CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

PHYLOGENY, NICHES, AND RELATIVE ABUNDANCE IN NATURAL COMMUNITIES

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Abstract. Community structure refers to the number of species in a community and the pattern of distribution of individuals among those species. We use a novel way of representing community structure to show that abundance within closely related pairs of co-occurring tree species in a highly diverse Mexican forest is more equitable than is abundance within more distantly related pairs. This observation is at odds with the fundamental assumption of neutral models of community structure, i.e., that species are interchangeable. The observed patterns suggest niche apportionment, in which interaction is focused pairwise between congeners but falls away from the phylogenetic structure above the genus level. Thus niche processes may significantly affect community structure through regulating relative abundance in a substantial proportion of species, which in turn potentially enhances community stability. One such mechanism of stable coexistence has already been shown to be active in this forest.

Key words: Chamela Biological Station, Jalisco, Mexico; community structure; differential sensitivity; fractional abundance; hierarchical niches; neutral theories; stable coexistence; storage dynamics; temporal niches.

INTRODUCTION

The two main approaches to the rules dictating organization in natural communities start at opposite ends of a spectrum: one, resource partitioning theory, posits an underlying structure of niches in which particular species excel at exploiting particular resources (MacArthur 1957, Preston 1962*a, b*, Armstrong and McGehee 1980, Sugihara 1980, Nee et al. 1991, Sugihara et al. 2003); the other rests upon the absence of any such structure, with species assumed to be interchangeable (MacArthur and Levins 1967, Bell 2000, Hubbell 2001, Volkov et al. 2003, 2005). In a niche-structured dynamic, abundance of any one species is directly affected primarily by the abundance of only one to several highly similar species. Species are not interchangeable and competition affects community composition through regulating population size and persistence of the species within a focused competitive interaction. In contrast, where species are assumed to be interchangeable, competition is by definition diffuse; species loss and change in population size is by chance alone, and the loss of a species is absorbed generally by the overall community.

That niches exist is hardly an issue (Engelbrecht et al. 2007). The larger question is to what extent they can or cannot be ignored in explaining community structure. If niches are highly relevant to community structure, they also must be of importance in determining the impact of immigration, extinction, and speciation rates and in turn the capacity of these processes to influence community composition, stability, and diversity. Both niche approaches (for example, the sequentially broken stick of Sugihara [Sugihara 1980, Nee et al. 1991, Sugihara et al. 2003] and the neutral models following Hubbell (Hubbell 2001, Volkov et al. 2003, 2005) have the ability to explain the ubiquitous (approximate) lognormal species abundance curve characterizing community structure. Both do this quite well, demonstrating that the distribution is not particularly informative of underlying processes.

Population-level studies have yielded evidence that stable competitive interactions can regulate relative abundance between closely related species in tropical deciduous forest through temporal niche processes (Kelly et al. 2001, Kelly and Bowler 2002, 2005; see also Chesson 2000). In the first-growth, undisturbed forest of Chamela Biological Station, Jalisco, Mexico, populations of highly similar, closely related tree species coexist interdigitated with one another (see Plate 1). The

model developed from these observations and additional ecological data describe a stable competitive dynamic between pairs of taxa, one of which is more sensitive to environmental fluctuations than the other and is also the better competitor. The more sensitive species is able to recruit when conditions are "good" and then able to outcompete its less sensitive competitor. The less sensitive species successfully recruits when the more sensitive is out of the picture. The observed relative abundances between investigated pairs of tree taxa are better explained by focused, pairwise competition rather than by the assumption that competition is primarily diffuse (Kelly and Bowler 2005).

Here we investigate whether focused, pairwise interactions of the kind envisaged by Sugihara and indicated by our earlier work are prevalent and forceful enough to be of significance at the level of the community. In the Sugihara model each bifurcation of an ecological niche dendrogram has a probability distribution for resource allocation, taken to be reflected in the relative numbers of the two species. This splitting function is the distribution of the fractional abundance in a pair, r, defined as $r = n_c/(n_c + n_r)$ where n_c is the number of individuals of the more common member of the pair and n_r of the less common. This splitting function may contain the signature of focused competition when the pairs are chosen from ecological bifurcations. In contrast, if all species are equivalent and there is no niche structure or focused competition, then composing pairs according to any meaningful biological algorithm should yield a distribution of fractional abundance indistinguishable from that of pairs chosen at random from the community.

