# CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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## A hierarchical framework for investigating epiphyte assemblages: networks, meta-communities, and scale

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Abstract. Epiphytes are an important component of many forested ecosystems, yet our understanding of epiphyte communities lags far behind that of terrestrial-based plant communities. This discrepancy is exacerbated by the lack of a theoretical context to assess patterns in epiphyte community structure. We attempt to fill this gap by developing an analytical framework to investigate epiphyte assemblages, which we then apply to a data set on epiphyte distributions in a Panamanian rain forest. On a coarse scale, interactions between epiphyte species and host tree species can be viewed as bipartite networks, similar to pollination and seed dispersal networks. On a finer scale, epiphyte communities on individual host trees can be viewed as meta-communities, or suites of local epiphyte communities connected by dispersal. Similar analytical tools are typically employed to investigate species interaction networks and meta-communities, thus providing a unified analytical framework to investigate coarse-scale (network) and fine-scale (meta-community) patterns in epiphyte distributions. Coarse-scale analysis of the Panamanian data set showed that most epiphyte species interacted with fewer host species than expected by chance. Fine-scale analyses showed that epiphyte species richness on individual trees was lower than null model expectations. Therefore, epiphyte distributions were clumped at both scales, perhaps as a result of dispersal limitations. Scale-dependent patterns in epiphyte species composition were observed. Epiphyte-host networks showed evidence of negative co-occurrence patterns, which could arise from adaptations among epiphyte species to avoid competition for host species, while most epiphyte meta-communities were distributed at random. Application of our "metanetwork" analytical framework in other locales may help to identify general patterns in the structure of epiphyte assemblages and their variation in space and time.

Key words: checkerboard distribution; co-occurrence; epiphyte; host trees; meta-community; nestedness; network; null model; Panamanian rain forest; plant assemblages; scale-dependent patterns; spatiotemporal variation.

#### Introduction

Vascular plants inhabit nearly every terrestrial environment on earth. But one of the most surprising and unappreciated places occupied by plants is the substrate provided by other plants. Upwards of 10% of all terrestrial plant species grow epiphytically on the branches of older, larger plants, typically trees (Benzing 1990). Nevertheless, the processes structuring local assemblages of epiphytes remain poorly resolved. This gap in our understanding of plant community ecology results in part from logistical difficulties associated with sampling epiphyte communities (Barker and Pinard 2001). However, another serious problem is the lack of a rigorous theoretical framework that could guide investigations of epiphyte assemblages (Kitching 2006).

To date, the majority of published epiphyte community studies are descriptive rather than analytical (Went 1940, Johansson 1974, Nieder et al. 2000), although there are increasing numbers of experimental studies addressing particular aspects of community structure and dynamics, e.g., the impact of vertical abiotic gradients on community stratification (Pittendrigh 1948, Hietz and

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Briones 1998), the effects of dispersal on community structure (Cascante-Marín et al. 2008), or the mechanisms behind change in time, e.g., succession (Ibisch 1996). The essence of their existence, the nonparasitic growth on other plants, highlights a unique feature of epiphytes: they depend on a living organism with varying physical and chemical characteristics, but also differences in architecture and phenology, which introduces its own spatial and biological dynamics. Although repeatedly mentioned in the literature, strict host specificity seems to be, at best, a rare local phenomenon (Zotz and Schultz 2008). However, a preference of epiphyte species for particular host tree taxa may be more widespread, as suggested by recent quantitative studies (Bernal et al. 2005, Laube and Zotz 2006). Thus, structurally dependent epiphyte communities may be strongly influenced by the composition of the local tree assemblage.

