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Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality

Robert E. Ricklefs^{1*} and Susanne S. Renner²

Patterns of species richness and relative abundance at some scales cannot be distinguished from predictions of null models, including zero-sum neutral models of population change and random speciation-extinction models of evolutionary diversification. Both models predict that species richness or population abundance produced by independent iterations of the same processes in different regions should be uncorrelated. We find instead that the number of species and individuals in families of trees in forest plots are strongly correlated across Southeast Asia, Africa, and tropical America. These correlations imply that deterministic processes influenced by evolutionarily conservative family-level traits constrain the number of confamilial tree species and individuals that can be supported in regional species pools and local assemblages in humid tropical forests.

Discussion of patterns in biodiversity and population size has been heightened during the past two decades by insights gained from the properties of random birth-death processes. Applied to species diversification within evolutionary clades, a particular random speciation and extinction process can produce a wide range in species richness, with a preponderance of small clades and a few large ones (1). Random births and deaths of individuals (ecological drift)

result in a similar distribution of the sizes of species populations (2), mimicking the effect of genetic drift on the frequency of neutral alleles within populations. In random birth-death models, each replication of the process over time is independent, and so the outcomes of separate iterations are uncorrelated. Pitman *et al.* (3, 4) used this logic to test for any correspondence in the number of species and individuals in tree families between terre firma tropical forests in Peru and Ecuador, following the earlier insight of Alwyn Gentry concerning what he called “family-level niches” (5). Although the two sites exhibited strong positive correlations, seemingly rejecting random models of diversification and population growth, shared history and ongoing

migration might have substantially homogenized these floras over the 1400 km separating the sites across the upper Amazon basin (SOM text).

Although floras within continents may lack independence, global comparisons between areas separated by tens of millions of years of independent evolutionary diversification allow valid tests of neutral theory, which assumes that random processes predominate in ecology and evolution (5). In one such comparison, regional floras in Ecuador, Madagascar, and Malaysia exhibited strong correlations (correlation coefficient $r = 0.65$ to 0.81) between the number of genera per order of flowering plants (Angiospermae) (6). Parallel correlations between temperate regional floras in eastern North America and eastern Asia were equally compelling. This result implies taxon-specific variation in either the propensity of these clades to diversify or in the capacity of the environment to support genera within each order.

The 25- to 52-ha plots established at several sites around the world and associated with the Center for Tropical Forest Science (CTFS) (www.ctfs.si.edu) now provide detailed information on species richness and local relative abundance of trees within family-level taxa (7). We compared the number of species and individuals in shared families between seven plots in three regions (Fig. 1 and Table 1) to test the prediction from neutral theory of random diversification and population change that diversity and abundance should be uncorrelated between independently evolved floras (8).

The number of families currently recognized by the Angiosperm Phylogeny Group (APG III) (9, 10) and represented by tree-sized species [>10 -cm diameter at breast height (dbh)] on the CTFS forest plots varied from 47 (Korup, Cameroon)

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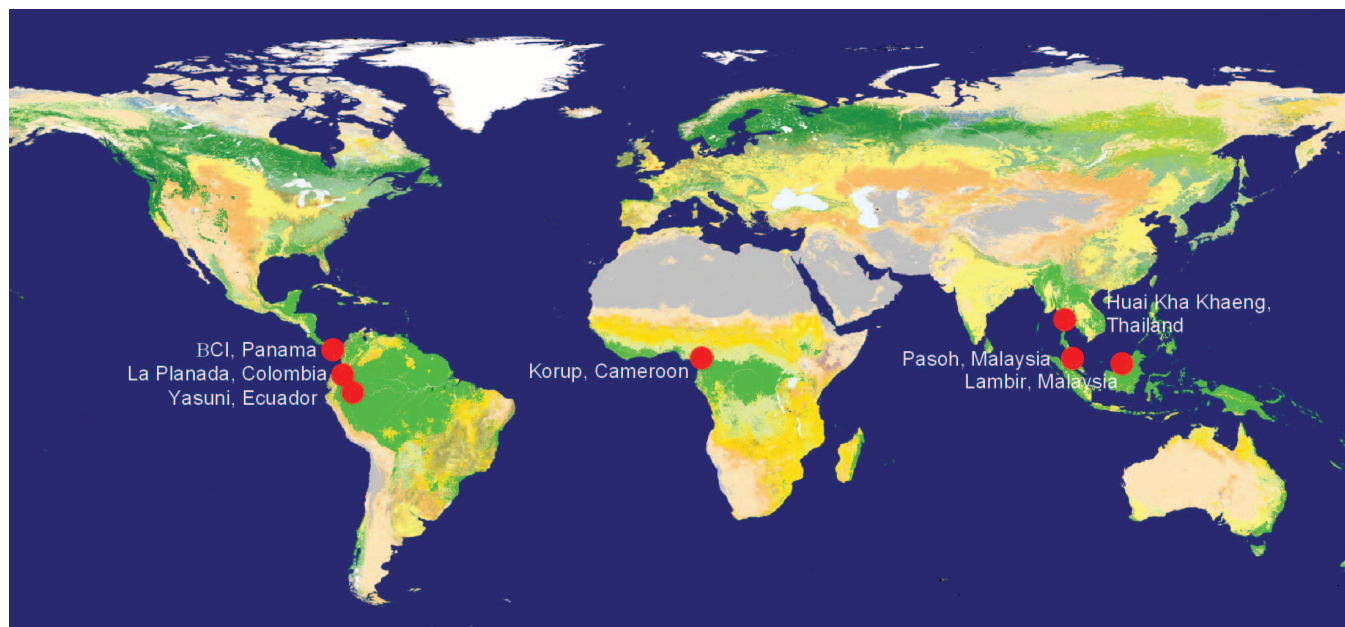