We paired species from the natural community at Chamela Biological Station according to evolutionary similarity and thus likely to possess similar niche requirements (Harvey and Pagel 1991) and obtained a novel and robust signal of population regulation through focused interactions within pairs. Pairs were identified through membership in terminal dichotomies in the phylogenetic structure of the community and naturally fell into two groups: (1) pairs in which both species are members of the same genus (congeneric pairs) and (2) pairs in which species do not have congeners within the data set but whose nearest relatives are members of the same family (non-congeneric pairs). We found the distribution of abundances in congeneric pairs to be very different from that of non-congeneric pairs and from pairs selected at random from the community. These observations are not consistent with the strict assumption that species within a community are effectively equivalent and promise to be highly relevant to understanding the processes governing structure in natural communities.

METHODS

The data set from the tropical deciduous forest of Chamela Biological Station provided an assessment of

PLATE 1. The tropical deciduous forest of the Estación de Biología de Chamela, Mexico. (Top) To determine growth rates in the tropical deciduous forest, woody individuals have to be measured at the end of the dry season, their point of greatest dehydration. Even during years of "normal" rainfall, natural variation in water uptake in the wet season can account for significantly greater increase in girth from one year to the next than can growth. (Bottom) Panoramic view of the forest of Chamela; the dark objects are canopy-level cacti. Photo credits: top, Meg Warren; bottom, C. K. Kelly.

frequency for a total of 193 co-occurring woody species. Abundances were determined over 14 Long-Term Ecological Research (LTER) plots for which were recorded a total of 11 868 woody individuals (Kelly et al. 2001). Competition in plants ultimately rests upon successful colonization of space, and we know for the Chamela data set whether surveyed individuals could be assumed to be established (canopy-level individuals together with observed minimum reproductive size for subcanopy individuals). The forest of Chamela Biological Station is a dry forest with the canopy quite short on the canyon sides and ridgetops where the survey took place; the general understory is of shrubs rather than species that qualify as permanent subcanopy trees.

The molecular phylogeny of angiosperms found in Soltis et al. (2000) provided a phylogenetic structure of
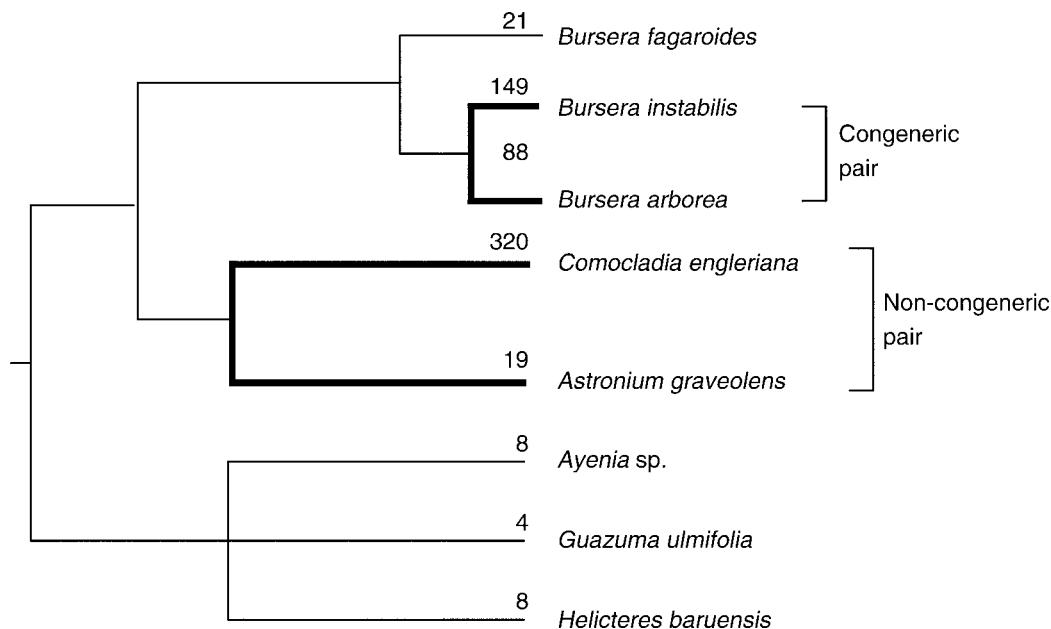
FIG. 1. Selecting species pairs. Comparison of resolved tip nodes pairs *Bursera instabilis* with *B. arborea* (congeners) and *Comocladia engleriana* with *Astronium graveolens* (non-congeners), with $r = 0.63$ for the former and 0.94 for the latter. *Bursera fagaroides*, not being a part of a terminal dichotomy, would not be used in the analysis. The species in the unresolved clade at the bottom of the figure would similarly all be excluded. Numbers above bars are numbers of individuals of each species. The Chamela phylogeny is 95% resolved, with 92 species occurring in resolved terminal dichotomies, approximately half of the species list.

