General patterns of taxonomic and biomass partitioning in extant and fossil plant communities

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A central goal of evolutionary ecology is to identify the general features maintaining the diversity of species assemblages[1–3]. Understanding the taxonomic and ecological characteristics of ecological communities provides a means to develop and test theories about the processes that regulate species coexistence and diversity. Here, using data from woody plant communities from different biogeographic regions, continents and geologic time periods, we show that the number of higher taxa is a general power-function of species richness that is significantly different from randomized assemblages. In general, we find that local communities are characterized by fewer higher taxa than would be expected by chance. The degree of taxonomic diversity is influenced by modes of dispersal and potential biotic interactions. Further, changes in local diversity are accompanied by regular changes in the partitioning of community biomass between taxa that are also described by a power function. Our results indicate that local and regional processes[2] have consistently regulated community diversity and biomass partitioning for millions of years.

Three broad categories of processes have been hypothesized to regulate local species richness across ecological communities: ecological interactions, phylogenetic history and historical contingency[1–6]. Their relative influence on communities has been the subject of debate[6–11], but singly or in combination, these processes ultimately determine the composition of ecological communities and how community biomass is divided into discrete systematic units. Here we use two large woody plant data sets to identify the relative importance and generality of the ecological, evolutionary and historical processes shaping the taxonomic structure and biomass division within local plant communities across the world.

We used 227 standardized one-tenth hectare samples of woody plant communities from around the world compiled by the late A.H. Gentry and the Missouri Botanical Garden[9,10]. The observed relationship between species and higher taxa is not a constraint envelope, as would be expected if certain taxa sometimes dominated locally species-rich communities (Fig. 1). Instead, our analysis shows that the relationships between the number of species, *S*, the number of genera, *G*, and the number of families, *F*, are described by simple power-functions, where $F \propto S^{0.68}$ and $G \propto S^{0.941}$ (Fig. 2; see also refs 4, 12 and 13). These exponents are statistically invariant across and within major biogeographic provinces, continents and physiognomic types (see Table 1a in the Supplementary Information). Furthermore, taxonomic exponents for palaeocommunities are indistinguishable from those of extant communities (Fig. 3 and Supplementary Information). As species richness increases, congeneric species and confamilial genera become proportionately more common because the observed exponents between species and higher taxa are less than 1. As a result, an increase in local diversity is paralleled by a proportional increase in taxonomic similarity between taxa within the community.

The consistent macroecological nature of the relationship between the number of species and higher taxa across continents supports the assertions of some palaeontologists and conservationists that the number of higher taxa can be used as a predictor of species richness within local assemblages[12–15] (see also ref. 16), although the relationship is not linear. Data from diverse taxa, including marine molluscs[13], birds, mammals (J.P.H., unpublished work) and ants (M. Weiser, personal communication) suggest that local communities of animals are also characterized by approximate power-functions. The presence of general functions that describe the partitioning of subunits into higher taxonomic groups is of importance to ecologists and palaeobiologists requiring quick and robust estimates of local taxonomic richness in both present and historical communities[12,13] and to theoretical and empirical ecologists studying the causes and consequences of biological diversity.

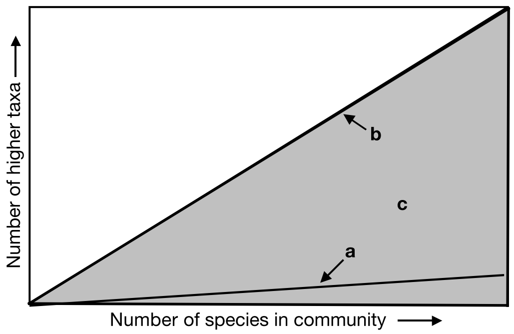

Figure 1 Three graphical hypotheses for the relationship between species richness and number of higher taxa within a local community. **a**, A positive relationship with a shallow slope: as species richness increases, the number of higher taxa (that is, genera or families) increases at a slower rate; additional species come from within an increasingly limited subset of higher taxa. **b**, A slope of unity represents the upper constraint boundary where increases in species richness result solely from the addition of higher taxa. **c**, The shaded area represents a constraint region in which the variance in abundance of higher taxa could be expected to increase with species richness: actual higher taxa abundance would be effectively unpredictable from species richness.

