

## Phylogenetic Balance and Ecological Evenness

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**Abstract.**—The frequency distribution of numbers of species in taxonomic groups, where many species belong to a few very diverse higher taxa, is mirrored by that of species in most communities, where many individuals belong to a few very abundant species. Various hypotheses mechanistically link a species' community abundance with the diversity of the higher level taxon (genus, family, order) to which it belongs, but empirical data are equivocal about general trends in the relation between rank-taxon diversity and mean abundance. One reason for this inconclusive result may be the effect of the semisubjective nature of rank-based classification. We assessed the relationship between clade diversity and mean species abundance for two diverse tropical tree communities, using both traditional rank-based analysis and two new phylogenetic analyses (based on the ratio of individuals to taxa at each node in the phylogeny). Both rank-based and phylogenetic analyses using taxonomic ranks above the species level as terminal taxa detected a trend associating common species with species-rich families. In contrast, phylogenetic analyses using species as terminal taxa could not distinguish the observed distribution of species abundances from a random distribution with respect to clade diversity. The difference between these results might be due to (1) the absence of a real phylogeny-wide relationship between clade abundance and diversity, (2) the influence of poor phylogenetic resolution within families in our phylogenies, or (3) insufficient sensitivity of our metrics to subtle tree-wide effects. Further development and application of phylogeny-based methods for testing abundance-diversity relationships is needed. [Borneo; Ecuador; phylogenetic tree balance; randomization test; relative abundance distribution; taxonomic hollow curves; tropical rain forest.]

It has long been noted that groups of a given taxonomic rank vary greatly in species richness (e.g., Willis, 1922; Dial and Marzluff, 1989). The shape of the frequency distribution of numbers of species in such groups (a so-called hollow curve), where many species belong to a few very diverse higher taxa (see Fig. 1a), is mirrored by that of the abundances of species in most communities, where many individuals belong to a few very abundant species (Fig. 1b; Preston, 1948, 1962; Gaston and Blackburn, 2000). The similarity in this taxonomic imbalance (Mooers and Heard, 1997) and ecological inequality is obvious, and biologists have asked whether there is a causal relationship between the diversity of a group (i.e., the number of species in that group, either locally or globally) and the community abundance of its members (e.g., Schwartz and Simberloff, 2001). These distributions reflect processes operating on very different temporal and spatial scales: longer term evolutionary processes creating imbalance in clade diversity versus shorter term ecological processes creating imbalance in species abundances (Hubbell, 2001), and the connection between these distributions is therefore not immediately obvious. Hypotheses have been proposed, however, that

link abundance and the probability of speciation and extinction, either via attributes of individuals and species or directly.

Some of the traits of species in diverse clades are shared by common species in communities, and this sharing may reflect the independent influence of attributes of individuals on ecology and on speciation and extinction rate. For example, the most diverse clades tend to contain species that are small bodied and highly mobile and have short generation times (Dial and Marzluff, 1988; Marzluff and Dial, 1991). The most common species in communities also tend to be small bodied and highly mobile and have short generation times (Brown, 1984, 1995; Gaston, 1994; Gaston and Kunin, 1997; Kunin and Gaston, 1997). Small body size, an individual-level attribute, may therefore be both a cause of high speciation and a cause of high local abundance. Other such individual-level key innovations with increased population density consequences may include latex canals (Farrell et al., 1991) and furanocoumarins (Berenbaum, 1983) in plants and swim bladders in teleosts (Liem, 1990; see Heard and Hauser, 1995: type II, increased fitness innovations). However, testing the significance of such associations is