the Chamela community to the family level, although in the end this proved irrelevant to our analyses: all terminal dichotomies, the criterion by which we paired species, occurred below the level of family. Where there were more than two species per family, the relatedness structure below the level of family was drawn from published material, with order of precedence given to molecular phylogenies (cladistic treatments) of more over fewer genes, molecular over morphological phylogenies, and phylogenetic over taxonomic treatments. A list of the authorities used is in Appendix A, together with the full phylogeny for the Chamela tree community.

Species pairs used in the analyses presented here were those forming resolved dichotomies at the tips of the phylogenetic tree for the data set, so that within pairs the two species were more closely related to one another than either were to any other species in the community; our selection algorithm is illustrated in Fig. 1. There were 26 congeneric and 20 non-congeneric species pairs. The remaining 101 species were either singletons or unresolved within a group of three or more. Abundances for the 92 species paired by our algorithm varied between 1 and 736, including the first and second most abundant species in the data set.

The distribution of fractional abundances (Sugihara et al. 2003) for the 26 congeneric pairs was compared with that for the 20 non-congeneric pairs (confamilials) with the two-sample Kolmogorov-Smirnov (K-S) test. The distributions of congeneric and non-congeneric fractional abundances were each compared with a distribution constructed by repeated sampling for 20 pairs randomly selected from the full Chamela tree community of 193 species, normalized for the sample size of the relevant group, using the one-sample two-stage δ-corrected Kolmogorov-Smirnov test (Khamis 2000).

RESULTS

The distributions of fractional abundances are shown in Fig. 2. Fig. 2a displays the distribution of fractional abundance for the 26 congeneric pairs, contrasted with that for random selection from the full community roster of 193 species. Fig. 2b shows the 20 non-congeneric pairs and the random selection. The smooth red curves are analytically calculated for random selection from a lognormal species abundance distribution of standard deviation 2.5. Such a distribution represents well the full Chamela data set and also those 52 species comprising the congeneric pairs (see Fig. 4) as well as the 40 species within the non-congeneric pairs. The smooth red curves are not used for statistical comparison but to illustrate how well Chamela conforms to the general expectation of a lognormal species abundance distribution, discussed further below (see Fig. 4).

We have tested two principal hypotheses: (1) That the abundance distributions for the congeneric and the non-congeneric pairs are drawn from the same underlying distribution; and (2) that the abundance distribution for
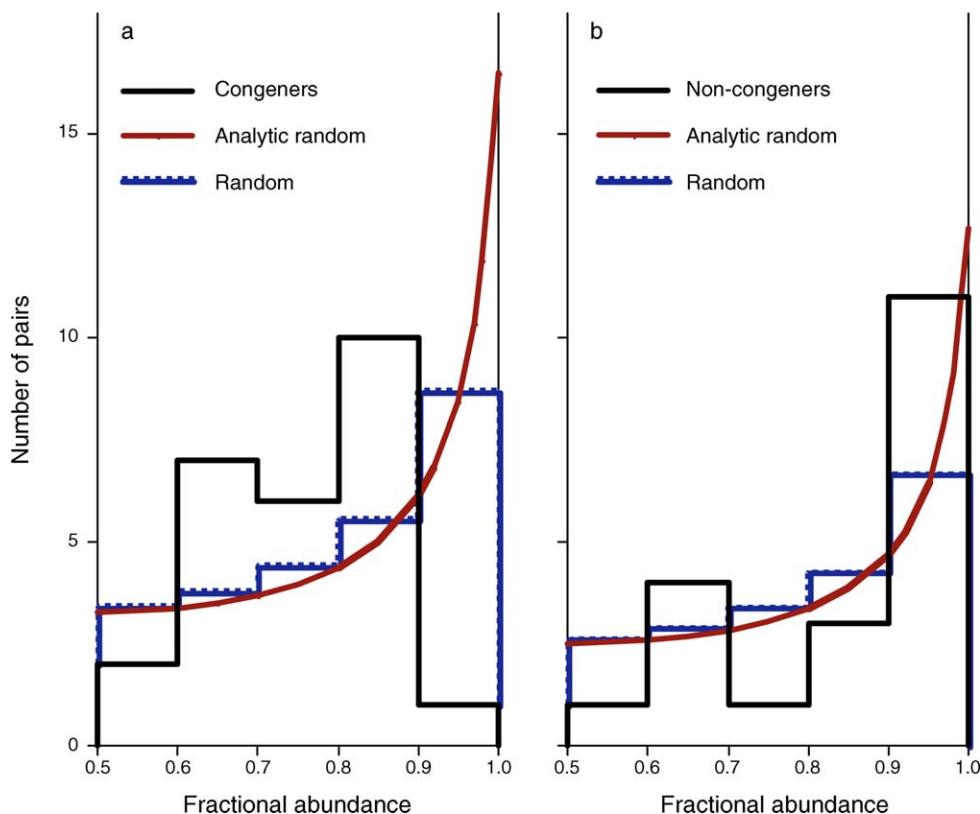
FIG. 2. Fractional abundance profiles for (a) congeneric and (b) non-congeneric pairs. Fractional abundances are calculated as the abundance of the more common species divided by the summed abundance of the two (Sugihara et al. 2003). The solid lines show the Chamela data; the red curves show, for a sample of that size, the expected count given random selection from a lognormal species abundance curve with a standard deviation of 2.5. The blue lines show the mean frequency distribution for repeated sampling for 20 randomly selected pairs ($n = 10\,000$), normalized for group sample size.