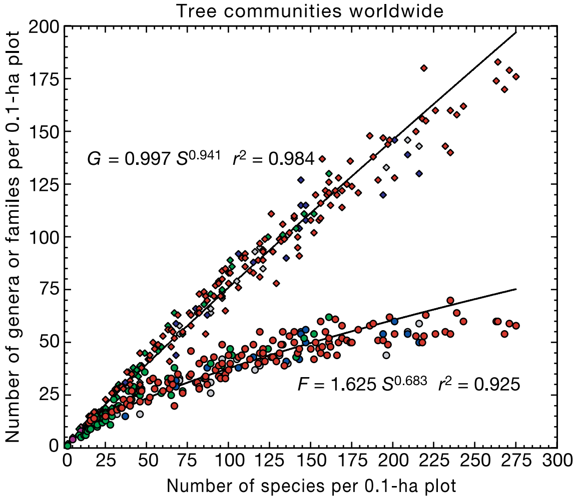

Figure 2 Relationship between the number of species and higher taxa across 227 0.1-ha sites from around the world. Species richness at individual sites ranges from 2 to 275. Diamonds, number of genera; circles, number of families. Colours correspond to samples from each continent (red, South America; blue, Asia; grey, Africa; green, North America; purple, Europe). Significant differences were not observed between the individual continents, hemispheres, and the world (see Table 1a,b in the Supplementary Information). *G*, number of genera; *S*, number of species; *F*, number of families.

To determine whether the local-scale taxonomic structure was significantly different from random samples of species pools of differing sizes, we constructed two Monte Carlo simulations. In all tests, assuming equal probability of colonization, the implicit null hypothesis is that the taxonomic structure of local communities is not distinguishable from a random sample of the species pool in which they were contained[17,18] (see Methods and Supplementary Information). Randomized communities assembled from global, regional, continental and local scales are characterized by significantly higher exponents than observed (Table 1b,c in the Supplementary Information and Fig. 4). For a given species richness, 'real' communities consist of fewer numbers of genera and families than communities randomly assembled from species pools of different sizes[4,5,18]. This accords with Elton's original observation[4], that local communities are more taxonomically similar than expected by chance. With increasing species richness, generic richness rises at a proportionately slower rate and familial richness rises at an even slower rate (for example, $\mathrm{d}F/\mathrm{d}S \propto S^{-0.26}$ and $\mathrm{d}G/\mathrm{d}S \propto S^{-0.06}$). If, during evolutionary diversification, traits associated with physiology, morphology and ecology are conserved within a taxon, then congeners (members of the same genus) are expected to be more ecologically similar and compete more intensely with one another than noncongeners[4–7,11,19]. As such, our observations are consistent with previous assertions[19–22] that an increase in community species richness is accompanied by both (1) an increase in the proportional degree of ecological similarity between species due to taxonomic exponents less than 1 (see refs 2, 3, 5 and 23), and (2) an overall increase in total morphological or character diversity due to a uniform increase in higher taxa[11,19,21–24], although at an ever-slowing rate.

Two fundamental processes are likely to explain why generic and familial richness do not rise as quickly with increases in species numbers in natural communities as they do in our null models. First, taxa are likely to vary widely in their ability to gain access to local sites (that is, poor mixing of taxa within a given species pool owing to dispersal limitation[2,19]). Second, biotic and abiotic features of a local site will influence the ability of taxa to colonize and survive within the site[19]. Patterns of residual variation (Fig. 1) support both of these hypotheses. For example, there is a significant negative residual correlation in generic and familial richness with local annual precipitation (genera: $r^2 = -0.155$, $n = 91$, $F = 16.33$, $P = 0.0001$; families: $r^2 = -0.148$, $n = 91$, $F = 15.51$, $P = 0.0002$), while there is a significant positive residual correlation for familial diversity and elevation (genera: $r^2 = 0.005$, $n = 145$, $F = 0.757$, $P = 0.386$; families: $r^2 = 0.101$, $n = 145$, $F = 15.98$, $P < 0.0001$). Thus, for a given species diversity, more dry and high-elevation sites have proportionally greater numbers of higher taxa than mesic low-elevation sites. This finding highlights the uniqueness of diverse high-elevation and dry forests[9,10]. There is, however, no significant correlation between residual variation in generic or familial diversity with variation in local stem density, maximum stem diameter, total community biomass and absolute latitude. Our observations accord with a recognized association between wind/long-distance dispersal with (1) local rainfall and (2) the degree of insularity/increasing elevation[25,26]. Thus, as indicated by our null model, deviation from the general taxonomic diversity function between sites (Fig. 1) seems to be significantly influenced by dispersal probabilities of a local flora.