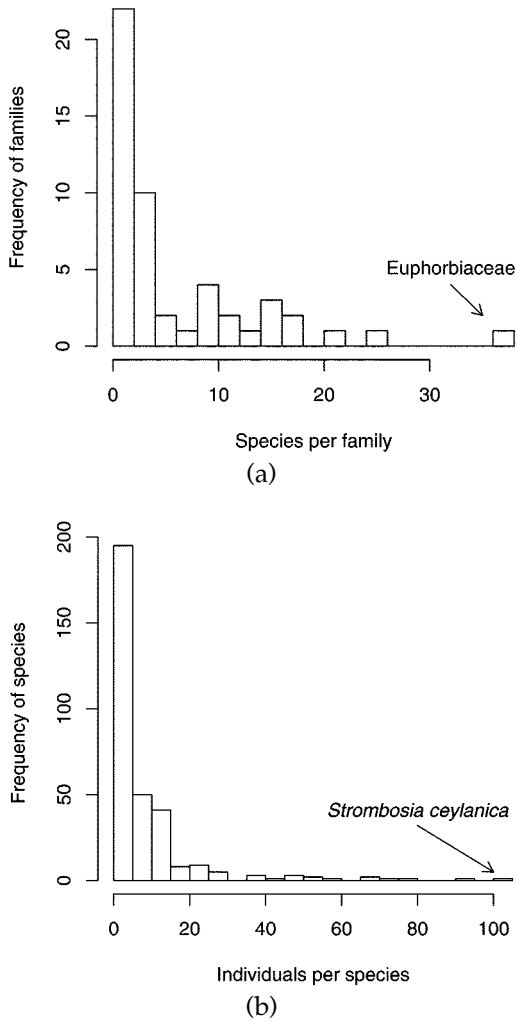


FIGURE 1. Frequency distributions of the number of species per family (a) and the number of individuals per species (b) for rain forest trees at Gunung Palung, Indonesia.

difficult (Heard and Hauser, 1995; de Queiroz, 1998; Hunter, 1998; Agapow and Isaac, 2002).

Commonness in local communities (a population-level attribute) may be directly linked to elevated speciation rates or reduced extinction rates (Darwin, 1859; Vermeij, 1987; Rosenzweig, 1995; Maurer, 1999), and thus may influence phylogenetic tree balance (Moors and Heard 1997). For example, Hubbell's (2001) null model of biodiversity and biogeography links a species' probability of speciation to its absolute abundance in the regional community, i.e., common taxa are more likely to speciate than are rare taxa.

In contrast to the above theories, which predict higher abundance in more speciose clades, classic ecological theory suggests that species in diverse clades should tend to be rarer than species in less diverse clades because the stronger competition expected between closely related, ecologically similar, undifferentiated species in diverse clades should result in low population densities (Hutchinson, 1957; MacArthur and Levins, 1967). The same pattern is also predicted if resource space is subdivided at each speciation event, and a species' abundance is a function of its resulting niche-breadth (MacArthur's [1960] broken-stick model). Key innovations that may lead to such ecological specialization include special jaw morphology in fish, feeding niche in bovids, or footpads in *Anolis* (Heard and Hauser's [1995] type III innovations).

In at least four recent studies, statistical correlations have been reported between the abundance of species and the diversity of the higher level taxa they belong to, although these correlations vary in strength and direction, and the studies have included widely different kinds of data and methodologies. In communities of western Amazonian trees (Pitman et al., 2001) and of North American and Hawaiian plants (Schwarz and Simberloff, 2001), rare species were associated with diverse clades. In contrast, in a study of carnivores and primates rare species were associated with species-poor taxa (Gittleman and Purvis, 1998), and the presence of latex-bearing canals in trees was associated with both high clade diversity and elevated local abundance in Peruvian rain forest (Farrell et al., 1991).

Schwartz and Simberloff (2001) suggested that the "differential species-naming conventions" between different groups of taxonomists (particularly between animal and plant taxonomists) may explain the different patterns of association observed. Insofar as traditional taxonomic approaches to the assignment of higher taxa contain elements of subjectivity, a move toward phylogenetic, rank-free tests should reveal more clearly the real associations in the data. The purpose of this article is to introduce some rank-free tests of the association between taxon abundance and clade diversity, using data for two tropical tree communities as an example. We compared the results of these new tests with those of correlation tests using traditional

taxonomic ranks. We conclude with a discussion of challenges and promising avenues for further research.