There is a long tradition of conceptualizing interactions between predators and their prey as food webs, or networks of interacting species (Cohen 1978, Pimm 2002). More recently, this approach has been used to investigate other types of species interactions, such as pollination and seed dispersal mutualisms (Bascompte and Jordano 2007). Network analyses can therefore be used to investigate a wide range of species interactions, including interactions between epiphyte species and their associated host tree species. Interaction networks are typically quantified as binary interaction matrices (i.e., qualitative data), in which rows represent one partner in the interaction (e.g., pollinators) and columns represent the other partner (e.g., flowering plants). Each cell in the resulting matrix is then filled with a "1" if the corresponding species pair interacts, or a "0" if a species pair does not interact. If a pair of species interacts, the species pair is said to form a "link." Species that form fewer links than expected by chance are known as specialists, whereas species that form more links than expected are generalists (see Proulx et al. 2005). Species interaction networks can also be characterized quantitatively by incorporating information on the frequency of interactions between individuals of each species pair (see Berlow et al. 2004). However, analytical tools to characterize quantitative matrices have yet to be established definitively. Thus we used binary matrices, which are the most straightforward way to characterize networks and meta-communities.

Species pairs with the same number of links do not necessarily interact with the same species, and binary interaction matrices can exhibit several distinct patterns in compositional structure (Lewinsohn et al. 2006). For example, networks can be "nested." Nestedness occurs when specialist species interact with proper subsets of the species that interact with generalists (Darlington 1957, Bascompte et al. 2003). Many types of species interactions are nested (but see Blüthgen et al. 2008), including plant–pollinator (Phillip et al. 2006), fruit–frugivore (Lázaro et al. 2005), ant–plant (Guimarães et al. 2006), clownfish–anemone (Ollerton et al. 2007), and

marine fish cleaning symbioses (Guimarães et al. 2007). Interaction networks can also be "checkerboarded." In this case, species replace one another in their interactions with the other player in the interaction (Diamond 1975, Gotelli and Graves 1993). Finally, compositional patterns in species interactions can also be consistent with randomized expectations generated by null models, and are then referred to as "neutral" (cf. Hubbell 2001).

Interactions between epiphytes and their host trees can accurately be viewed as networks, and network analyses can be used to determine coarse-scale patterns in the structure of epiphyte assemblages (Burns 2007). However, network analyses can mask important interactions occurring on finer scales. Individual host trees form discrete patches of habitat that can be colonized by epiphytes belonging to many different species. Individual host trees can therefore contain diverse communities of epiphytes that may, or may not, be similar to those found on other trees belonging to the same host species (Laube and Zotz 2006). Therefore, each host species supports an epiphyte "meta-community," or a suite of local epiphyte communities on separate trees that are linked together by seed dispersal (Leibold et al. 2004). In quantitative terms, each row in the epiphyte-host interaction network is an amalgamation of multiple trees belonging to the same host species, each of which houses its own assemblage of epiphytes. Therefore, epiphyte-host networks are a composite of many epiphyte meta-communities, and can mask complex patterns in epiphyte species richness and composition. Each host species forms its own binary matrix, in which epiphyte species are listed as columns and trees are now rows. The same analyses used to investigate interaction networks are typically employed to assess patterns in meta-community structure (Leibold and Mikkelson 2002, Almeida-Neto et al. 2007). Therefore, epiphyte meta-communities and host-epiphyte networks may show similar structural patterns (nested, checkerboarded, or neutral). On the other hand, they may show distinct structural patterns if different processes operate on coarse (network) and fine (meta-community) scales.

We introduce a new, hierarchical approach to investigate epiphyte assemblages (Fig. 1). On a coarse scale, epiphyte–host species interactions can be evaluated as bipartite networks. On a finer scale, similar analyses can be used to evaluate structural patterns in epiphyte meta-communities on individual host trees of a given species, each of which are embedded within each row of the bipartite matrix (i.e., host species). We apply this "meta-network" framework to investigate the distribution of epiphytes in a Panamanian rain forest and demonstrate how different structural patterns in epiphyte assemblages can occur on coarse (network) and fine (meta-community) scales.