Analysis of taxonomic exponents across size classes (a proxy for plant age) suggests a slight but significant decrease in the degree of taxonomic and hence ecological similarity as individuals within the community mature. By comparing the fitted regression parameters of the largest one-third of individuals with those of the smallest one-third we see a slight increase in the taxonomic exponent for both genera and families. The generic scaling exponent from the largest individuals ($b = 0.979 \pm 0.023$) falls outside the 95% confidence interval predicted by the smallest individuals ($b = 0.942 \pm 0.001$). The magnitude of the change for families is less than that observed for genera (largest $b = 0.776 \pm 0.032$; smallest $b = 0.754 \pm 0.020$;). We cannot assess whether a greater proportion of smaller-sized taxa generates this directional change in the taxonomic exponent. However, the observed directional shift agrees with the prediction that disproportionate competitive thinning of related taxa influences local richness[1,4,6]. The observed patterns of residual variation in taxonomic diversity are in accord with interpretations that the probabilities of local species establishment and extinction[19,21–24,27] are governed in part by dispersal ability and the degree of ecological similarity of the interacting taxa, both of which are mediated by the local abiotic environment[5–8,18–20].

Our analyses exclude the possibility that the taxonomic structure influences the total biomass within natural assemblages[19–21]. As the total standing aboveground dry biomass, M_{tot}, is approximately constant with local richness ($M_{\mathrm{tot}} \propto S^0$), increasing species richness within natural communities results in a finer division of biomass between taxa rather than an increase in total biomass[10,28]. Instead, observed patterns of biomass partitioning are consistent with zero-sum models of community assembly (see refs 2 and 28) where a change in local richness is compensated for by a concomitant

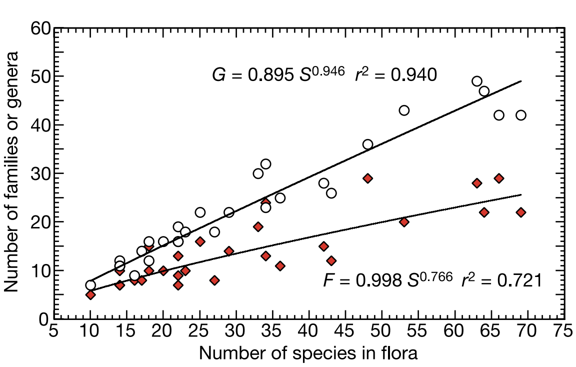

Figure 3 Relationship between the number of species and higher taxa across 28 local palaeoflora sites ranging from 4.5 to 45 Myr ago. Each point represents a single sampling locality (see ref. 10 and Supplementary Information). Open circles, the number of genera for a given number of species; filled diamonds, the number of families per species. Species richness at individual sites ranges from 10 to 69.