congeneric pairs is drawn from the distribution of pairs selected at random from all recorded species in the data set. Hypothesis 1 was rejected ($P = 0.005$), as was hypothesis 2 ($P = 0.015$). The difference between the fractional abundance distribution of congeneric pairs and that of pairs sampled randomly was established with the one-sample two-stage δ-corrected Kolmogorov-Smirnov test (Khamis 2000). In the one-sample Kolmogorov-Smirnov test the cumulative fractions of the data are compared with a parameter-free continuous curve drawn from the random sorting, with the K-S statistic constructed about the point of largest difference in cumulative fractions (Fig. 3a). The same procedure compared distributions of non-congeneric and randomly selected pairs.

The difference between the distributions for pairs of congeners and pairs of non-congeners was established with the two-sample Kolmogorov-Smirnov test. Analogous to the one-sample test, the two-sample Kolmogorov-Smirnov statistic (Siegal and Castellan 1988) is evaluated at the largest difference of the cumulative fractions of the two data sets (Fig. 3b).

If all species in the tree community were interchangeable, as in the family of neutral models (Hubbell 2001,

Volkov et al. 2003, 2005), neither hypothesis should have been rejected. We also asked whether the distribution of non-congeneric pairs could be the same as that for random pairs; this was not rejected ($P = 0.15$). Thus the distributions of fractional abundance have revealed that there is something distinctive about species within congeneric pairs and that the supposition that all species are interchangeable cannot be strictly true.

The Chamela Preston plot and uses of the analytic lognormal approximation for distributions not heavily veiled

It may be asked whether the differences between the distribution of congeners and those of non-congeners and randomly selected pairs may be, for some unknown reason, a property merely of species having congeners in the data set and not due to the close relationship within a congener pair. If so, the species that are members of congeneric pairs would cluster somewhere in the species abundance distribution but they do not (Fig. 4). Instead, within congeneric pairs high abundance goes with high abundance, low with low (Fig. 5). We further quantified this by testing whether the fractional abundance distribution for our selected congeneric pairs is drawn

from the distribution formed by all possible pairings of the 52 species and found that it is not ($P = 0.04$). Thus our second result is that the close relationship within congeneric pairs is important for the distribution of fractional abundance.

Exploring the shape of the fractional abundance distribution

An analytic lognormal approximation can be used to explore the shape of the fractional abundance distribution (and other representations of the same thing) as a function of the width, σ_2, of the Preston plot, under the assumption that one species is as good as another. The curves in Fig. 2 were obtained from this approximation for $\sigma_2 = 2.5$, matching the Chamela data.

For the analytic lognormal, the number of species with N individuals is represented by

$$S(N) \propto \exp\left[-\frac{(R - R_0)^2}{2\sigma_2^2} \right]$$

where $R = \log_2 N$ and the suffix on σ_2 is a reminder that R is the logarithm to the base 2.

For a given pair, the fractional abundance is $r = n_1/(n_1 + n_2)$ (where $n_1 > n_2$ and r is between 0.5 and 1.0) and $\ln(n_1) = \ln(n_2) + \ln(r/1 - r)$.

