is a strong proxy for ecological similarity. This assumption will undoubtedly be violated in some, if not many, cases particularly on fine taxonomic scales (e.g., [75–77]). A further difficulty with the phylogenetic approach is that even if relatedness is a decent indicator of overall similarity, co-occurring species may have their co-occurrence dictated by one or a few axes of function and whether or not these individual axes are phylogenetically conserved is not known. In other words, even if nine of ten axes of plant function are phylogenetically conserved, one critical axis of function may not be and this would result in a faulty inference regarding the mechanisms underlying community structure and dynamics.

Given the difficulties with inferring mechanisms from phylogenetic patterns, tropical plant ecologists have increasingly sought to conduct community-wide inventories of plant functional traits. As noted above, these traits are often selected because they are feasible to measure for each species in a diverse assemblage and they are believed to be quantitative indicators of plant ecological strategies. The first study of this type that I am aware of comes from Swenson and Enquist [78] where we analyzed the community-wide diversity in wood density across temperate and tropical tree plots. The results found that the diversity in this trait was maximized in warmer and wetter forests suggesting that in these less abiotically challenging environments wood density was allowed to vary more widely between co-occurring species. We inferred that this was evidence for competition for light and water resources in these environments where divergent species were more likely to co-occur and similar species competing for similar "niche space" were not [78]. While this was the first study to explicitly investigate the functional trait similarity of co-occurring tropical trees in forest inventory plots, the investigation was limited to a single plant functional trait. A stronger investigation into the community assembly of tropical trees would come from quantifying multiple functional traits in an entire

community rather than just a single axis of function. One of the first studies to accomplish such a community-wide inventory of multiple functional traits in a tropical tree community was conducted by Kraft et al. in Yasuní, Ecuador [79]. Specifically, Kraft et al. quantified several leaf traits, maximum diameter, wood density and seed mass for most of the >1,000 species found in the Yasuní Forest Dynamics Plot. This data was then used to quantify whether co-occurring species in this forest tended to be more similar in their trait values than expected from a null model where random communities were generated by randomly pulling from the pool of species known from the forest plot. The study found that the observed patterns of trait similarity were often nonrandom and therefore lent support for a niche-based model of community assembly. In particular, most traits were locally convergent, or more similar than expected, between co-occurring species supporting an abiotic filtering mechanism whereas a few, seed mass and maximum diameter, were locally divergent indicating the importance of biotic interactions.

Soon after the Kraft et al. [79] study a similar investigation from a dry forest dynamics plot in northwestern Costa Rica was published by Swenson and Enquist [68]. Their study quantified several of the same traits and used similar null modeling analyses as Kraft et al. [79] therefore making it a nice comparative piece of evidence. The Swenson and Enquist [68] study also found nonrandom trait similarity patterns and interestingly they found similar trait specific patterns. That is, leaf and wood traits tended to be locally convergent while seed and size traits were locally divergent. Thus, Swenson and Enquist [78] inferred that rather than just abiotic filtering or biotic interactions driving community assembly, these opposing mechanisms are likely operating simultaneously albeit on different axes of species function. In such a scenario, it may be expected that a few functional axes determine whether or not species can meet the abiotic challenges in an environment and additional axes of function sort out the biotic interactions within those environments to ultimately determine the co-occurrence of species. This scenario is similar to that generally envisioned by physiological ecologists that view the spatial distribution of species as the outcome of that species first passing through an abiotic filter and second through a biotic filter hierarchically [80]. An additional important aspect of the Swenson and Enquist [68] study was that it contrasted the trait similarity results with previously published phylogenetic similarity analyses from the same dry forest plot [67]. They demonstrated that the opposing assembly mechanisms operating on different axes of function often produced a pattern of phylogenetic randomness and showed that mapping phylogenetic patterns to trait similarity is often difficult if not impossible.

Since the above two original studies investigating multiple functional traits within a single community many more have been published (e.g., [53–57, 81–85]). Some such as Paine et al. [81] and Swenson et al. [56] have utilized very similar traits and analytical approaches across several tropical tree plots and have found very similar results to Kraft et al. [79] and Swenson and Enquist [68]. Thus, there appears to be some generality in trait dispersion across several different tropical forest types suggesting the general importance of the functional axes being quantified in determining the distribution and co-occurrence of tropical trees. Further, these studies have generally analyzed the trait similarity of co-occurring species across various spatial scales within forest plots. These analyses have generally revealed similar scale dependencies where nonrandom patterns of trait similarity are more likely on finer spatial scales again signaling the potential for similar mechanisms being at play across disparate forests.

Additional studies have focused less on the functional trait similarity of all of the tree species in a tropical forest and have focused more on the functional trait similarity and co-occurrence of the members of a lineage. For example, Becerra [86] has investigated the functional similarity of co-occurring *Bursera* species in Mexican dry forests to show that divergence in function promotes species co-occurrence. The axis of function that Becerra [86] analyzed was the leaf chemical composition of *Bursera* as an indicator of their interactions with the local herbivore assemblage. If differentiation between *Bursera* species in their chemical interactions with herbivores promoted their coexistence, Becerra [86] predicted the leaf chemical composition of co-occurring species should be divergent. This expectation was supported and the study remains one of the clearest examples of nonrandom herbivore related trait dispersion in a tropical tree lineage.