Fig. 1. Location of seven CTFS forest plots. The distribution of tropical rainforest is indicated in bright green within tropical latitudes. BCI, Barro Colorado Island. Base map from http://eoimages.gsfc.nasa.gov/images/news/NasaNews/ReleaseImages/LCC/Images/lcc_global_2048.jpg.

to 76 (Lambir, Malaysia). The number of families shared between plots varied from 29 to 59 (27 to 44 in between-region comparisons; i.e., South America, Africa, Southeast Asia). Few genera are shared between plots in different regions, consistent with the independence of species diversification between regions (SOM text). For example, the plots at Yasuni, Ecuador, and Pasoh, Malaysia, share 44 of their 65 (68%) and 76 (58%) families, respectively, but only 35 of their 296 (11.8%) and 259 (13.5%) genera.

Time-calibrated molecular phylogenetic reconstructions available for some families emphasize the distant connections between and the general independence of the tree floras of the three floristic regions included in this study. For example, species in the families Annonaceae, Lauraceae, Meliaceae, and Myrtaceae occurring at Yasuni, Ecuador, and Pasoh, Malaysia, have most recent common ancestors no younger than the early Oligocene, ~30 million years ago, and mostly older (SOM text). Because the ancestors of the

species in Malaysia and Ecuador mostly coalesce within each of the regions, with connections within families between the regions being older, the predicted correlation in the species richness of families between the regions under neutral theory is essentially zero.

Spearman rank correlation coefficients (r_s) between the number of species per family recorded in the seven ~50-ha plots are all significant, and many of them are quite high ($r_s > 0.60$, $P < 0.0001$) (Figs. 2 and 3 and table S1). Correlations between sites in the Neotropics and Southeast Asia (all but one $r_s > 0.60$) even approach those within floristic regions, where dispersal tends to homogenize local floras, and many more genera are shared between sites [for instance, 177 genera out of 259 (68%) and 261 (68%), respectively, and many species, between Pasoh and Lambir, Malaysia]. With respect to the numbers of individuals per family, the correlations within Southeast Asia and within the Neotropics are significant (r_s , $P < 0.01$); the correlations between Southeast Asia and the Neotropics also are significant (r_s , $P < 0.05$); and the correlations between these two regions and the African site are weaker, although most are significant. All are positive; none remotely approach zero.

Correlations of number of species per taxon also are strong above the family level within angiosperm orders, but not below the family level within genera. For example, between Yasuni, Ecuador, and Pasoh, Malaysia, the numbers of species are highly correlated among the 19 shared orders ($r_s = 0.86$), but not among the 35 shared genera ($r_s = 0.037$). In general, the number of species per genus is correlated within regions (six comparisons, all $r_s > 0.39$, $n > 44$ genera, $P < 0.001$), but not between regions (15 comparisons, all $r_s < 0.31$, $n < 35$ genera, $P > 0.05$), which is suggestive of the homogenizing effect of shared ancestry and dispersal within regions and further emphasizes the independence of floras between regions.

Representation of families within regions over time appears to be conservative, also contradicting the predictions of neutral theory (11). The most abundant families identified from the Paleocene Cerrejón megafossil flora of northern Colombia (12) are among the most abundant families in present-day Neotropical rainforests, a point also emphasized by Wing *et al.* (12). For example, 25 of 33 Cerrejón macrofossils assignable to modern families are referable to the 15 most species-rich of 76 families in the contemporary Yasuni flora (likelihood ratio $G = 30.7$, $P < 10^{-6}$); the numbers of species per family in the Paleocene and modern floras, separated by ~58 million years, are significantly correlated ($r_s = 0.45$, $P < 0.0001$) (Fig. 4).