## METHODS

### *Field Data and Diversity Data*

We used data from large tree inventories carried out independently in lowland tropical forest in Amazonian Ecuador and Indonesian Borneo. In both forests, trees were sampled in small plots scattered across the landscape. The Ecuadorean network consists of 16 1-ha plots in unflooded forest, sampling 9,510 trees  $\geq 10$  cm diameter of breast height (dbh) and 1,004 species. Plots in Ecuador were established by N. Pitman, C. Cerón, D. Neill, W. Palacios, and M. Aulestia and have been described in detail (Pitman et al., 1999, 2001; Pitman, 2000). The Borneo network consists of 28 0.1-ha plots, sampling 2,862 trees  $\geq 10$  cm dbh and 324 species in unflooded forest of Gunung Palung National Park. These plots were described in detail by Webb and Peart (1999, 2000). At both sites, edaphic (soil) and topographic conditions varied from plot to plot, but climate did not.

In each plot, every free-standing tree was measured and identified to species or morphospecies. For the analyses described here, we removed from each data set a small proportion of trees that were not identified to family (ca. 2% of the stems). Species abundances were calculated as the total number of individuals of a species recorded at a site (i.e., at Gunung Palung and at Yasuní).

### *Taxonomic (Rank-Based) Analyses*

We used a nonparametric correlation statistic (Spearman's rho) to examine the relationships between two measures of family diversity and three measures of abundance. Family diversity was estimated as the number of species in a family at a given site recorded in a site's inventory (local diversity) and as the number of species in a family at the global scale, *vide* Mabberley (1997; global diversity). Abundance was measured as (1) the total number of individuals of a family, (2) the mean number of individuals per species recorded for each family, and (3) for each family the proportion of rare species (defined as having densities of  $< 1$  individual/ha in the inventories). The

correlation of total number of trees per family with the local number of species in a family is trivial and was not calculated because families with more species recorded locally will on average have a higher number of individuals in the family.

The use of mean species abundances in analyses can be fraught with hidden null expectations (Gotelli and Colwell, 2001). However, after careful consideration (R. Colwell, pers. comm.), we determined that our use of these ratios was free from misleading behavior. The sample of trees at each site represents a single draw from the population, and we expect both species:family and individual:species ratios to reflect the population values without sampling bias. Additionally, where tested, the significance of the relationships was insensitive to rarefaction of the number of individual trees sampled (Gotelli and Colwell, 2001).

The five resulting correlation tests were carried out separately for the Ecuador and Borneo data sets. In all analyses for a site, only the abundances and diversity of taxa present at that site were used (i.e., there were no zeros in the correlation).

### *Phylogenies*

Hypotheses for the phylogenetic relationships of the 1,004 species at Yasuní (Ecuador) and the 324 species at Gunung Palung (Borneo) were constructed separately using previously published phylogenetic studies. This process was automated by the Phylomatic database and assembly tools (Webb and Donoghue, 2001). Phylomatic is based on a single, hand-assembled supertree (Sanderson et al., 1998) or tree of trees that grows continuously as new phylogenies are attached and changes as major branches are rearranged as the result of new work; full assembly rules for this supertree are given on the Phylomatic website (Webb and Donoghue, 2001). The tree backbone is the most recent all-angiosperm three-gene tree (Soltis et al., 2000), to which strict consensus trees from other studies are attached, with the clade arrangement in more phylogenetically focused studies overriding those in less focused studies. An online program then translates the input list of taxa into a phylogeny for those taxa, attaching unrecognized species to a polytomous genus node and unrecognized genera to a polytomous

family node. The supertree database used in this study was revision L20011010, containing 38 sources of data (all versions of the supertree are archived). The phylogenies used here thus represent best current hypotheses for the relationship of our taxa based on up to 38 other studies of a wide range of genes and morphology. However, the position of most genera in families and the position of all species within genera were unresolved. NEXUS versions of our supertrees for Borneo and Yasuní are available from the authors. The supertrees used are only working hypotheses, and their construction involves some subjective decisions. An assessment of the influence of using alternatively resolved phylogenies is therefore generally indicated when using these phylogenies (e.g., Webb, 2000). Our purpose here, however, is primarily methodological, and we therefore did not perform sensitivity analyses on alternative phylogenies.