A similar study to the *Bursera* study by Becerra [86] has recently been conducted using the diverse Neo-tropical genus *Inga*. In particular, Kursar et al. [87] investigated the phylogenetic and functional similarity of co-occurring species of *Inga* in Peru and Panama. Again the functional similarity of species was characterized with anti-herbivore defense traits. As in the Becerra [86] study, the Kursar et al. [87] study found significant divergence in defense traits between co-occurring species in the genus again supporting the expectation that differentiation in defense promotes coexistence in diverse tropical tree assemblages.

The final lineage specific functional trait analysis that I am aware of comes from Sedio et al. [85] who studied the functional similarity of co-occurring species of *Psychotria* in Panama. A large number of morphological and physiological traits were quantified for the species locally represented from this diverse genus and the authors asked whether the trait similarity of co-occurring species in the genus deviates from a random expectation. Similar to community-wide investigations, this lineage-specific analysis found nonrandom trait dispersion in assemblages and the directionality of this dispersion depended on the axis of function being analyzed. The work nicely demonstrated that traits related to plant hydraulics play a critical role in determining the spatial distribution and co-occurrence of the species in this important genus. Similar to the other lineage-specific analyses described above, Sedio et al. [85] array their trait data on a phylogenetic tree. Across studies many of the traits measured are not phylogenetically conserved suggesting that patterns of phylogenetic similarity within these highly diverse groups may not reflect patterns of functional similarity.

Although static analyses of the functional similarity of co-occurring tropical tree species have been successful and

will likely become more common in the literature in the coming years, several key challenges remain. A challenge that was almost immediately recognized was that of intraspecific trait variation. The studies mentioned above have generally utilized a species mean trait value for each species in their study systems. This is potentially problematic given that individual-level variation is believed to be generally important and some traits are known to vary widely within species and even within individuals. Thus, it was not surprising that almost immediately after the initial inventories of Kraft et al. [79] and Swenson and Enquist [68] a number of investigations into intraspecific trait variability in tropical trees were published. One of the first came from Messier et al. [88] in Panama suggesting that leaf functional trait values can vary widely within species, but the functional composition of communities may not be as variable suggesting that the overall distribution of community function may be more informative than population-level variation for understanding the mechanisms underlying community assembly. Additional work published shortly thereafter sought to partition the variation in trait values within individuals, across individuals and across species and found that while there is often large variation within species, species can be differentiated on the basis of their mean functional trait values so long as that mean is estimated by sampling, in many cases, greater than 10 individuals [89]. Additional work from French Guiana has measured individual level trait values across several forest inventory plots to successfully demonstrate the importance of individual level values when attempting to identify community assembly mechanisms [81]. In particular, Paine et al. [81] demonstrated that trait dispersion patterns were more nonrandom when using individual-level trait values than when using species mean trait values calculated from multiple forests plots arrayed across a region. Similarly, Swenson et al. [55] have demonstrated that the functional dissimilarity of tree assemblages along an elevational gradient in Puerto Rico is accentuated when incorporating population-level trait differences suggesting the importance of intraspecific functional responses to abiotic changes along the elevational gradient. The sum total of this evidence can be boiled down to a few important points. First, population-level variation in trait values can be substantial enough to significantly influence a study and when possible this variation should be quantified. Second, within a forest species can be differentiated by their traits so long as the population is sampled adequately and that intraspecific variation within that population is likely small enough that a species mean trait value for that population is sufficient for most analyses. Of course, quantifying individual-level variation would be preferred, but in practice this is not feasible due to the large number of stems (>100,000) in many forest plots nor is it ethical particularly when coring each individual bole to quantify wood density. Third, if a local trait value is not available incorporating the species level trait value collected from another part of the species range is likely a better estimate of function and certainly is preferred over excluding the species from the analysis.

A second major challenge for static analyses of trait similarity in tropical trees is linking the results to demographic rates. While the ultimate presence of species in tropical forest plots is the result of their ecological interactions with broad scale environmental gradients and the vagaries of their biogeographic history, the dynamics and coexistence of species on contemporary time scales boils down to their demography. Thus it is imperative that we are able to link static patterns of trait similarity to the demography of the species co-occurring in our dataset. Making this direct link is generally not possible from static patterns. Some have attempted to make this link by analyzing the trait similarity of species in different size classes [68], but such analyses are flawed due to the loose correlation between size and individual age in tropical trees. Thus, functional ecologists investigating community assembly and species co-occurrence from static patterns will need to seek alternative approaches to directly link patterns of trait similarity to species demography. In the next subsection I will discuss the few such analyses to date that have taken advantage of temporally dynamic datasets.