Our analyses show that the number of species, as well as the total number of individuals, per family of trees in tropical forests is conserved across floristic regions widely separated in space and time on the globe and across tens of millions of years within the same region. This

Table 1. Attributes of the seven CFS forest plots. Data are from www.ctfs.si.edu. Negative latitudes are south of the equator; negative longitudes are west of the Greenwich Meridian. Lat, latitude; Long, longitude; Fam, number of families; Spp, number of species; Inds, number of individuals.

Location	Lat (°)	Long (°)	Elevation (m)	Plot size (ha)	Fam	Spp	Inds (>10-cm dbh)
Yasuni, Ecuador	-0.69	-76.40	215–245	50	65	846	17017
La Planada, Colombia	1.16	-77.99	1796–1891	25	50	179	14620
Barro Colorado Island, Panama	9.15	-79.85	120–160	50	53	251	21051
Korup, Cameroon	5.07	8.85	700–850	40*	47	281	24188
Pasoh, Malaysia	2.98	102.31	70–90	50	73	700	27955
Lambir, Malaysia	4.19	114.02	104–244	52	76	1009	31465
Huai Kha Khaeng, Thailand	15.63	99.22	549–638	50	55	247	21524

*Four 10-ha plots.

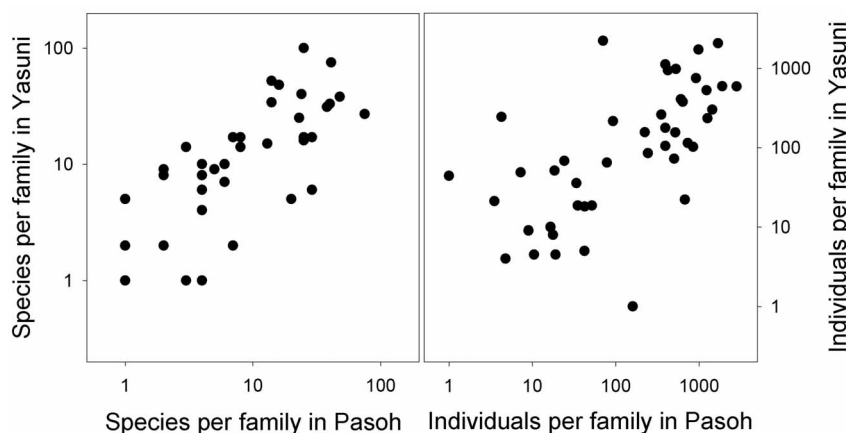


Fig. 2. Relation between the number of species per family and the number of individuals per family in Pasoh, Malaysia, and Yasuni, Ecuador. Correlation coefficients are Spearman (rank) values.

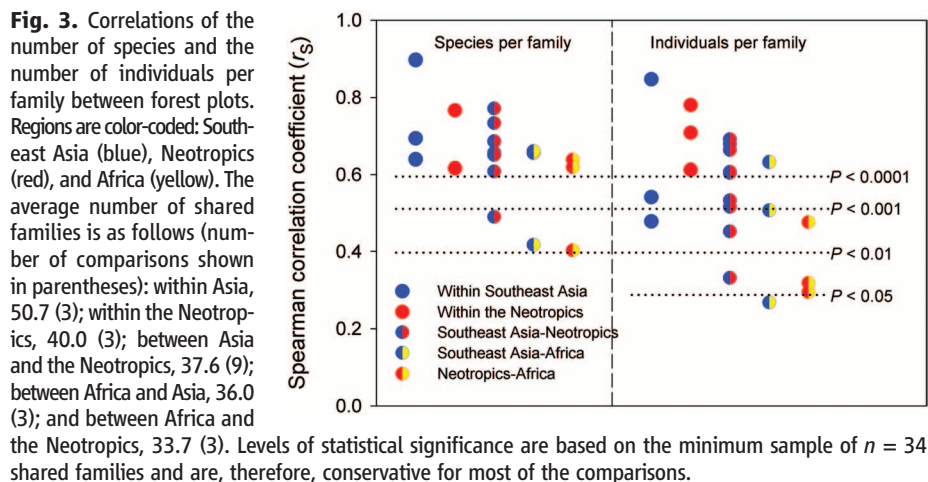


Fig. 3. Correlations of the number of species and the number of individuals per family between forest plots. Regions are color-coded: Southeast Asia (blue), Neotropics (red), and Africa (yellow). The average number of shared families is as follows (number of comparisons shown in parentheses): within Asia, 50.7 (3); within the Neotropics, 40.0 (3); between Asia and the Neotropics, 37.6 (9); between Africa and Asia, 36.0 (3); and between Africa and the Neotropics, 33.7 (3). Levels of statistical significance are based on the minimum sample of $n = 34$ shared families and are, therefore, conservative for most of the comparisons.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6067/464/DC1
Materials and Methods
SOM Text
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Heavy Livestock Grazing Promotes Locust Outbreaks by Lowering Plant Nitrogen Content