#### *Phylogenetic Analyses*

The simplest way to assess abundance–diversity relationships over a whole phylogeny is to calculate the mean number of individuals per species at every node. We began by calculating for every node in the community phylogeny the number of species distal to that node and the sum of the individuals accounted for by those species. To achieve a standard metric that could be compared across communities, all abundances and all species numbers were first converted to proportions. The nodes index metric  $I_n$  was therefore calculated as the mean of the ratio of summed proportional individuals to summed proportional species at every node, i.e.,  $I_n = \text{mean} [\text{sum}(n/N)/\text{sum}(s/S)]$  over all nodes, where  $N$  is the total number of individuals in the community and  $S$  is the total number of species in the community.  $I_n$  is a higher-rank-free metric where the terminal taxa are species, but it will be influenced by the method used to group species into terminal taxa where terminal taxa are groups of more than one species.

To be able to compare results from this type of metric to the rank-based tests directly, we developed a tips index metric,  $I_t$ , for just the terminal taxa:  $I_t = \text{mean} [(n/N)/(s/S)]$ , over terminal nodes. In a species-level analysis, the number of taxa in the terminal clade ( $s$ ) is equal to 1, and  $I_t$  becomes meaningless.

Because there are many more nodes containing a few species than nodes containing many,  $I_n$  is heavily weighted toward patterns in the tips of the phylogeny rather than expressing the pattern throughout the whole tree. To address this bias, we calculated a third metric,  $I_a$ , based on the averaged accumulation of both taxa and individuals as a tree is traversed from the tips to the base. We calculated a series of ratios for every terminal taxon; one ratio (of individuals to species) at every node along the route traced back from the terminal taxon to the root of the phylogeny. Deep nodes and shallow nodes were therefore weighted equally. The cumulative (scaled) abundance can be plotted against the cumulative (scaled) number of species (Lorenz, 1905). If all species in the phylogeny are of equal abundance, the ratio of individuals to species  $[\text{sum}(n/N)/\text{sum}(s/S)]$ , will be constant at each more basal node (see Figs. 2b, 2c: Even). If species in more diverse clades have fewer individuals per species than species in less diverse clades, the ratio of individuals to species will be lower than average in the route taken to the base from a terminal taxon in the diverse clade and higher than average in the route taken to the base from a terminal taxon in the less diverse clade (Figs. 2b, 2c: Base-wards). However, there will be absolutely more nodes with below-average  $\text{sum}(n/N)/\text{sum}(s/S)$ , hence the mean trend will be for  $\text{sum}(n/N)$  to accumulate proportionally more slowly than  $\text{sum}(s/S)$ . If species in more diverse clades have more individuals per species than species in less diverse clades, the overall trend will be reversed (Figs. 2b, 2c: Tip-ward). Because  $\text{sum}(n/N)$  and  $\text{sum}(s/S)$  are scaled to 1, the area under the accumulation curve ( $A$ ) becomes a standardized measure of the deviation from the null hypothesis that clade abundance is independent of clade diversity (Gini, 1912).

Our third metric, the accumulation index,  $I_a$ , is then defined as the mean of  $A$  for routes to the base from each terminal taxon, i.e.,  $I_a = \text{mean}(A)$ . If low-diversity clades are disproportionately abundant (Fig. 2, Base-ward), then  $I_a$  will have a value  $<0.5$ ; if high-diversity clades are disproportionately abundant, then  $I_a$  will have a value  $>0.5$ . The hypothetical case illustrated in Figure 2 is based on the simplest possible imbalanced tree, and the particular shape of the mean curve for all terminal-to-base routes in more