3.3. Dynamic Analyses of Functional Similarity in Tropical Tree Communities. In many ways I see the analysis of functional similarity in dynamic datasets as the way forward for functional trait-based investigations of tropical tree communities. Dynamic datasets are those that track the growth and survival of individual trees through time. By linking the function of these individuals and their immediate neighbors to their growth and survival rates many of the direct hypothesis tests unapproachable via static analyses can be conducted. For example, a static analysis of trait similarity may report that co-occurring species or individuals may be functionally dissimilar but such a result fails to make the link that functional similarity negatively impacts the growth and survival of an individual. A dynamic analysis, on the other hand, could analyze whether the functional identity of the species or individuals surrounding a focal individual does nonrandomly influence the demographic fate of that focal individual. This brings us a step closer to the mechanisms underlying community assembly and dynamics and may bring us the closest we will come to identifying the important mechanisms in lieu of experimental studies which are generally not representative or at least not feasible for complex and diverse tropical assemblages.

The first truly dynamic analysis of individual-level tropical tree demography, co-occurrence and function was published by Uriarte et al. [90]. The Uriarte et al. [90] approach built upon a tradition in forest ecology that seeks identify the mechanistic linkages between abundance, size, and the spatial proximity and similarity of neighboring trees (e.g., [91–97]) and I will describe it in detail.

The neighborhood modeling framework assumes that each individual has a species-specific maximum growth or survival rate. Individual growth or survival is predicted by adjusting the species-specific maximum rates to account for the size of the individual and the spatial structure of its neighborhood. The model predicts individual growth as:

$$g = g_m \cdot \delta \cdot \nu, \tag{1}$$

and survival as:

$$s = s_m \cdot \delta \cdot \nu, \qquad (2)$$

where s is the predicted survival, g is the predicted growth, s_m is an estimated species-specific maximum survival rate, g_m is an estimated species-specific maximum growth rate, δ is the size effect and ν is the neighborhood effect. Size effects (δ) in these models are calculated using a traditional logarithmic function, that is empirically supported (e.g., [95]) and flexible, as:

$$g = g_m \cdot \exp\left(-\frac{1}{2}\right)\left[\frac{\ln(dbh/X_0)}{X_b}\right]^2,$$
$$s = s_m \cdot \exp\left(-\frac{1}{2}\right)\left[\frac{\ln(dbh/X_0)}{X_b}\right]^2, \qquad (3)$$

where dbh is the diameter of the focal individual, X_0 is the dbh at which maximum growth or survival occurs, and X_b determines the breadth of the function.

The neighborhood effects (ν) are the net effect of a neighboring tree on the growth and survival of the focal individual and they are assumed to vary positively as a function of the size of the neighbor and inversely with distance to the neighbor [94]. This effect is then multiplied by a scalar (λ_s), ranging from zero to one, which allows for differences among species in their competitive effect on the focal individual. A neighborhood crowding index (NCI) for each focal individual can then be computed by combining the size, distance, and competitive effects as:

$$\mathrm{NCI}_{\mathrm{focal},\,k} = dbh_{\mathrm{focal},\,k}^{\gamma} \sum_{i=1}^{S} \sum_{j=1}^{n_i} \lambda_{ik} \frac{dbh_{ij}^{\alpha_k}}{\mathrm{Distance}_{ij}^{\beta_k}}, \qquad (4)$$

where $dbh_{\mathrm{focal},\,k}^{\gamma}$ is the diameter of the focal individual weighted by the exponent γ that characterizes the size-sensitivity of an individual of focal species k to neighborhood effects. The model includes the number of species (S) and individuals of each species (j) in the neighborhood of a focal individual where the neighborhood is defined as having a radius of R. The α_k and β_k parameters allow for non-linear scaling of neighborhood effects and are uniform across species in order to keep the model tractable [96]. The pairwise competition coefficient, λ_{ik}, is scaled from zero to one reflecting the per capita effect of species i on species k. Depending on the analysis, this variable will be scaled based on trait distance, where a value of one signifies identical individuals (i.e., conspecifics) [90].

The overall neighborhood effects used in the model, ν, are then translated into an actual effect on growth or survival using a negative exponential function as:

$$\nu = \exp^{-C \cdot \mathrm{NCI}_i^D}, \qquad (5)$$

where, NCI_i is the NCI for focal individual i and C and D are species-specific estimated parameters. If $D = 1$ this function takes the form of a standard negative exponential function, but if $D > 1$ the function will be sigmoidal with a flexus when $\mathrm{NCI} = 1$. A negative exponential indicates

a high sensitivity to crowding while a sigmoidal function represents a resistance to crowding up until a particular threshold [95, 96].