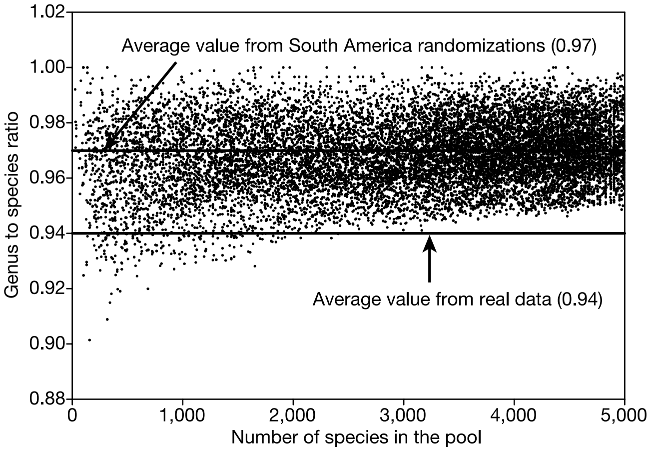

Figure 4 Relationship between species pool size and the results of randomization experiments using the total number of sampled sites from South America. The expected exponent describing the number of genera per species is relatively constant above a small pool size; and, except for the smallest pool sizes, it is consistently greater than the observed exponent. These results indicate that fewer genera (and families) comprise real world communities than would be expected by chance and that this result is largely independent of species pool size.

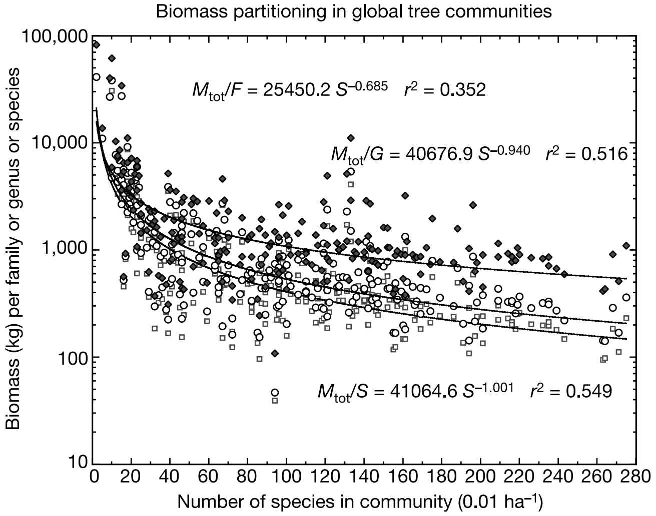

Figure 5 Biomass partitioning between species (open squares), genera (open circles), and families (filled diamonds) across global woody plant communities. The fitted inverse power-functions indicate a decrease in biomass per taxon with increasing richness. Although the relationships are statistically significant, patterns of residual variation indicate potential influences of other environmental and/or historical features on community biomass partitioning. $M_{\rm tot}$, total standing aboveground dry biomass.

change in the amount of biomass contained within a given taxon. Thus, within a given community, the amount of biomass partitioned per family, $M_{\rm tot}/F$, decreases with increasing species richness, where $M_{\rm tot}/F \propto S^0/S^{0.683} \propto S^{-0.683}$. Similarly, the amount of local community biomass partitioned per genus and species must decrease as $M_{\rm tot}/G = S^{-0.94}$ and $M_{\rm tot}/S = S^{-1.0}$ respectively (Fig. 5).

Our results suggest that ecological communities have phylogenetic structure[11], reflected in the fact that general taxonomic and biomass partitioning functions describe species richness in woody plant communities. The presence of a power-function probably identifies the hierarchical and self-similar nature of phylogenetic diversification across a pool of species as reflected by systematic rankings[2] (see also ref. 16). We have used these empirical observations as a functional baseline by which to test null models of local composition and the importance of dispersal syndromes and biotic interactions.

The presence of a similar power-function that accounts for over 90% of the variation in taxonomic structure across contemporary and fossil woody plant communities suggests that the processes that promote and/or limit ecological similarity within communities (1) operate in a regular manner across broad geographical gradients, (2) reflect the ecological and evolutionary processes that dictate local composition, (3) uniquely quantify their net influence on community taxonomic structure, and (4) have probably operated in a consistent fashion across woody plant communities for millions of years. Our conclusions do not eliminate important roles for environment, history and other factors in shaping regional floras composed of many local communities, but they do suggest that these features are secondary in their influence on the patterns of local species coexistence. ☐