#### METHODS

Study site, species, and sampling

Field data used in this study were collected at the San Lorenzo Canopy Crane site near the Atlantic coast of

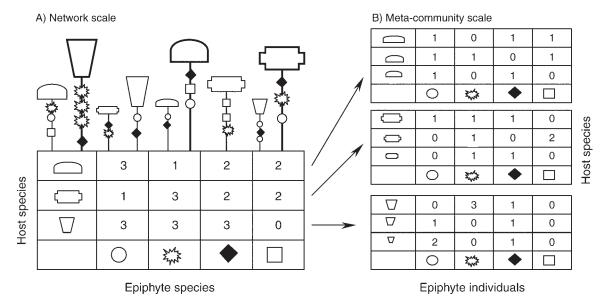


Fig. 1. Schematic illustrating the meta-network analytical framework. (A) An epiphyte-host species interaction network, with an illustration of a hypothetical forest composed of three host species, each of which is represented by three trees that are inhabited by four epiphyte species. Below the forest diagram is the corresponding interaction matrix whose entries are the interaction frequencies of each species pair. (B) The three host-specific epiphyte meta-communities, which are amalgamated into single rows in the epiphyte-host interaction network.

the Republic of Panama. For a detailed description of this lowland forest see Wright et al. (2003), and for its epiphyte community see Zotz and Schultz (2008). Briefly, each of 1373 trees (dbh  $\geq$  1cm) in a roughly square area of  $\sim$ 0.4 ha was inspected for the occurrence of vascular epiphytes by use of a canopy crane. This census yielded more than 13 000 individuals out of 103 epiphyte species. A majority of both the tree and epiphyte species were rare, but eight tree species were represented in the plot by at least 10 individuals each. We restricted our analyses to these common tree species to facilitate analyses both within species (i.e., among trees) and among species (see Table 1).

Network degree and meta-community richness null models

We conducted a simple simulation, following Burns (2007) to test for nonrandom column totals in epiphyte—host species interactions and epiphyte meta-communities. Coarse-scale analyses of epiphyte—host species interactions tested for patterns in the number of links maintained by each species. A "link" was noted when at least one individual of an epiphyte species was found growing on at least one individual of a host tree species. Fine-scale analyses of epiphyte meta-communities tested for patterns in the species richness of epiphytes on individual host trees. The simulation procedure used at each scale was identical.

Table 1. Results from meta-network analyses of epiphyte distributions in a Panamanian rain forest.

	Sampling			No. links		T			
Species	No. trees	No. epiphytes	Matrix fill		Expected	Observed	Expected Expected	Observed	Expected
Brosimum utile Geonoma congesta Lozania pittieri Marila laxiflora Perebea xanthochyma Protium panamense Socratea exorrhiza Unonopsis panamensis	11 11 13 40 38 10 31	2396 23 73 496 227 63 354 77	0.22 0.15 0.11 0.08 0.07 0.15 0.11 0.16	51 8 26 49 32 24 39 12	72.2 ± 1.9*** 14.1 ± 1.9*** 26.9 ± 2.7 53.2 ± 2.7 42.4 ± 2.8*** 24.9 ± 2.6 48.5 ± 2.8** 27.6 ± 2.6***	12.2 52.9 23.2 8.6 11.8 33.1 11.5 20.9	$\begin{array}{c} 9.4 \pm 1.6 \\ 40.9 \pm 8.9 \\ 20.4 \pm 3.9 \\ 9.4 \pm 0.9 \\ 10.9 \pm 1.5 \\ 27.6 \pm 4.1 \\ 13.6 \pm 1.6 \\ 20.7 \pm 3.9 \end{array}$	25.0 1.2 5.2 8.4 3.4 19 9.4 17	$25.8 \pm 0.8$ $1.2 \pm 0.04$ $5.1 \pm 0.2$ $8.4 \pm 0.2$ $3.1 \pm 0.1**$ $19.9 \pm 1.1$ $9.1 \pm 0.2*$ $16.6 \pm 1.3$

Notes: The numbers of trees and epiphytes sampled, in addition to matrix fill (proportion of occupied cells in the binary, meta-community matrix) are given in the columns under the "Sampling" heading. The last six columns show observed and expected (mean  $\pm$  SD) values for number of links maintained by each host species, temperatures from null model tests for nestedness in host species-specific meta-communities, and c scores from null model tests for negative co-occurrence patterns in host species-specific meta-communities.

<sup>\*</sup> P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001.