Uriarte et al. [90] used this neighborhood modeling framework to link individual growth and mortality to the trait neighborhood of that focal individual, while taking into account effects of individual size and local stem density. Their analyses were conducted on a trait-by-trait basis for several species of trees in a Luquillo Forest Dynamics Plot in Puerto Rico. The results showed that the functional identity of neighboring individuals often had a significant influence on the growth and survival rates of focal individuals in this forest plot. As with static analyses, the results were often trait-specific with similarity in some traits positively influencing focal individual growth and survival with other traits negatively influencing these demographic rates. Further, the results were not consistent across species suggesting that the interaction between demographic rates, trait similarity, and coexistence is much more complex than what may be believed from static analyses.

A second study that focuses on neighborhood analyses was published by Paine et al. [98]. This research focused on whether seedling demography in French Guiana was related to the functional identity of neighboring individuals. The analytical approach taken by Paine et al. [98] that utilized generalized linear mixed models is less complex than the Uriarte et al. [90] approach, but conceptually it is very similar with the same ecological questions being posed. The results from French Guiana indicate that the overall functional similarity of neighboring individuals is negatively related to the mortality rate of the focal individual. In other words, they found that the more functionally similar the neighbors the greater the survival rate. This finding does not support a model of negative competitive interactions. Rather it provides supports for abiotic filtering of similar functions. The analyses focused on the overall functional similarity of species and individuals and did not perform trait specific analyses making it not possible to discern whether the findings were or were not generalizable across all axes of plant function. The results from Uriarte et al. [90] and from static analyses of trait dispersion in tropical tree assemblages suggest this is likely not the case such that there are likely axes of function where trait dissimilarity increased growth and survival rates. Paine et al. [98] also sought to test the Janzen-Connell [99, 100] hypothesis, that shared enemies promote negative density dependence and coexistence, using phylogenetic relatedness in the models, but the degree to which the traits and interactions underlying this hypothesis are phylogenetically conserved is not well known with conflicting evidence depending on the taxonomic scale [86, 87, 101–103]. A second key finding in the Paine et al. [98] work is that the magnitude of differences in seedling mortality explained by seedling height is larger than that explained by the functional neighborhood indicating the central importance of size specific demographic rates and the need to incorporate this information into any such neighborhood models in the future. Aside from the original Uriarte et al. [90] and Paine et al. [98] neighborhood modeling studies no other such analyses have been performed on tropical tree

assemblages. Given the power of analyzing dynamic datasets over analyzing static datasets I expect many more trait-based neighborhood modeling studies to be published in the near future. It will be useful if these future analyses use similar methodologies that will allow for the comparison across different tropical forest types and continents as well as across latitude.

An alternative dynamic analysis to neighborhood models is to quantify the temporal turnover in the functional composition of tree assemblages. In particular, does the functional composition of an assemblage nonrandomly shift directionally or stay static? It is known that there is a temporal decay in the similarity of tropical tree species composition through time in a spatially defined area [104]. The degree to which this decay in similarity is driven by neutral or niche-based processes is frequently debated. Answering this question is not only central to basic ecological research, but also terribly important for those focusing on the dynamics of tropical forests as they experience increasing human pressure via direct disturbance (e.g., timber logging) and indirect disturbance (e.g., climate change). A central difficulty in addressing this issue is that analyzing the temporal turnover of species compositions is an incredibly information-poor exercise and likely leads to faulty inferences [54–57]. This problem may be especially acute in tropical tree assemblages where multiple species likely have very similar functional strategies such that a species could be replaced through time by a functionally analogous species in less disturbed forests. Studying the dynamics of Latin binomials in this case may lead a researcher to declare temporal decay in the composition and potentially neutral ecological drift, but a functional analysis would show that the functional composition is decidedly not drifting and a neutral model should not be exclusively supported. In more disturbed tropical forests we may expect that priority effects and neutrality may dominate the successional trajectory or that the harsh environmental conditions in a disturbed forest may strongly filter the community composition and deterministically drive its successional trajectory. I argue that answering such a question requires functional information and ignoring this information could lead us seriously astray. Inspired by this thought experiment, James Stegen and I spearheaded a project to investigate the functional and phylogenetic compositional turnover of one disturbed tropical forest dynamics plot in Luquillo, Puerto Rico and one less disturbed forest dynamics plot on Barro Colorado Island, Panama. Using trait data collected in Panama by Wright et al. [32] and in Puerto Rico by myself and phylogenetic trees published by Kress et al. [69, 70], we quantified whether the phylogenetic and functional composition of trees in subplots turned over more or less than expected given the known levels of species and individual turnover. The phylogenetic results were inconclusive and generally suggested that the phylogenetic composition turned over randomly in each forest albeit with some interesting and not well investigated nonrandom spatial patterns. The functional results on the other hand were much more interesting. In the disturbed Luquillo forest we found that the functional composition turned over much faster than that expected given the species

turnover. The trait-specific patterns through time generally followed what would be expected by a functional ecologist studying succession [105, 106] with an increase in wood density and seed mass and a decrease in leaf nutrient content through time in assemblages. While these results may seem intuitive and obvious to a functional ecologist there were some interesting spatial patterns with respect to the spatial turnover through time. The less disturbed regions of this forest plot functionally turned over consistently through time whereas the more disturbed regions in the plot were functionally static for the first two censuses after Hurricane Hugo where pioneer species colonized and dominated for around 5–10 years. This period was followed by a very rapid shift in the functional composition towards a more functionally diverse composition over the course of the next 5–10 years suggesting that the functional recovery in a disturbed tropical forest may be much more rapid than previously expected.