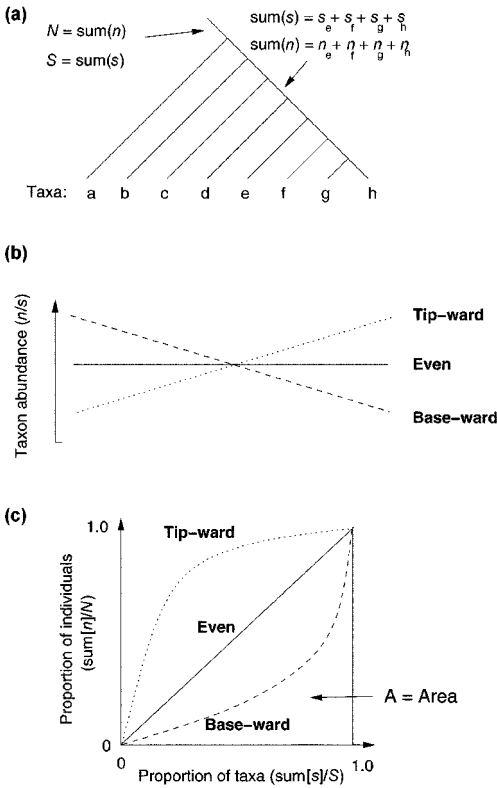


FIGURE 2. Calculation of phylogenetic metrics. (a) Hypothetical phylogeny of eight taxa. Taxa may be species (where each  $s = 1$ ) or higher taxa (where each  $s > 1$ ), and each represents  $n$  individuals; species and individuals can be summed at each node for all distal branches. The phylogeny is maximally imbalanced for simplicity. (b) Distribution of individuals across taxa can be tip-ward (more diverse clades have relatively more individuals), even, or base-ward (less diverse clades have relatively more individuals). (c) The trend (averaged over all  $S$  taxa) for accumulation of proportional taxa and proportional individuals. The metrics produced here are the tips index,  $I_t = \text{mean}(n/s)$  for terminal taxa (lettered taxa a-h), the nodes index,  $I_n = \text{mean}[\text{sum}(n)/\text{sum}(s)]$  for all nodes (lettered taxa plus the interior seven nodes), and the accumulation index,  $I_a = \text{mean}(A)$  for each accumulation curve of the terminal taxa.

complex trees will depend upon the particular distribution of species abundances ( $n/s$ ) across the phylogeny.

The behavior of the three metrics was examined across a simple pectinate phylogeny of 16 taxa, with abundance distributions constructed to be base-ward, even, random, or tip-ward (Table 1). In the base-ward or tip-ward cases, the abundances of adjacent taxa increased or decreased exponentially. The same abundance patterns were also used on

TABLE 1. Comparison of behavior of three metrics of abundance–diversity equality with variation in correlation of terminal clade  $n/s$  and terminal clade  $s$  and changing arrangement of  $n/s$  versus  $s$  imbalance on a simple pectinate phylogeny (see Fig. 2).  $I_t = \text{mean}[(n/N)/(s/S)]$  for terminal groups;  $I_n = \text{mean}[\text{sum}(n/N)/\text{sum}(s/S)]$  for all nodes;  $I_a = \text{mean}(A)$ .

Direction of high $n/s$	Metric	Correlation of $n/s$ with $s$		
		Negative	$s = 1$	Positive
Tip-ward	$I_t$	$>1$	1	$<1$
	$I_n$	$>1$	$>1$	$<1$
	$I_a$	$>0.5$	$>0.5$	$>0.5$
Even or random (balanced phylogeny)	$I_t$	$>1$	1	$<1$
	$I_n$	$>1$	1	$<1$
	$I_a$	0.5	0.5	0.5
Base-ward	$I_t$	$>1$	1	$<1$
	$I_n$	$>1$	$<1$	$<1$
	$I_a$	$<0.5$	$<0.5$	$<0.5$

a perfectly balanced (bifurcating) phylogeny of the same 16 taxa. The metrics respond to (1) the amount of imbalance in species abundance (i.e., variation in  $n/s$ ; see Fig. 2b), (2) the correlation of species abundance ( $n/s$ ) with the number of species in the terminal group ( $s$ ) (i.e., the primary biological pattern to be detected), (3) the degree of imbalance in the topology of a phylogeny (i.e., perfectly imbalanced vs. perfectly balanced), and (4) the direction of abundance–diversity imbalance in an imbalanced phylogeny (Fig. 2, base-ward vs. tip-ward). The precise relationship among these parameters is complicated and awaits further analysis, but two gross patterns in the metrics are clear and of value for this study (Table 1): (1) metrics  $I_t$  and  $I_n$  respond to the correlation of species abundance ( $n/s$ ) with the number of species in the terminal group ( $I_t, I_n > 1$  indicates a positive correlation;  $I_t, I_n < 1$  indicates a negative correlation), and (2) metric  $I_a$  responds to the direction of distribution of abundance imbalance across an imbalanced phylogeny ( $I_a < 0.5$  indicates an overabundance in base-ward taxa;  $I_a > 0.5$  indicates overabundance in tip-ward taxa; see Fig. 2).