The probability of drawing a pair at random in unit intervals of R_1 and R_2 is proportional to

$$\exp\left[-\frac{(R_1 - R_0)^2}{2\sigma^2} - \frac{(R_2 - R_0)^2}{2\sigma^2} \right]$$

and for fixed n_2,

$$dR_1 = d\log_2 n_1 \propto \frac{dr}{r(1 - r)},$$

The shape of the frequency distribution of the fractional abundances is, in this approximation, obtained by integrating out $R_2 = \log_2 n_2$ and the shape is then

$$\exp\left\{ -\left[\log_2\left(\frac{r}{1 - r} \right) \right]^2 / 4\sigma_2^2 \right\} \frac{dr}{r(1 - r)}$$

where ($\log_2 x = \ln x / \ln 2$).

For large σ_2, $1/r(1 - r)$ is dominant, flat near $r = 0.5$ but spiked as $r \rightarrow 1$. This spike is increasingly tamed as σ_2 decreases. The curves in Fig. 2 were obtained from the expression for $\sigma_2 = 2.5$ (matching the Chamela data), and it is simple to follow the collapse of the bin 0.9–1.0 in the fractional abundance distribution as σ_2 decreases (Fig. 6). The quantity σ_2 has to be below 1.7 before the distribution function has flattened off. For even smaller values (narrower lognormal curves), fractional abundances near 0.5 are increasingly favored. For all values of the standard deviation the curves turn over before reaching unit fractional abundance, as can be seen from the analytic expression. For a standard deviation of 2.5 the curve turns over at 0.9975.
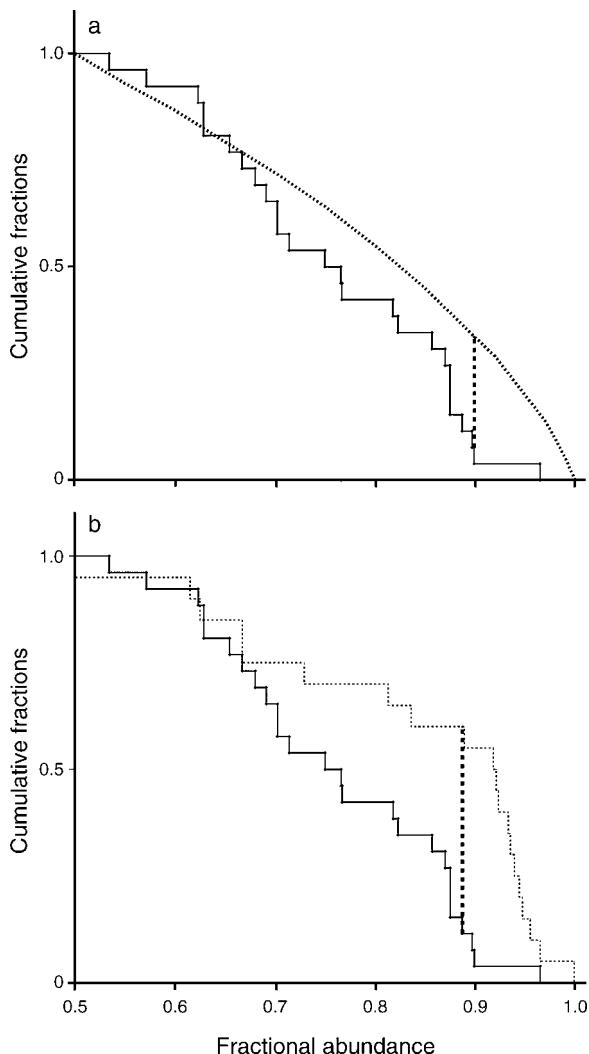

FIG. 3. (a) Abundances (estimates of population sizes) of congeneric pairs are more similar than expected by chance. The solid line shows the cumulative fraction of the number of congeneric pairs with fractional abundance, counting from a fractional abundance of 1. The smooth curve was reconstructed from selecting 20 pairs at random from the full data set, 10 000 times. The vertical dashed line shows the point of greatest difference between the compared distributions. (b) Abundances of congeneric pairs are more similar to one another than are those of non-congeneric (con-familial) pairs. This is equivalent to the statement that the fractional abundance pattern of congeneric pairs (Fig. 2a) is significantly different from that of non-congeneric (con-familial) pairs (Fig. 2b). The solid line and vertical dashed line are as in panel (a). The dotted line shows the cumulative fractional abundance distribution for non-congeneric species pairs.