The results from the less disturbed Barro Colorado Island forest dynamics plot were the exact opposite of the results from the disturbed Puerto Rican plot. In particular, the functional composition of the Barro Colorado Island plot was essentially static over the >20 year period investigated. Thus, as an individual died in this forest, it was replaced by an individual that was more functionally similar to it than expected from random. This result stands in stark contrast to the strong temporal decay in the species compositional similarity previously reported for this forest plot [104]. I have been frequently asked whether there is enough mortality in this forest plot to detect anything but functional stasis, but it is important to recall that over half of the individuals in the original census of the plot in 1982 have died and have to a great extent been replaced though the total number of individuals in the plot has declined through time. Thus, while the species composition appears to be drifting neutrally through time in this forest the functional composition is not leading me to call this an instance of drifting binomials with functional stasis underscoring the importance of measuring species function. An additional implication of this work is that it may not be possible for an ecologist to predict the future *species* composition of a plot of tropical forest even using functional information, but we are likely in a position to predict the *functional* composition. That is, it might not be possible to predict the presence or absence of a particular species in a subplot, but we should be able to predict the type of functional strategies that will be present in that subplot in disturbed or less disturbed forests. This is promising for research focused on predicting the distribution and dynamics of ecosystem function in future environments, but it is not particularly promising for those focused on predicting the distribution of individual of species. Similar to the neighborhood modeling studies from Puerto Rico and French Guiana, my work on the functional turnover of tree assemblages through time comes from very few forests and from only a handful of functional axes. A great deal more research is needed from additional forest types and biogeographic regions using more axes of function before we can generalize, but the results thus far suggest that analyzing

dynamic tropical tree datasets will become an increasingly utilized and powerful approach in trait-based research.

4. Functional Genomics of Tropical Trees

Despite the many advances made by functional trait analyses of tropical tree communities, there are clear disadvantages to this approach. The clearest weakness is that only a few functional traits are generally measured. These traits, often called "soft traits," are generally only correlates of an actual physiological traits, often called "hard traits," or process of interest. This approach is taken because it is often not feasible to conduct detailed physiological measurements on multiple individuals of every species even in moderately diverse species assemblages. Another problem that arises with the functional trait approach is that it is not possible *a priori* to know all aspects of organismal function that are important in determining the assembly and dynamics of communities. Thus, even if field biologists could measure all aspects of organismal function that they wish to measure, inevitably there will be several other important axes of plant function that the investigator is ignorant of and will not quantify. Therefore, the functional trait approach to community ecology is fundamentally limited by the inability of a field biologist to measure all aspects of organismal function that one believes to be important and those that are important but not yet known. Functional ecologists have recognized these deficiencies of the functional trait approach to community ecology and integrated phylogenetic information into their research as a way to potentially estimate the similarity of the species on those axes of function not captured by the measured functional traits (e.g., [64–66]). While this phylogenetic bet-hedging approach may seem reasonable, it is susceptible to violations of the central assumption that phylogenetic similarity truly reflects functional similarity. I therefore suggest that while functional trait approaches to community ecology have been shown to be powerful in many studies, this approach will always be subject to the above limitations. Thus researchers in this field must begin to consider how to enhance their research programs through the integration of alternative tools and perspectives to address fundamental and important questions regarding the assembly and dynamics of communities.

In the above I highlighted several limitations to functional trait-based investigations in community ecology. These limitations will be extremely difficult to overcome in the best-case scenario when only using functional traits or by integrating phylogenetic trees with functional traits. I argue that by adding a genetic dimension to this existing research program these limitations can be mitigated. Often the genetic dimension of biodiversity has been integrated into tree community ecology by examining intraspecific genotypic diversity to investigate questions regarding the spatial distributions of individuals and the ecological interactions of different genotypes (e.g., [64, 66]). Generally research on the genetic diversity in ecological communities has not examined the genomic diversity within community samples aside from metagenomics research on microorganisms. One

reason for this that it is currently not feasible to sequence and assemble the genomes of all species in a community as it is generally not possible to assemble the genomes of non-model organisms particularly those distantly related from model organisms. Whole community inventories of transcriptomes, the portion of the genome being transcribed in a tissue, on the other hand are becoming feasible [107–112] and this development could potentially transform community ecology. Specifically, next generation sequencing (NGS) or massively parallel sequencing facilitates the rapid and cost effective sequencing of transcriptomes and sequences from "deep" paired-end transcriptome NGS can be readily assembled for non-model organisms [107, 108]. Thus, it is now possible to quickly inventory and analyze what parts of the genome are being transcribed by each species in the community and therefore permits the rapid inventory of the functional composition of a community. In other words, NGS will lead to the development of an integrative research program that I term "community functional genomics" or "community functional phylogenomics."