All three metrics were compared with null model results to determine whether the observed inequality between clade diversity and abundance was more or less than expected by chance. In all three cases, the appropriate null model is to reassign abundances at random among terminal taxa. Metrics were calculated and null models run in a C-language program available from the authors.

We applied these metrics and the associated significance tests to the tree community abundance data from Yasuní and Gunung Palung. For each site, we used a phylogeny to family (the pruned species phylogeny, see above) with the local number of individuals ( $n$ ) in each family and the local number of species ( $s$ ) in each family, and a species-level phylogeny (i.e.,  $s = 1$ ) and abundances ( $n$ ) for each species across the whole site. Index  $I_t$  is meaningless when  $s = 1$ , and thus two combinations are not presented. Hence, a total of 10 metrics were calculated and tested: (3 metrics  $\times$  2 phylogenies  $\times$  2 sites) – 2 combinations.

## RESULTS

### *Taxonomic (Rank-Based) Analyses*

Six of the 10 rank-based correlation tests gave significant results, and all 6 were significant in the same direction, rare species being associated with families that are relatively species-poor (Table 2). In both forests, we found a significant positive relationship between the mean abundance of species in a family and the local diversity of that family, and we found a consistent negative relationship between the proportion of rare species in a family and the local diversity of that family. In neither forest was there an association between global diversity and mean species abundance per family or proportion of rare species. However, in both forests there was a positive association between global diversity and total family abundance.

### *Phylogenetic Analyses*

A visual examination of the phylogeny of families reveals that both species and indi-

viduals are distributed without a clear relationship to the imbalance evident in the angiosperm tree (Fig. 3).

For the phylogenetic analyses using families, metrics  $I_t$  and  $I_n$  supported the result found by simple family-level correlations. Metric  $I_t$  is a tip-level analysis and is therefore rank based where  $s$  is not equal to 1. The direction and significance of  $I_t$  was consistent with the simple correlations. For both Yasuní and Gunung Palung (GP), local mean species abundance in a family was positively correlated with local family species richness (Yasuní  $I_t = 0.952$ ; GP  $I_t = 0.854$ ; Table 3). Metric  $I_n$  integrates the extent of abundance–diversity inequality over the whole tree. The significant positive correlation of species abundance with local family diversity at the tips ( $I_t$ ) was also significant with metric  $I_n$  (Yasuní  $I_n = 0.988$ ; GP  $I_n = 0.871$ ), indicating that the inequality effect was deeper than just at the tips. Metric  $I_a$  was not significantly different from the null expectation at either Yasuní or Gunung Palung. However,  $I_a$  responds to the direction of abundance imbalance on an imbalanced phylogeny and may indicate that for Yasuní ( $I_a = 0.482$ ) the overabundant taxa lie in the base-ward clades (i.e., Ranalean groups in the highly imbalanced angiosperm phylogeny), whereas for Gunung Palung ( $I_a = 0.510$ ) the overabundant taxa may lie in the tip-ward (Asterid-ward) clades.

None of the four phylogenetic analyses using species as terminal taxa showed a significant deviation from the null expectation that species abundances are distributed at random with respect to clade diversity (Yasuní and GP,  $I_n$  or  $I_a$ ). The parameters do, however, hint at differing patterns at the two sites (see Table 1), consistent with using families as terminal taxa. Yasuní appeared

TABLE 2. Results of the rank-based tests of abundance–diversity inequality for two rain forest tree communities, using two measures of family diversity (local and global) and three measures of family abundance (total number of trees per family, mean number of trees per species in each family, and proportion of species with trees of density <1 tree/ha). Significance was tested with Spearman's rank correlation ( $\rho$ ). The correlation of total number of trees per family with the local number of species in a family is trivial and is not shown.