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The simulation randomly placed all individual epiphytes that were encountered during sampling onto individual host trees. All epiphytes were assumed to be functionally equivalent and therefore had identical life history characteristics, including dispersal potential and competitive ability. The total number of epiphytes placed on each tree during each simulation replicate was always held constant to that observed. Therefore, the total abundance of each epiphyte species, the total abundance of epiphytes on each host tree, and the total abundance of epiphytes on each host species were fixed. This randomization procedure was replicated 1000 times in R (R Development Core Team 2007) for both the epiphyte-host species network and the epiphyte metacommunity maintained by each host species. On a coarse scale, the average number of links formed by each host tree species across all simulation replicates was taken as the expected network degree. On a finer scale, this procedure was repeated to obtain the expected number of epiphyte species present in the epiphyte community on each host tree.

Our matrix fill methods did not explicitly consider how the aggregation of conspecifics on a given host tree might influence network and meta-community structure. However, our null model test for nonrandom network degree and meta-community richness addresses this problem indirectly, because it randomly populates host species and individual trees within host species from the total pool of individuals found on each species and tree, respectively. Consequently, if the null model generated expected values that were larger than observed, it would indicate that individuals are over-dispersed among hosts. Alternatively, expected values that were smaller than observed would indicate that individuals were under-dispersed among hosts, or, in other words, with epiphyte individuals showing a clumped distribution, either among host species or host trees within host species. A different approach, which may be adopted by future work, would be to include individual aggregations into null model simulations, and to compare these null model results to empirical results (see Gotelli and McGill 2006).

Differences between the observed and expected number of links maintained by each tree species in the epiphyte-host species network were evaluated by obtaining a z score and corresponding two-tailed P value from the normal distribution of expected values generated in the simulation. Differences between observed and expected numbers of epiphytes present on individual trees with host-specific meta-communities were assessed using the general linear model procedure in SPSS (2002). The observed number of species was used as the dependent variable, the average expected value was included in the model as a covariate, and the host species was treated as a fixed factor. Differences in the slope and intercept of relationships for each host species were assessed following Engqvist (2005). If relationships between observed and expected epiphyte

species richness were found to be similar among host species, the data were pooled and subjected to ordinary least squares regression. The 95% confidence limits for the slope and y-intercept estimates of this relationship were obtained to evaluate whether expected values consistently predicted observed values. A one-to-one relationship between observed and expected values of network degree and epiphyte species richness would be consistent with the hypothesis that epiphytes are randomly distributed among host trees.

#### Compositional null models

Two types of null models were used to test for nonrandom compositional patterns in network and meta-community structure. First, we used Ulrich's Nestedness software to test for nestedness (Ulrich 2006). The nestedness temperature calculator (NTC) is the most commonly used test for nestedness (Atmar and Patterson 1993). It characterizes nestedness with a metric called matrix temperature, which is calculated by first reorganizing the matrix in order of increasing row and column sums. When the matrix is "maximally packed" after reorganization, a curve (isocline) is fit through the matrix in a way that best separates occupied cells from unoccupied cells. Deviations from this curve are used to calculate matrix temperature. To evaluate whether the observed temperature differs from randomized expectations, the positions of entries in the matrix are randomly shuffled in a computer simulation. Differences between observed and expected temperature values are used to establish whether the observed matrix is structured nonrandomly.

Unfortunately, NTC suffers from several well-described problems. These problems are associated not only with how temperature is calculated (Rodríguez-Gironés and Santamaría 2006), but also with the null model that it employs (Ulrich and Gotelli 2007). Therefore, we did not use NTC. Instead we used Nestedness software, which uses a modified procedure to calculate temperature, in addition to a modified null model, which corrects for some of these problems and results in a more conservative test for nestedness relative to NTC (Ulrich 2006). The epiphyte-host interaction network and the epiphyte meta-community comprising each host species were evaluated using default settings (100 simulation replicates, maximum distance to borderline = 0.5, matrix packing according to richness) using fixed row and column totals and the sequential swap method of matrix fill. Therefore, row and column totals never differed from those observed in all simulation replicates. Two-tailed Type I error rates were calculated based on the z value obtained in the output.