As with many developing technologies it is often easy to generate a lot of data, as it is with NGS, but the difficulty will be determining how to utilize that information to answer fundamental biological questions. I foresee two initial ways in which transcriptomic diversity can be quickly and meaningfully integrated into tropical tree community ecology. One approach is to address fundamental questions about what aspects of function regulate the spatial distributions of individuals within species along important environmental gradients in a forest. A second approach seeks to integrate the interspecific transcriptome diversity in a community with the phylogenetic and functional trait diversity to perform community functional phylogenomics analyses. This second approach could be beneficial to tree community ecology in two ways. First, it will allow researchers to quantify the transcriptomic similarity of co-occurring species. This frees ecologists from having to pick and choose a few plant functional traits to quantify in a community and allows them to instantly quantify all aspects of the genome that are being transcribed (i.e., that are functional). Second, community functional phylogenomics can truly integrate the phylogenetic, functional, and transcriptomic (genetic) dimensions of biodiversity into a single analysis. Specifically, recent research has introduced the concept of "functional phylogenomics" where a phylogenetic inference is first made using the transcriptomes from many species and subsequent analyses quantify the degree to which certain parts of the transcriptome do or do not support each node in the inferred phylogeny [108]. This pioneering study analyzed species from across the plant tree of life, but generating such an analysis for all species in a plant community could just as easily be accomplished. By performing a similar study in a plant community, one would be able to quantify the phylogenetic structure of ecological community using the phylogenomic tree and to determine what aspects of the transcriptome underlie that phylogenetic community structure. In particular it is now easy to quantify whether a node in a phylogenetic tree is over- or under-represented in a plant community, but it is far from trivial to determine

what is significant functionally about the species subtended by that node (e.g., [68]). This difficulty in disentangling the phylogenetic structure of communities may be alleviated by quantifying which parts of the transcriptome support, or do not support, the particular nodes of interest. For example, knowing that parts of the transcriptome related to drought tolerance tend to be conserved between species subtended by a node in the phylogeny that is over-represented in a community would provide evidence for abiotic filtering and would quickly help "unpack" the observed phylogenetic structure.

Of course in many cases parts of the transcriptome that appear to be strongly related to the observed ecological patterns may have no known function at present. Thus, in such scenarios candidate genes or gene families can be identified for future detailed investigations. Thus instead of measuring a few plant traits ecologists believe to be important and not measuring many others that are important, directed research can be undertaken by analyzing transcriptomes and identifying the genes or gene families that are the best predictors of the ecological patterns of interest.

Plant ecologists quantifying functional traits in plant communities have begun to explicitly incorporate intraspecific trait variance into their analyses. This work has shown that intraspecific trait variation can be particularly important when comparing multiple forest plots. The importance of intraspecific trait variation within forest plots and whether it explains local species distributions along local environmental gradients is less well understood and additional research on this topic is needed. Further observational studies of the intraspecific variation in transcriptomes are greatly needed for a number of reasons, but here I list two. First, the magnitude of intra- versus interspecific variation has not been well quantified and understanding this relative magnitude will be fundamental to the development of transcriptome-based analyses of communities. Second, comparative studies of the intraspecific variation in transcriptomes across species can help reveal whether similar aspects of the transcriptome respond in the same way across local environmental gradients and how this similarity or dissimilarity influences patterns of species co-occurrence. Thus while I expect many more functional trait studies to be published in tropical tree community ecology, NGS-enabled functional genomics or transcriptomics on a community-scale may become more common within the next few years and will substantially expand the functional space ecologists can investigate in the field.

5. The Functional Diversity of Tropical versus Temperate Trees and the Latitudinal Gradient in Species Richness

The latitudinal gradient in species richness is perhaps the most ubiquitous and analyzed pattern in all of ecology and biogeography. A prominent hypothesis for the latitudinal gradient in species richness is that the relative lack of strong abiotic pressures and the increased degree of biotic interactions in the tropics may explain, in part, the gradient in species richness. For example, Fischer [3] proposed that

relatively benign and stable tropical climates and strong biotic interactions have driven increased net diversification in the tropics through an expansion of niche space. Thus, increased tropical species richness should positively correlate with an increase in the range of functional strategies in these ecosystems. This prediction would also be supported if limiting similarity dictates community membership whereby the addition of species can only arise from an expansion of strategy space. Similar to the local scales studies of tropical tree community assembly that we discussed above, addressing this hypothesis requires information regarding the functional convergence and divergence in species along the gradient.

Most of the studies investigating the convergence and divergence of functional strategies across latitude have come from the zoological literature. For example, Ricklefs and colleagues [113, 114] have tested the prediction of limiting similarity that the morphological trait volume of species assemblages should increase with species richness towards the tropics. The original research on this topic demonstrated support for limiting similarity [113, 114], but recent work with expanded sampling has thrown this into question suggesting that species simply pack more tightly into morphological space in the tropics than in the temperate zone. Additional work tends to show a similar pattern where the morphological or functional volume of tropical assemblages increases with species richness [115], but only to a point and that the packing of species in that volume increases more rapidly than volume expansion.