Site	Family diversity	Measure of abundance					
		Total trees/family		Mean trees/species		Proportion of rare species	
		$\rho$	$P$	$\rho$	$P$	$\rho$	$P$
Yasuní	Local			0.3655	0.002	–0.415	0.0004
	Global	0.384	0.007	0.138	0.255	–0.173	0.151
Gunung Palung	Local			0.520	0.0002	–0.340	0.018
	Global	0.334	0.0057	0.09	0.54	0.067	0.65

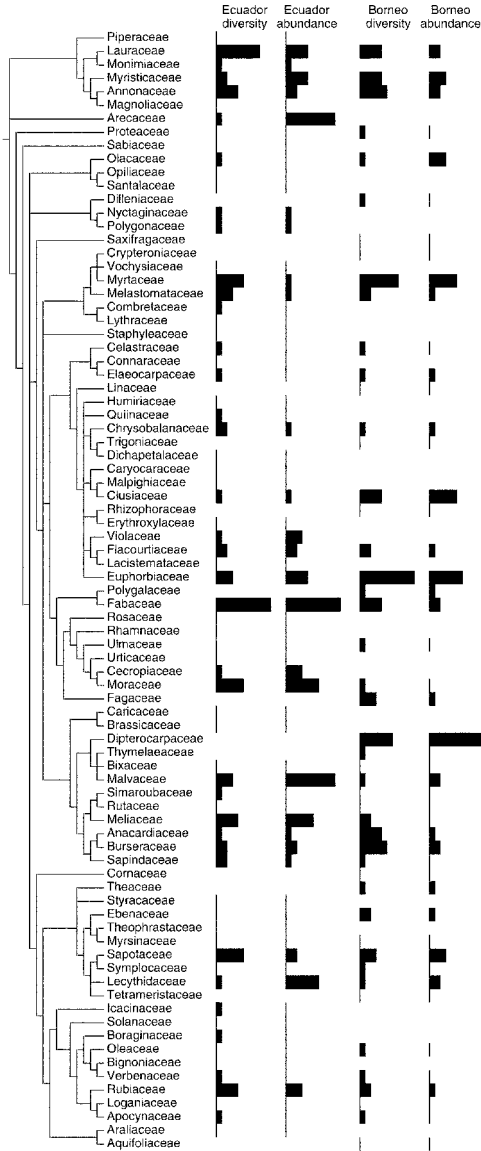


FIGURE 3. Ecological and phylogenetic imbalance in tree communities of Yasuni National Park, Ecuador, and Gunung Palung National Park, Borneo. The sizes of the four bars to the right of each family indicate (1) the proportion of all Yasuni species accounted for by that family, (2) the proportion of all individual trees in Yasuni accounted for by that family, (3) the proportion of all Gunung Palung species accounted for by that family, and (4) the proportion of all individual trees in Gunung Palung accounted for by that family. Missing bars indicate that the family was not recorded in the respective inventory.

to have overabundant taxa distributed base-ward ( $I_a = 0.483$ ), whereas Gunung Palung had them distributed tip-ward ( $I_a = 0.510$ ).

DISCUSSION

Our rank-based and phylogenetic analyses (using families as terminal units) support the conclusion that in both forests tree species in larger families tend to be more common than species in smaller families. Thus, hypotheses predicting a positive relationship between clade diversity and mean species abundance (e.g., Rosenzweig, 1995; Hubbell, 2001) appear to be supported in these diverse forest systems. At the larger scale of comparison among studies, however, these results do little to clarify the confusing picture of the relationship between diversity and abundance. The positive association reported here between common species and diverse plant families conflicts with strong trends in the opposite direction reported previously (Pitman et al., 2001; Schwarz and Simberloff, 2001). This scattering of positive, negative, and insignificant correlations between abundance and diversity has also been found for several other floras, even when consistent methods have been applied (M. Schwarz, pers. comm.).