Dynamics within pairs

The previous results were based on the differences between distributions of fractional abundance, but the shapes of those distributions are informative in themselves. If species are assigned to pairs without biological significance, the shape is governed by the species abundance distribution. For the congeneric pairs in the
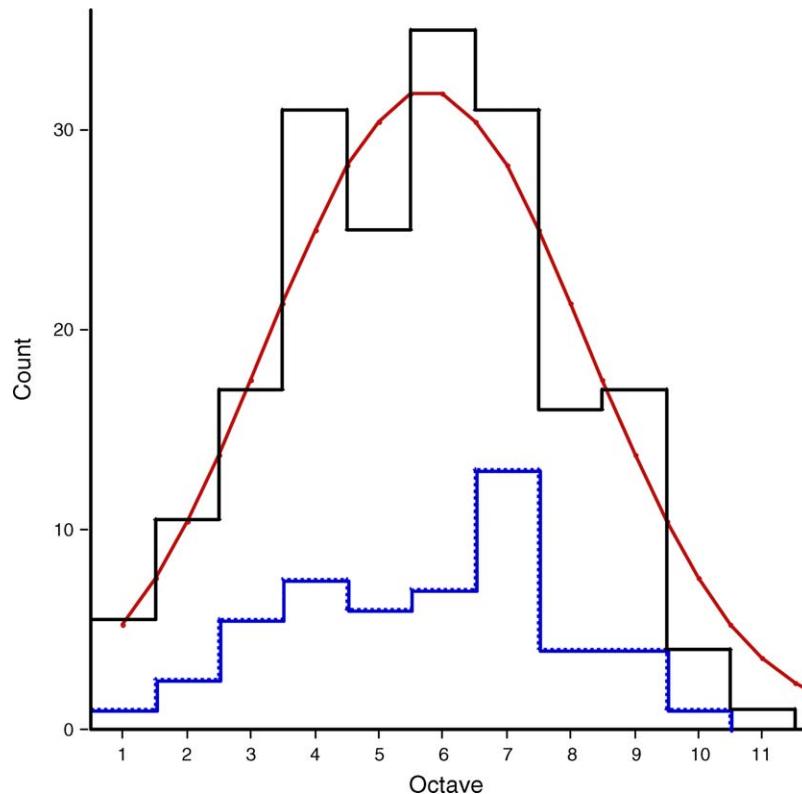
Fig. 4.   Lognormal species abundance curve for the Chamela data set. Bins show the number of species per octave; the solid black lines denote the bin count for the full 193 species. The blue line represents only those 52 species in the congeneric pairs and does not differ from the full community. The curve shown in red is a (log-)normal with standard deviation, σ_2, of 2.5. The term "octave" follows Preston's (1962) use as bin labels. The numbers on the x-axis signify that the upper value of the bin is 2 to that power.

Chamela data set, the shape of the fractional abundance distribution reveals that the pairing has biological significance and yet that the species coexisting within congeneric pairs are not identical. If they were, the fractional abundance distribution would peak at 0.5, but the distribution in Fig. 2a is concentrated in the middle of the range 0.5–1. It is similarly unlikely that the observed congeners distribution of Fig. 2a can be explained by the left-skewed curve (loading most heavily into the 0.9–1.0 bin) expected from progressive competitive exclusions (see Appendix B for a development of these results). That the coexistence of closely related species is unlikely to be trivial in either of the above senses is our final result from the study of fractional abundance distributions.

DISCUSSION

Our primary result is that there is a community structuring process at Chamela dependent upon species identity. The distribution of fractional abundance for congeneric pairs at Chamela is more equitable than for random pairs (Figs. 2a and 4). The observed pattern is a fact and is not based on assuming any sort of niche axis or niche variable. We have made no assumptions about the correctness or otherwise of Sugihara's niche hierarchy model. We applied the fractional abundance

algorithm because it seemed a promising way of determining whether niches might be important to community structure. It appears that it is.

From the observed differences among fractional abundance distributions, we conclude that the closely related members of congeneric pairs must interact with one another differently than do members of randomly selected species pairs. This observation is at odds with the assumption that species are interchangeable, which underpins neutral theory in any of its current forms (Hubbell 2001, Volkov et al. 2003). If species were interchangeable, then any reasonable pairing algorithm would yield a fractional abundance distribution consistent with pairing at random. The fractional abundance distribution of our paired congeners, comprising >25% of the censused woody species at Chamela and >60% of all woody species with congeners, is notably different from random. Previous studies have raised doubts over neutrality's predictions (Graves and Rahbek 2005, Dornelas et al. 2006); our results query the fundamental assumption, showing that dynamics that depart from strict neutrality regulate a large proportion of the same sort of community that gave rise to neutral theory, tropical trees.