There are surprisingly few botanical investigations into the fundamental question of how functional diversity and species richness relate across latitude. To the best of my knowledge, the majority or all of this work has come from my laboratory. My first investigation into this issue examined the diversity of the key plant trait wood density in over 150 0.1 ha forest inventory plots arrayed across North and South America [78]. Specifically the research asked whether diversity in this trait was higher or lower than that expected given the species richness of the inventory plot and how this varied across latitude and climatic gradients. The research showed that there was a higher than expected variance in wood density values in tropical tree assemblages than expected given their species richness. It is common knowledge to tropical tree researchers that their study organisms widely vary in their wood density, but this result suggests that this variation is even higher than expected given the species richness and suggests that niche differentiation is likely important in determining the composition of these forests and that this variation exceeds that expected given a random sample of the global pool of possible wood densities.

We recently followed up our original study on wood density in forest plots by examining the diversity of multiple traits in map grid cells across North and South America. Specifically, using a database of over 5 million geo-referenced plant specimens and a large composite plant trait database we asked whether functional diversity increased towards the Equator more than expected given the increase in species diversity [116]. In many cases we found that the functional diversity did increase as expected by Fischer [3], but the

finding was not consistent across traits and substantial variation in trait dispersion patterns within the tropics were evident. The heterogeneity of the spatial and trait datasets used in this work make it difficult to generalize and draw broad conclusions. Future research that utilizes complete forest inventories and complete inventories of traits are needed to fully address this most fundamental question regarding the distribution of perhaps the most important axes of biodiversity-functional diversity.

6. Future Directions and Conclusions

At many times while writing this paper I have been simultaneously surprised by how much functional research has been accomplished on diverse tropical tree assemblages in recent years and by how much more work we have to do. When presenting my work I am frequently asked what are the next steps for functionally based investigations of tropical tree assemblages and where should this research program go. A natural and easy answer is that we need more comparative investigations to determine how generalizable research to date is really. Tropical ecology has often been dominated by research findings from a few major research sites and mostly from one region of the world, the Neotropics, and the time is now to determine how much that work is applicable to other forests. That said, just advising the field to replicate previous work, but just in different regions is not very appealing or forward-looking. I therefore suggest that we begin to explore how functional genomics may transform functionally based investigations of tropical tree communities as I described above, but below I will suggest three additional areas where I perceive a desperate lack of knowledge and an opportunity for major advances.

6.1. Plant Defense and Natural Enemies—The Big Black Box of Tropical Tree Functional Ecology. The Janzen-Connell hypothesis [99, 100] surely must be one of the all time favorite hypotheses to test for tropical tree ecologists. The hypothesis posits that natural enemies should mediate the spatial distribution of offspring in relation to parents and ultimately the coexistence of species through space and time. Despite the enormous time, money and brainpower devoted to addressing this hypothesis we have generally failed to quantify the functional relationships between plants and enemies in tropical tree assemblages and how those relationships vary between coexisting species. In the above I have reviewed a few important studies that have impressively accomplished this in *Bursera* and *Inga*, but additional examples are hard to find perhaps outside of *Piper*. Rather, tropical ecologists have resorted to functionally uninformed analyses or analyses of phylogenetic similarity to infer the relative importance of natural enemies mediating coexistence. There is, of course, a good reason for this deficiency. First, it is not trivial to develop and implement the methodologies necessary to quantify things such as the chemical composition of leaves or to pay for such analyses. For example, some methodologies may require the analysis of fresh or flash frozen plant material thereby immediately

ruling out investigations in all but the most developed field research stations. Second, in those instances where the chemical composition can be characterized, it is difficult to annotate the function to the chemical and how that function mediates plant-enemy interactions. For example, we might be able to identify a compound shared or not shared by coexisting species, but determining whether that compound influences rates and types of herbivory requires very detailed additional information and perhaps experimentation. Third, simply documenting the plant-enemy interaction network in a tropical ecosystem likely requires substantial effort and funding over decades. For example, the plant-lepidopteran inventories in Guanacaste, Costa Rica and Wanang, New Guinea have yielded an unbelievable amount of invaluable natural history information for a relatively low cost [117, 118], but collecting such information requires a substantial amount of time—the type of long-term detailed inventories our funding agencies emphasize less compared to short-term hypothesis testing studies.

Thus the challenge is clear and I would argue so are the solutions. First, tropical ecology would greatly benefit from more detailed inventories of natural enemies with the most progress likely coming from large-scale plant-lepidopteran surveys. As sequencing costs continue to drop, I expect meta-genomic environmental sampling of presumed enemies will increase where ecologists will sample soil and leaf environments to build plant-pathogen interaction networks. The difficultly with this is that many of the organisms can not be cultured at all or easily making direct linkages unobtainable and making analyses of the functional relationships between plants and enemies impossible. This issue might be mitigated by obtaining massive sample sizes and building statistical relationships between environmental samples and plant species, but this will require substantial funding and will reveal little fundamental natural history information from which future research can be built and no information regarding the functional interactions between plants and enemies.