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Current paradigms generally assume that increased plant nitrogen (N) should enhance herbivore performance by relieving protein limitation, increasing herbivorous insect populations. We show, in contrast to this scenario, that host plant N enrichment and high-protein artificial diets decreased the size and viability of *Oedaleus asiaticus*, a dominant locust of north Asian grasslands. This locust preferred plants with low N content and artificial diets with low protein and high carbohydrate content. Plant N content was lowest and locust abundance highest in heavily livestock-grazed fields where soils were N-depleted, likely due to enhanced erosion. These results suggest that heavy livestock grazing and consequent steppe degradation in the Eurasian grassland promote outbreaks of this locust by reducing plant protein content.

Plant nitrogen (N) content has long been linked to the performance and dynamics of herbivorous insects (1). Most nitrogen in plants is in the form of protein, and current paradigms generally assume that increased plant N content will enhance herbivore performance by relieving any constraints on growth and reproduction due to limitations of available protein (2). Because plants in many terrestrial ecosystems are N-limited (3), it is often assumed that primary consumers would be as well (2). However, studies performed on the basis of the geometric framework (4) have shown that many animals have specific dietary intake targets for protein, carbohydrates, and other nutrients. Interestingly, such studies have found that excess protein decreased life span in fruit flies (5) and that herbivores and omnivores (including humans) will overeat carbohydrates but are unlikely to overeat protein (6). Thus, animals may sometimes be impaired by

ingesting excess protein (7). Indeed, the Australian plague locust, *Chortoicetes terminifera* (Acrididae: *Oedipodinae*), grew slowly on one host plant because it obtained excess protein relative to carbohydrate (8). Given that humans have substantially altered ecosystem N cycling through fossil fuel combustion, agricultural fertilizer application (9), and domesticated animal production (10), they may also affect insect dynamics in unexpected ways by altering plant nitrogen supplies. Understanding these anthropogenic impacts is critical to developing sustainable land management practices that minimize economically damaging insect outbreaks.

Oedaleus asiaticus (Acrididae: *Oedipodinae*) is a nonmodel [e.g., (11)], economically damaging locust of the north Asian steppe (12, 13), part of the largest grasslands in the world (Fig. 1A). We examined the effects of increases in the N content of host plants due to fertilization inputs of 175 kg N ha⁻¹ year⁻¹ on growth and viability of this locust in both laboratory and field cage experiments (14). This level of N addition is similar to the fertilization rates of most crops (15). We then used artificial diets varying in their protein:carbohydrate ratio to assess effects on dietary preference and growth rates.

In contrast to the existing paradigm of limitation of insects by low content of plant protein, our results show that N fertilization and high-protein artificial diets can have consistent negative effects on the performance of the locust. Survival decreased strongly with N fertilization in the field (Fig. 1B). The decreased survival of *O. asiaticus* in N-fertilized field plots could have been due to many possible consequences of fertilization, such as changes in plant structure or chemical content, species composition, predators, or microclimate. However, results from lab experiments that controlled for these factors indicated that growth rate, size, and development rate were all reduced when locusts were fed N-fertilized plants (Fig. 1C), indicating that the field survival results were due to effects associated with plant N status. Furthermore, when offered complementary artificial diets [e.g., (16)], locusts selectively consumed a protein:carbohydrate ratio of 0.5, which most correlated with maximal survival (Fig. 1, D and E). Performance (growth rate × survival) was significantly reduced when locusts were confined to artificial diets with a protein:carbohydrate ratio above 1:1 (Fig. 1E), consistent with the hypothesis that the mechanism by which N fertilization reduces survival of this locust in the field is elevation of plant protein content.

In addition, plant N content was closely associated with the relative amounts of different food plants consumed when locusts were offered a palette of the six most common local plants collected from unfertilized plots (five grasses and one sedge) (Fig. 2A). Indeed, contrary to expectations from protein-limitation paradigms, *Stipa grandis*, the grass with the lowest N content, was the most highly consumed over 36 hours [a period long enough for locusts to take multiple meals and regulate nutrient intake on the basis of internal conditions (17)]. Direct behavioral observations confirm that low-N *S. grandis* was the most highly consumed plant under field conditions (18).

We compared food selection over 8 hours between N-fertilized and unfertilized *S. grandis*, using dried, ground leaves to control for toughness and water content (8, 19). Locusts strongly favored unfertilized *S. grandis* leaves over *S. grandis*

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