Neutral theory has evolved from treating all individuals in a guild as identical in all life-history parameters
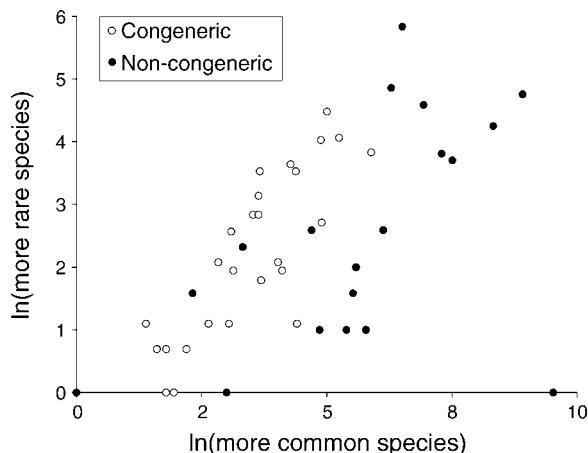
FIG. 5. Plot of ln-transformed abundances in species pairs. The figure displays all data for the resolved terminal dichotomies and shows the relations between the more common and more rare members of pairs holding over a wide range of abundances.

(Hubbell 2001) to treating all individuals as identical in certain parameters only (Volkov et al. 2003) to lately treating all species in a guild as identical (but not all individuals) (Volkov et al. 2005). It will probably evolve further, but in any event it must be remembered that the assumption of interchangeability is questionable and at odds with the patterns documented here. If species are not equivalent, then the interpretation of parameters fitted in a model presupposing equivalence (e.g., the relaxation time of Azaele et al. [2006]) must be viewed with caution.

We note that even with strong evidence of dynamics other than neutral in over a quarter of its species, the Chamela community species abundance curve exhibits the slightly skewed lognormal distribution of the kind generated by the Hubbell family of models (Hubbell 2001, Volkov et al. 2003, 2005). Moreover, an equally good lognormal with a similar standard deviation applies to only those Chamela species included in our congeneric pairs (Fig. 4). A lognormal distribution of this sort is also generated by the Sugihara niche hierarchy model (Sugihara 1980, Nee et al. 1991, Sugihara et al. 2003). Sugihara's splitting function for sequential "stick breaking" is similar to the distribution of fractional abundance of the congeneric pairs in the Chamela data set. A natural interpretation of our fractional abundance pattern then is of a splitting function at the tips of a niche dendrogram (Sugihara 1980, Sugihara et al. 2003), coinciding with our congeneric pairs at the tips of the Chamela phylogenetic tree.

In Sugihara's niche hierarchy model a communal niche space is split up sequentially by component species (Sugihara 1980); the splits define an ecological dendrogram and niche interfaces. Successive splits could be driven by either ecological or evolutionary forces, or

even something as simple as who gets there first, but Sugihara's model does not provide a mechanism to generate his splitting function; such functions have been extracted empirically from data on two species communities (Sugihara 1980) and from abundances in ecological dendrograms (Sugihara et al. 2003). Both splitting functions are equitable and the distribution of fractional abundance of our 26 congeneric pairs is consistent with either.

The comparative difference between the standard deviations of Chamela and the classic canonical lognormal is consistent with an earlier conjecture that niche structure may narrow the lognormal (Chave et al. 2002) and raises the question of whether, on Barro Colorado Island (BCI), the community carries niche dynamics that have thus far escaped the methods used to characterize its structure. The standard deviation of a "canonical" lognormal for 200 species is ~4.0 (Preston 1962a, b). With the same binning algorithm as that originally used by Preston (Preston 1948, McGill 2003), the standard deviation of the curve shown in Fig. 4 for Chamela (for which 45% of species have congeners) is 2.5. The similarly derived lognormal of the 50-ha BCI plot (with ~55% congeners) is 2.98 (Volkov et al. 2003). The information necessary to count only established individuals is not, to our knowledge, readily available for the BCI data set.