A second step should be to conduct detailed chemical ecology investigations in those places where plant-enemy interactions networks have been well documented on a large spatial scale. Research to date has often focused on a single lineage presumably because it is difficult to inventory entire communities and the chemical diversity that surely exists between all of the lineages present. This is understandable, but it fundamentally limits the research by ignoring all interactions between non-congeneric species and the findings therefore may be difficult to scale-up to communities. Chemical ecology investigations in well-characterized plant-enemy networks presumably would also make annotating the function of the different chemicals identified much more tractable and applicable to the hypotheses of interest to a tropical tree community ecologist.

In sum, given the near obsession of tropical tree community ecologists with the Janzen-Connell hypothesis, it is shocking how little information we have regarding the functional relationship between plants and enemies outside of a few outstanding efforts on a few genera. If we are to seriously consider this hypothesis we need to become more

serious about developing methodologies or opportunities for inventorying natural enemy assemblages, obtaining the fundamental natural history information regarding plant-enemy associations and identifying the functional linkages between plants and enemies. This will require substantial time, effort and funding, but it would surely be worth it.

6.2. Analyzing the Evolution of Tropical Tree Function.

A second major future direction for tropical tree functional biology should be analyzing the evolution of tropical tree function. Tropical tree diversity is the result of an increase in net diversification through space and time and the present day spatial distribution of this diversity is governed by the functional relationship between trees and their environment. We are increasingly accumulating information regarding how tropical tree function relates to the distribution of species and communities through space and time, but we have little information regarding when, where, and why that functional diversity evolved in the first place. Community phylogenetics studies of tropical trees are now beginning to map functional traits onto community phylogenies, but the evolutionary inferences that can be drawn when the taxonomic sampling is so sparse are severely limited. An alternative is to analyze the evolution of functionally important traits within specific lineages where taxonomic sampling will be much more dense. The majority of such studies to date have focused on defense or reproductive traits, but additional studies are now being produced where those traits often quantified by community ecologists are being mapped onto phylogenies. This research allows us to begin to understand the degree to which evolutionary history dictates the present day coexistence of functionally similar or dissimilar species. A clear limitation to this approach is that requires a densely sampled and well-resolved phylogenetic tree, which is often very difficult to achieve for tropical plant lineages. In other words, molecular systematics and collaborations between systematists and functional ecologists will be foundational to the success of this approach. A second difficulty is that lineage-specific approaches are difficult to scale up to the community-level. Ultimately, the goal should be to have a tree and map of life and a complete inventory of plant function, but in the near-term these data will not be available. Therefore, it is logical to begin with the major lineages in a flora that compose a significant fraction of the species or functional diversity and to analyze the evolution of important axes of function and how those axes determine the distribution of species in the lineage through space and time.

6.3. Mapping the Spatial Distribution of Tropical Trees.

A major shortcoming in tropical botany is how poorly we know the spatial distributions of tropical plants. Mapping the distributions of tropical plants, much less collecting and identifying specimens, is obviously not an easy task and those doing this work should not be faulted for our lack of spatial information. Rather this lack of information is due to a lack of resources flowing to those dedicated to inventorying tropical biodiversity. Whether these resources are to be used for collecting today or for training the future major collectors of tomorrow, who undoubtedly will and should come from tropical countries not the United States or Europe, we simply need more time and effort dedicated to collecting the fundamental information that facilitates all ecological and evolutionary investigations in tropical botany.

Several groups are now striving to map the distributions of tropical plants using techniques such as ecological niche models, but these efforts critically rely on existing geo-referenced occurrence data and therefore will reach a ceiling of data availability and will not yield strong predictions of actual ranges. A major benefit of these efforts will be the identification of regions that are under-sampled either in reality or due to the collections from this region not being geo-referenced. For example, a compilation of global tropical plant collections should be able to quickly map whether a particular region of the neo- or paleo-tropics has been severely under-collected making for a compelling argument for funding future spatially targeted biodiversity inventories. If such inventorying does not occur in the near future our knowledge of the ecology and evolution of tropical plants will be embarrassingly limited to what we have learned from a few intensively studied sites. Simply put, if we are ignorant of the distribution or existence of tropical plant species we cannot really study tropical plant biodiversity in a meaningful and effective way.

Acknowledgments

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[118] Y. Basset, V. Novotny, S. E. Miller, G. D. Weiblen, O. Missa, and A. J. A. Stewart, "Conservation and biological monitoring of tropical forests: the role of parataxonomists," *Journa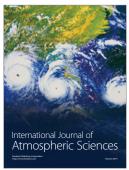l of Applied Ecology*, vol. 41, no. 1, pp. 163–174, 2004.