There are a number of ways to interpret these equivocal results among various studies. First, the relationship between abundance and diversity, like many others in ecology, may be site dependent rather than general and may differ from community to community. This would be the case, for example, if a taxonomic character associated with diverse clades (e.g., latex-bearing canals in trees; Farrell et al., 1991) provided a competitive advantage in some environments but no advantage (or a disadvantage) in others. Second, different types of key innovation should promote different relationships between diversity and abundance. Innovations with a positive effect on local fitness and abundance should lead to a positive relationship, whereas innovations that result from ecological specialization should lead to a negative relationship (Heard and Hauser, 1995, type II vs. type III). Third, the relationship between abundance and diversity may take different forms at different spatial scales. The abundance data used by studies to date have been sometimes derived from local inventories (this study; Pitman et al., 2001), sometimes taken from global surveys (Schwarz and Simberloff, 2001), and sometimes based on geographic range sizes. Likewise, the diversity data used by studies to

TABLE 3. Results of the phylogenetic tests of abundance–diversity inequality for two rain forest tree communities. The taxonomic rank of the terminal taxon and the source for the number of species of the terminal taxon is indicated. The metric rank refers to the sorted position of the observed value compared to 1,000 random shufflings of the abundances ( $n$  of terminal taxa). A rank of  $<25$  or  $>975$  is equivalent to a two-tailed  $P$  value of 0.05.

Site	Terminal clade rank	Terminal clade diversity ( $s$ )	$I_t$		$I_n$		$I_a$	
			Value	Rank	Value	Rank	Value	Rank
Yasuní	Family	Local	0.952	1	0.988	5	0.482	272
	Species	1			1.048	775	0.483	149
Gunung Palung	Family	Local	0.854	1	0.871	1	0.510	395
	Species	1			0.978	336	0.510	753

date have been variously local, regional, or global. Our own results showed that global estimates of taxon diversity were not associated with mean species abundance in a family but were associated with total abundance of a family, suggesting a correlation between global taxon diversity and local taxon diversity.

Alternatively, these contradictory results may be an artifact of taxonomic classifications (Schwarz and Simberloff, 2001). Because division into families and other higher taxonomic groups also occurs at an arbitrary level from a phylogenetic standpoint (e.g., Doyle and Donoghue, 1993; de Queiroz and Gauthier, 1994; Mishler, 2000), there may be no relation between the classes recognized by taxonomists and the distribution on the phylogeny of the characters that may truly influence abundance. For example, if the angiosperm phylogeny were divided into taxonomic classes that corresponded with ancestral acquisitions of latex, there might be a very clear positive relationship between taxon diversity and mean local species abundance (Farrell et al., 1991).

Our own tests of phylogeny-wide abundance–diversity associations with families as terminal groups continued to show a significant positive association between clade local diversity and local mean species abundance, suggesting that the clade abundance–diversity inequality exists as a real phenomenon in the phylogeny. However, all the analyses that started with species as the terminal taxa showed no significant relationship; i.e., after removing all predefined classes from the phylogeny, there was no significant association between abundance and diversity at a node. This failure to detect an association has three possible explanations: (1) there is no real phylogeny-wide relationship between clade abundance and diversity, (2) the lack of

phylogenetic resolution within families in our phylogeny hid real clade-abundance inequalities, or (3) the sensitivity of our metrics was insufficient to pick up tree-wide effects. Although extreme clade abundance–diversity inequality in the test data was detectable by all three metrics, we have yet to explore sensitivity to more subtle patterns. Application of these metrics to communities with fully resolved phylogenies will be important in the development of these techniques. Other important issues to address include incorporation of phylogenetic branch-length information, determination of the effect of using local diversity and local community phylogenies to represent global patterns of diversification (taxon sampling issues, e.g., Ackerly, 2000), and assessment of the conceptual and practical improvement of correlating actual diversification rates (derived using node dates, e.g., Magallon and Sanderson, 2001) with local abundances rather than numbers of extant taxa in an area.

Further exploration of the relationship between clade abundance and diversity will be an important step in better understanding the links between ecological and evolutionary processes and will no doubt become a more common activity for ecologists (see Webb et al., 2002). Evolutionary biologists too have much to gain by explicitly considering the likely ecological context of speciation events. The uneven diversity among clades or imbalance in phylogenetic trees (see other articles in this issue of *Systematic Biology*) may be as much a function of population-level ecological control of abundance as of the individual-level evolutionary innovations usually considered. Given the relative ease of constructing supertree phylogenies for ecological communities, the use of phylogenetic analyses to complement traditional rank-based analyses should become standard. The metrics



described here are a first step in developing tools for the phylogeny-based analysis of community abundance structure.

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