Methods

Data analysis

We analysed plant community data from a global data set collected by A.H. Gentry[9,10]. The Gentry data set is remarkable in its coverage and uniform standardization. The data set includes 227 sites across six continents of tropical and temperate, closed canopy, forest communities ranging between 60.4° N to 40.43° S latitudes and elevations between 20 m and 3,050 m. Within each site, all plants with stem diameters of 2.5 cm at breast height (d.b.h.), including lianas, were sampled along ten 2 m × 50 m transects, totalling 0.1 ha at each site. Across sites, species diversity and number of individuals ranged between 2 and 275 and 52 and 1,005, respectively. The complete data set contains a total of 83,121 individual plants. Because the sample area is constant and the number of individuals per plot is approximately constant (see ref. 20), concerns related to sampling biases caused by differences in sample size or numbers of individuals are not important. Additional information is available through http://www.mobot.org/MOBOT/Research/gentry/transect.shtml. To test whether patterns observed in extant woody plant communities are consistent with those observed in geologic time, we compiled a similar database summarizing 29 floral samples ranging from 4.5 to 45 Myr ago from western North America (see Supplementary Information).

Statistical analysis

We first reassigned species randomly with equal sampling probabilities and with replacement to communities 1,000 times from a species pool composed of species from the world, eastern and western hemispheres, and individual continents. The number of species at each site was held constant. The log number of higher taxa was then regressed against the log number of species, just as in the original analysis. To preserve biological reality and to facilitate comparisons with the ratios from individual sites, the intercepts of the regressions were constrained to equal 0 ([1,1] in arithmetic space). In all but one case, the resulting average simulated exponents are larger than that observed in the real data (see Table 1 of the Supplementary Information). Only in the family-level analysis for Europe, where the sample size is extremely small ($n = 5$), was the average randomized exponent larger than the observed exponent at $P = 0.05$. Second, for South America we used a slightly more sensitive test by examining the ratios of the log number of higher taxa to the log number of species at individual sites. Specifics on this second test are listed in the Supplementary Information.

We also tested the effect of changing species pool size at individual sites in the South American data. This tests the effect of geographic scale on the taxonomic structure of the randomized communities. To quantify the effects of random reassignment and the size of the species pool, richness at each site was held constant, while the pool from which the species were drawn was increased sequentially by adding species from the next nearest sites, starting with only the nearest sites and working toward all sites on the continent. Again, species were drawn with equal probabilities within each spatial scale. Nearest-site distance, D, was calculated using a nearest euclidean neighbour distance algorithm: $D_{ij} = [(X_j - X_i)^2 + (Y_j - Y_i)^2]^{1/2}$ where X and Y represent the latitude and longitude of each site, i to j, respectively. Although the variance was influenced at extremely small pool sizes (that is, less than 500 species), that impact diminished quickly with pools composed of species from more than about 5–10 sites. We note that pool size is also an approximate measure of increasing geographic distance. The estimates of the exponents produced by the second analysis are plotted against the size of the species pool (Fig. 4). The result displays a curvilinear relationship between the randomized exponent and the size of the species pool but only at the smallest species pools.

Calculation of community and taxonomic biomass

We used empirical data reported in the literature from representative communities growing in latitudes and elevations equivalent to those communities in the Gentry data set to estimate above ground dry biomass from d.b.h. Biomass values are the same as those reported in ref. 28.

Received 18 December 2001; accepted 5 August 2002; doi:10.1038/nature01069.

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Supplementary Information accompanies the paper on *Nature*'s website (➧ **http://www.nature.com/nature**).

Acknowledgements We thank J. H. Brown, S. Collins, R. Colwell, M. J. Donoghue, N. J. Gotelli, D. Post, S. P. Hubbell, C. J. Humphries, W. P. Maddison, K. J. Niklas, N. Pittman, F. A. Smith, M. Weiser, J. Williams, R. Whittaker and the members of the NCEAS Body Size Working Group and Phylogenies and Community Ecology Working Group for critical discussions and/or comments on earlier drafts. In particular, C. O. Webb provided valuable comments. This work stems in part from the Body Size in Ecology and Evolution Working Group (F.A. Smith, Principal Investigator) sponsored by The National Center for Ecological Analysis and Synthesis (NCEAS, a national centre funded by the NSF, the University of California Santa Barbara and the State of California). B.J.E. was supported by the NSF and NCEAS. J.P.H. was supported by a student internship from NCEAS. Computer resources for the simulations were provided by the UNM Department of Biology, Sevilleta Long Term Ecological Research site and NCEAS.