Second, we used Ulrich's *co-occurrence* software (Ulrich 2006) to test for checkerboard, or negative co-occurrence patterns. This analysis uses the c score index, which is obtained by calculating the number of checkerboard units (cu) for each species pair: cu =  $(O_i - S)(O_i - S)$ , where  $O_i$  is the total number of host

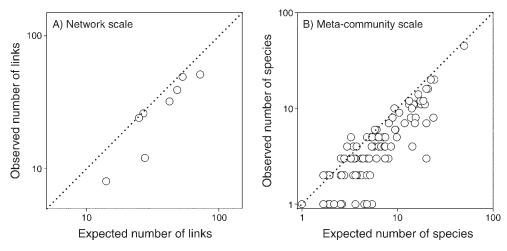


Fig. 2. Relationships between observed and expected patterns in (A) the number of links (i.e., epiphyte species interactions) maintained by each host species (network scale) and (B) the number of species inhabiting individual host trees (meta-community scale). Expected values were generated in a null model analysis that randomly populated hosts with individual epiphytes.

species occupied by each epiphyte species i,  $O_j$  is the total number of host species occupied by epiphyte species j, and S is the number of host species occupied by both species (Stone and Roberts 1990). Similar to null model tests for nestedness, the observed c score is compared to expected c score values generated by randomizing the positions of entries in the matrix in a computer simulation. The epiphyte—host interaction network and the epiphyte meta-community composed of each host species were evaluated using default settings (100 simulation replicates, fixed row and column totals, and sequential swap method of matrix fill). A c score higher than null model expectations would indicate support for checkerboard compositional patterns.

#### Effects of rare species

Rare species interactions can play an important role in determining patterns in network structure (Blüthgen et al. 2008). Therefore, the observed patterns might change if species interactions were redefined to include only those species pairs that interact frequently. To assess whether results hinge on the inclusion of rare species, we repeated all of our analyses after restricting our attention to species pairs that interacted at least three times. More specifically, compositional null models (i.e., tests for nestedness and negative co-occurrence patterns) were repeated after removing all (nonzero) cell values that were less than three. Therefore, cell values that were less than three were replaced by zeros before converting quantitative matrices to binary matrices prior to analyses. Network degree null models were repeated after redefining epiphyte-host species interactions as those that were represented by three or more individual interactions. Similarly, metacommunity richness null model analyses were repeated after redefining epiphyte species richness as the sum of all epiphyte species that were represented by three or more individuals on host trees. After removing rare species interactions, the size of meta-communities in four host species (*Geonoma congesta*, *Unonopsis panamensis*, *Lozania pittieri*, *Protium panamense*) became too small for accurate analyses (i.e., their matrices had less than five rows and five columns). These species were therefore removed. The size of the epiphyte–host network (i.e., coarse-scale analyses) remained unchanged.

#### RESULTS

Network degree and meta-community richness null models

Our data set encompassed 3709 individual epiphytes belonging to 77 species that were growing on 173 host trees belonging to eight species. These tree species were colonized by a minimum of 8 (Geonoma congesta) and a maximum of 51 epiphyte species (Brosimum utile). In most cases there were fewer links between host tree and epiphyte species than expected by chance (Brosimum utile, Geonoma congesta, Perebea xanthochyma, Socratea exorrhiza, Unonopsis panamensis), whereas the number of links maintained by the remaining species (Lozania pittieri, Marila laxiflora, Protium panamense) did not differ from randomized expectations (Table 1, Fig. 2). Similar results were obtained in analyses of species richness within host meta-communities. The number of epiphyte species on each host tree was positively related to expected richness values generated by the null model  $(F_{1,157} = 291.9, P < 0.001)$ . The covariate and fixed factor did not interact ( $F_{7,157} = 0.87$ , P = 0.53), indicating that the slopes of relationships for each species did not differ. The independent effect of the fixed factor was not significant either ( $F_{7,164} = 1.05$ , P = 0.40), indicating that the y-intercept of relationships for each species did not differ. Therefore, all host tree species showed similar relationships between observed and expected species richness values (Fig. 2). Combined analyses of species richness patterns among meta-communities showed that observed species richness within host trees was linearly

related to expected species richness values ( $r^2 = 0.83$ , P < 0.001). This relationship had a y-intercept that did not differ from zero (mean = -0.074, 95% CI = -0.074– 0.007) and a slope that was less than one (mean = 0.81, 95% CI = 0.76–0.87). Therefore, epiphyte species richness within host meta-communities was lower than expected by chance and differences between observed and expected richness values increased with the total number of epiphyte species present.