Although there is no particular reason for the patterns revealed here to be specific to dry forests, if it were so that result would be curious and informative. It would also be important because seasonally dry forest comprises >40% of all tropical forest area (Murphy and Lugo 1986) and is disappearing at an even greater rate
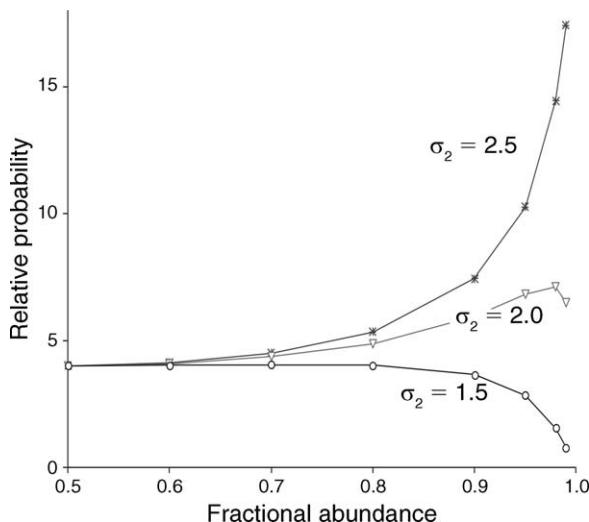

FIG. 6. Analytically derived shapes of fractional abundance distributions for random sampling for selected values of σ_2, the standard deviation of a lognormal curve. These probability distributions have not been normalized to the same (unit) area, for clarity.

than that of the more publicized tropical rain forest (Janzen 2004, Miles et al. 2006).

The shapes of the fractional abundance curves themselves contain further information and may provide insight into the ecological processes structuring the forest, over and above the species abundance plot associated with Preston. In particular, the data show a fingerprint of phylogeny in community dynamics suggesting that phylogenetic similarity is important insofar as it can lead to phenotypic similarity sufficient to dictate ecological interaction. Beyond that level of similarity, ecology does not map onto phylogeny. It is the ecological interactions, not phylogenetic relatedness, that directly regulate population-level characteristics, a process summarized in relative abundance within pairs of closely related species. This adds an important extra step to the expectation that phylogenetic or genetic similarity simply result in similar population processes and thus similar abundances (Anderson et al. 2004). In the same vein, studies that assume a simple correlation between degree of relatedness and degree of interaction (an intermediate relatedness means intermediate interaction, a low level of relatedness induces a low level of interaction) have failed to find a community-level signal of phylogeny (e.g., Silvertown et al. 2006). This could be because competition does not work this way (cf. Kelly and Bowler 2005) or because the postulated niche axis was not the best determinant of interaction, but it could also be because signal has been swamped by "noise" from higher levels of the phylogenetic structure of the community, where phylogeny becomes extraneous to ecology.

The fractional abundance measure has nothing to say about mechanism, but temporal dynamics (differential sensitivity of two competing species to environmental fluctuations) are capable of generating the form of distribution shown by the congeneric species pairs, disfavoring highly inequitable distributions (C. K. Kelly and M. G. Bowler, *unpublished calculations*). Models of nontemporal niche dynamics could generate the observed distribution of fractional abundances (for example by a suitable choice of carrying capacities in the Lotka-Volterra equation), but we know of no explicit models that do so.

Although the results reported here indicate that species interaction can be an important regulator in community structure and that that regulation has a strong phylogenetic component, they also suggest that above the level of the genus, the phylogenetic structure of a community is largely irrelevant to its ecological structure. Recent work has shown that with measures previously employed (e.g., Webb et al. 2002), the appearance of phylogenetic "clustering" or "overdispersion" within a community may not be separable from artifact (Swenson et al. 2006). The metric used here offers an assumption-free means of more directly investigating the influence of phylogenetic relatedness on community processes and structure.

CONCLUSIONS

The distribution of fractional abundances is a powerful new tool for investigating community structure. Although potentially applicable to any community, this static measure has the capacity to reveal the strength and prevalence of stabilizing (niche) dynamics in communities of high diversity and long-lived organisms. The observed distribution of fractional abundances reported here reflects a regulation of populations within congeneric pairs not active between species in either randomly selected or non-congeneric pairs (the congeners are more equitable) and a nontrivial stabilization mechanism is in place. An assumption of strict neutrality is not adequate to describe the structure of this forest, and the results suggest that niches are of considerable importance.

There is good reason to believe that the niche structure our results suggest will affect community stability and diversity. Population regulation within genera creates the sort of compartmental structure that has been shown elsewhere to lend stability to communities (Rozdilsky and Stone 2001, Rozdilsky et al. 2004). The temporal niche axis demonstrated in our earlier work is a stabilizing force and could serve as a mechanism within this phenomenological theory. Competitive compartments may also support greater diversity, either through "packing" species within compartments or compartments within broader niches, although the evidence suggests that any such broader niche structure does not map onto phylogeny.

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APPENDIX A

Phylogenetic trees of woody plants and woody species abundances at Chamela Biological Station, Jalisco, Mexico (*Ecological Archives* E089-057-A1).

APPENDIX B

Dynamics within congeneric pairs (*Ecological Archives* E089-057-A2).