Competing interests statement The authors declare that they have no competing financial interests.

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Genetic similarity between mates and extra-pair parentage in three species of shorebirds

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Matings between close relatives often reduce the fitness of offspring, probably because homozygosity leads to the expression of recessive deleterious alleles[1–5]. Studies of several animals have shown that reproductive success is lower when genetic similarity between parents is high[4–7], and that survival and other measures of fitness increase with individual levels of genetic diversity[8–11]. These studies indicate that natural selection may favour the avoidance of matings with genetically similar individuals. But constraints on social mate choice, such as a lack of alternatives, can lead to pairing with genetically similar mates. In such cases, it has been suggested that females may seek extra-pair copulations with less related males[4], but the evidence is weak or lacking[4,5]. Here we report a strong positive relationship between the genetic similarity of social pair members and the occurrence of extra-pair paternity and maternity ('quasi-parasitism') in three species of shorebirds. We propose that extra-pair parentage may represent adaptive behavioural strategies to avoid the negative effects of pairing with a genetically similar mate.

Molecular studies of socially monogamous birds have shown that broods often contain offspring that are not related to one of the parents tending the nest[12]. Extra-pair fertilizations can result from females engaging in copulations with extra-pair males (extra-pair paternity; EPP), or from males copulating with extra-pair females that lay their eggs in the male's nest (quasi-parasitism; QP). Generally, EPP is common in passerines (songbirds) and, although other hypotheses cannot be discarded, it may be explained by females seeking 'good genes' for their offspring[12,13]. In contrast, EPP is less common in non-passerine birds[14], in which its adaptive significance remains unexplained. QP is rare among birds and poorly understood[15]. Here we propose an adaptive explanation for the occurrence of EPP and QP in non-passerine birds and show that it is over-represented in pairs with genetically similar mates.

We examined genetic parentage in western sandpipers *Calidris mauri*, common sandpipers *Actitis hypoleuca* and Kentish plovers *Charadrius alexandrinus*. Multilocus DNA fingerprinting identified low rates of EPP in these birds (Table 1), comparable to those found in most other shorebirds (ref. 16, and references therein). In contrast to previous studies, however, we also found evidence for QP in two of the species examined (Table 1). Thus, our study species are predominantly genetically monogamous, with alternative reproductive behaviours occurring at low frequencies.

The females laying the quasi-parasitic eggs may have been either mated (and thus were having extra-pair copulations) or unmated (floaters). Because we did not identify extra-pair parents in our study, we do not have evidence that can directly separate these two possibilities. If quasi-parasites were mated, however, we would expect their parasitic eggs to be fathered by their social mate (unless those females have extreme control over paternity). Given the low rate of EPP and the lack of intraspecific brood parasitism (only two cases documented in the Kentish plover; C.K., unpublished data), it seems more likely that the quasi-parasites were floaters. Observations suggest that female floaters are present in the common sandpiper (M.A., unpublished data), but information for the other species is lacking. In all cases of QP the clutch sizes were not increased, suggesting that the parasitic female (or the receiving

Table 1 **Frequency of extra-pair fertilizations in three species of shorebirds determined by DNA fingerprinting**

Species	Number of broods (number of chicks)	EPFs % (*n*)	EPP % (*n*)	QP % (*n*)
Kentish plover	65	4.6 (3)	1.5 (1)	3.1 (2)
	(170)	2.9 (5)*	0.6 (1)	1.2 (2)
Western sandpiper	25	8.0 (2)	8.0 (2)	0 (0)
	(61)	6.6 (4)	6.6 (4)	0 (0)
Common sandpiper	15	20.0 (3)	6.7 (1)	13.3 (2)
	(53)	7.5 (4)	1.8 (1)	5.7 (3)

Only broods where both putative parents were fingerprinted are included. EPF, extra-pair fertilization; EPP, extra-pair paternity; QP, quasi-parasitism.
*Two EPF chicks could not be classified as EPP or QP owing to high band-sharing between pair members.