#### Compositional null models

Coarse-scale analyses of the network of host–epiphyte species interactions showed no evidence for nestedness. The observed temperature (T = 14.3) was statistically indistinguishable from expected temperature values generated in null model analyses ( $T = 15.8 \pm 1.1$ , mean  $\pm$  SD; Z = -1.42, P = 0.16). However, negative cooccurrence patterns were indicated by the observed c score (c = 124.7), which was higher than most simulation replicates of the null model ( $c = 116.6 \pm 1.6$ , mean  $\pm$ SD; Z = 5.19, P < 0.001). Different results were obtained in fine-scale analyses of host meta-communities. No evidence for nestedness was found in any of the eight host tree meta-communities (see Table 1). Two host tree meta-communities (Perebea xanthochyma, Socratea exorrhiza) had higher c scores than expected, indicating support for negative co-occurrence patterns, whereas the six remaining host tree meta-communities showed no such patterns.

### Effects of rare species

The exclusion of rare species in additional analyses changed the previous results only slightly. All eight host tree species still housed fewer epiphyte species than expected by chance in coarse-scale analyses of network degree (P < 0.021 for all). Consistent results were also obtained in analyses of species richness within host meta-communities. The number of epiphyte species on each host tree was positively related to expected richness values generated by the null model ( $F_{1.62} = 155.28$ , P <0.001). The covariate and fixed factor did not interact  $(F_{3,62} = 0.55, P = 0.65)$ , indicating that the slopes of relationships for each species did not differ. The independent effect of the fixed factor was not significant either ( $F_{3.62} = 0.89$ , P = 0.45), indicating that the yintercept of relationships for each species did not differ. Combined analyses showed that observed species richness within host trees was linearly related to expected species richness values ( $r^2 = 0.72$ , P < 0.001). This relationship had a negative *y*-intercept (mean = -0.828, 95% CI = -1.092 to -0.563) and a slope below unity (mean = 0.850, 95% C.I. = 0.724-0.977), indicating that epiphyte species richness within host meta-communities was consistently lower than expected by chance.

Compositional null models also showed broadly similar results after excluding rare species. The observed temperature of the epiphyte–host network (T=14.40) was statistically indistinguishable from expected tem-

perature values generated in null model analyses ( $T=16.56\pm1.73$ , mean  $\pm$  SD; Z=-1.24, P=0.108), indicating no support for nestedness. However, the observed c score (c=61.11) was higher than most simulation replicates of the null model ( $c=57.81\pm1.24$ ; Z=2.661, P=0.003), indicating support for negative co-occurrence patterns. Fine-scale, compositional analyses of host tree meta-communities provided support for nestedness and negative co-occurrence patterns in one species. Perebea xanthochyma had a temperature value (T=14.14) that was lower than expected ( $T=22.42\pm4.25$ ; T=1.948, T=1.948, T=1.948, T=1.948, and an observed T=1.948, and an observed T=1.948, T=1.948, and an observed T=1.948, T=1.948, T=1.948, T=1.948, T=1.948, and an observed T=1.948, an

#### DISCUSSION

We developed a hierarchical analytical framework to investigate epiphyte assemblages. On a coarse scale, epiphyte assemblages can be viewed as species interaction networks. On a finer scale, epiphyte assemblages are represented as host-specific meta-communities. This "meta-network" approach allowed us to resolve several structural patterns in epiphyte assemblages in a Panamanian rain forest. Host tree species typically formed fewer links with epiphyte species than expected by chance. Similarly, epiphyte species richness on individual host trees was generally lower than randomized expectations. Therefore, similar relationships between epiphyte abundances and species occurrences were observed at both the network and meta-community scales. On the other hand, scale-dependent compositional patterns were observed as well: the epiphyte-host network was significantly checkerboarded, indicating that epiphyte species tend to form exclusive distributions among host tree species, whereas the composition of epiphyte metacommunities within host species was generally consistent with randomized expectations. These results remained largely the same after rare epiphyte species were removed. This suggests that similar processes may regulate the number of epiphyte species interacting within hosts, whereas the processes shaping compositional patterns are scale dependent.

At both the network and meta-community scales, fewer epiphyte species were found associated with hosts than expected from their abundances. In other words, the distribution of epiphyte species among host trees and host species was "clumped." One explanation for clumped epiphyte distributions at the meta-community scale is that epiphytes may disperse more seeds within the host tree than among host trees. Limitations to dispersal could lead to high abundances of a relatively small number of species on individual hosts. Dispersal limitation seems to be common in tropical tree communities (i.e., trees rooted terrestrially; Hubbell et al. 1998; see also Etienne et al. 2006, Vázquez et al. 2007, Krishna et al. 2008). Several studies on the population genetics of orchids (e.g., Trapnell and Hamrick 2004,

Chung et al. 2007), in addition to both descriptive and experimental work at the community level (e.g., Zotz et al. 1999, Cascante-Marin et al. 2008), suggest that dispersal limitation may also be common in epiphytes. Future work should explore this possibility further by incorporating dispersal limitations into simulations.

Analyses of compositional patterns in the epiphytehost network indicate that species interactions were checkerboarded. This evidence for negative co-occurrence patterns at the network scale suggests not only that epiphyte species have preferences for particular host species, but also that these host preferences differ nonrandomly among epiphyte species. Epiphyte species tended to interact preferentially with different host species. For example, almost 40% of all Guzmania subcorymbosa plants occurred on the few individuals of Socratea exorrhiza. Similarly, almost 70% of all individuals of another bromeliad (Tillandsia bulbosa) were found on Brosimum utile (Zotz and Schultz 2008). Negative co-occurrence patterns are widespread in nature (Gotelli and McCabe 2002) and are commonly attributed to interspecific competition, although neutral processes may also generate negative co-occurrence patterns that are consistent with the predictions of competition theory (Ulrich 2004). Because hard evidence for or against competition is lacking, it remains unclear whether competition or other processes are responsible for the observed patterns in these epiphyte meta-communities. However, in lowland rain forests vascular epiphytes typically use only a small proportion of the available bark surface, which argues against the importance of competition (Nieder et al. 2000, Zotz and Vollrath 2003; G. Zotz, unpublished observation).

On the finer scale, compositional patterns in epiphyte distributions within host tree meta-communities were generally consistent with randomized expectations. Although the epiphyte meta-communities within two host species were "checkerboarded," most meta-communities were "neutral." Slightly different results were obtained when rare species were removed. In this case, one species was both "checkerboarded" and "nested," while the rest were "neutral." Evidence for checkerboard compositional patterns at the network scale, but weaker support at the meta-community scale has important implications for the processes shaping epiphyte assemblages. Weak support for negative co-occurrence patterns among trees within host species again suggests that epiphytes do not compete in situ for the use of individual host trees, whereas strong support for negative co-occurrence patterns in the epiphyte-host species network suggests that epiphyte species are differentially adapted to exploit different host tree species. This interpretation is consistent with the low proportion of bark surface utilized by epiphytes in lowland forests and the substantial differences in ecophysiological traits of epiphyte species (Zotz and Hietz 2001). Abiotic conditions in tree crowns of moist tropical lowland forests are severe and host tree characteristics most likely play a major role in successful establishment and survival. We suggest that the interaction of epiphyte ecophysiology and host traits (architectural traits, e.g., branch angles and diameters, chemical and morphological bark characteristics, phenological patterns, moisture availability) explains the observed differences in network and meta-community structure. This interpretation also implies that competition should be more important in montane forests, where epiphytes are typically much more abundant (Benzing 1990).

Little evidence for nestedness was observed, both at the network scale and at the meta-community scale. Therefore, the distribution of epiphytes in this Panamanian rain forest appears to be quite different than the distributional patterns resolved in the only other study evaluating the network properties of epiphyte–host interaction networks. Burns (2007) analyzed an epiphyte–host interaction network in a temperate rain forest located in New Zealand and found one of the highest levels of nestedness in any type of species interaction observed to date. Therefore, the structural processes shaping epiphyte distributions in the relatively species-poor system in New Zealand appear to be quite different from those occurring in a much more diverse Panamanian rain forest.

In the only previous study on epiphytes using a metacommunity perspective, Burns (2008) assessed the distribution of epiphytes among host trees belonging to a single host species in British Columbia, Canada. Unlike the epiphytes in New Zealand and Panama, this assemblage was composed mostly of facultative epiphytes, i.e., species with most individuals growing terrestrially. Meta-community structure in these facultative epiphytes was neither nested nor checkerboarded. Rather, their distributions were compartmentalized, indicating that groups of epiphyte species tended to occur jointly on host trees, leading to sharp compositional turnover among host trees. Therefore, there appears to be greater similarity between host-specific epiphyte meta-communities in British Columbia and Panama. However, tests for compartmentalization were not made in this study and future studies would benefit from searching for this type of structural pattern elsewhere.

Epiphyte assemblages can form very different types of meta-communities, depending on their dependency on an arboreal lifestyle. Most species of epiphytes are restricted to tree canopies and are referred to as obligate epiphytes (Benzing 1990). Meta-communities composed of obligate epiphytes, such as the Panamanian epiphytes analyzed here, form "classical" or "Levins-type" metacommunities. Classical meta-communities lack a "mainland" setting and are instead composed of relatively similar-sized communities connected by dispersal. However, other epiphyte assemblages, particularly in temperate zones, are composed of species that commonly occur on the forest floor and only grow as epiphytes facultatively. Meta-communities composed of facultative epiphytes do not form "classical" meta-communities. Instead they form "mainland-island" metacommunities, in which the terrestrial environment forms the "mainland" and the tops of host trees form "islands" (Burns 2008). Future comparisons of meta-community structure between different geographic localities may help to determine spatial variation in the type of meta-communities formed by epiphytes.

In this paper, we outline an analytical framework to evaluate the structure of epiphyte assemblages. It uses the same set of analytical and conceptual tools to assess epiphyte distributions on multiple scales. Similar to any other general model in ecology, our network approach captures just a few important elements of epiphyte communities, while ignoring others. For example, our approach is neither spatially explicit (compare, e.g., Zotz and Schultz 2008) nor does it incorporate host tree size, which is a proxy for both structural complexity and available time for establishment (Flores-Palacios and García-Franco 2006, Laube and Zotz 2006). Our analyses are also restricted to common host species, so the effects of rare host species on meta-community and network structure remain unknown. However, our approach goes beyond most studies on epiphyte communities, which vary strongly in methodology and are largely qualitative. Hence, quantitative comparisons between studies are rarely possible beyond the level of species numbers or taxonomic participation (but see Cardelús et al. 2006, Laube and Zotz 2006).

Although we developed this framework explicitly for vascular epiphytes, research on other ecological communities with structurally dependent partners could similarly benefit from this approach. For example, the meta-network approach might usefully be applied to algal epiphyte communities on aquatic plants or macroalgae (Chung and Lee 2008), bacterial communities on plant leaves (Hempel et al. 2008), assemblages of epiphyllous or epiphytic lichens, mosses and liverworts (Zartman 2003, Löbel et al. 2006), or assemblages of arthropods in phytotelmata (Stuntz et al. 2002, Jabiol et al. 2009). By demonstrating the utility of analyzing both species-level and individual-level interactions concurrently, we hope that our meta-network approach will stimulate new approaches to complex species interactions, such as flower-pollinator, fruit-frugivore, or antplant mutualisms. However, most importantly we believe that our meta-network approach can help to answer a variety of questions that will bridge key gaps in our understanding of epiphyte community ecology. For example, how often are the patterns resolved at the meta-community scale different from the network scale? Is it appropriate to treat epiphyte networks as being spatially homogeneous (as most studies in food webs), or do the patterns resolved within this 0.4 ha vary sharply through space? Does the structure of epiphyte assemblages change consistently with latitude? Without a unifying analytical framework, answers to these questions will continue to elude us and our understanding of epiphyte assemblages will continue to lag behind that of terrestrial-based plants.

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