Analyzing Tropical Forest Tree Species Abundance Distributions Using a Nonneutral Model and through Approximate Bayesian Inference

Franck Jabot[1,2],* and Jérôme Chave[1]

1. Laboratoire Evolution et Diversité Biologique, Centre National de la Recherche Scientifique, Université Paul Sabatier, Bâtiment 4R3, 31062 Toulouse, Cedex 4, France;   2. AgroParisTech, École Nationale de Génie Rural des Eaux et des Forêts (ENGREF), 19 avenue du Maine, 75732 Paris, France

abstract: The neutral theory of biodiversity challenges the classical niche-based view of ecological communities, where species attributes and environmental conditions jointly determine community composition. Functional equivalence among species, as assumed by neutral ecological theory, has been recurrently falsified, yet many patterns of tropical tree communities appear consistent with neutral predictions. This may mean that neutral theory is a good first-approximation theory or that species abundance data sets contain too little information to reject neutrality. Here we present a simple test of neutrality based on species abundance distributions in ecological communities. Based on this test, we show that deviations from neutrality are more frequent than previously thought in tropical forest trees, especially at small spatial scales. We then develop a nonneutral model that generalizes Hubbell's dispersal-limited neutral model in a simple way by including one additional parameter of frequency dependence. We also develop a statistical method to infer the parameters of this model from empirical data by approximate Bayesian computation. In more than half of the permanent tree plots, we show that our new model fits the data better than does the neutral model. Finally, we discuss whether observed deviations from neutrality may be interpreted as the signature of environmental filtering on tropical tree species abundance distributions.

Keywords: neutral theory, environmental filtering, community modeling, approximate Bayesian computation.

Introduction

The processes that govern the assembly and functioning of ecological communities are varied and complex (Chesson 2000; Chase and Leibold 2003). They include species interactions (MacArthur 1972; Diamond 1975; Tilman 1982); dispersal limitation, that is, the inability of an or-

* Corresponding author; e-mail: franck.jabot@m4x.org.

ganism to disperse or send offspring to a remote locale (MacArthur and Wilson 1967; Clobert et al. 2001); and environmental filtering. Environmental filtering refers to the fact that individuals immigrating into a community will be able to establish only if they pass through the various environmental filters present in this community (Mueller-Dombois and Ellenberg 1974; Zobel 1997; Keddy 1992). These filters may include abiotic stresses and biotic pressures such as herbivory (Hillebrand et al. 2007).

Modeling the dynamics of ecological communities is difficult due to the inherently complex dynamics of interacting species (Lawton 1999; but see Simberloff 2004), and for this reason, progress toward integrated community dynamics models has been slow. One radical step toward the construction of a simple and tractable community model is Hubbell's theory of biodiversity (Hubbell 2001; Bell 2003). This theory is radical in assuming that all individuals have the same prospects of reproduction and death irrespective of their age and size and of the species they belong to. Hubbell (2001) considered that in a local community, individuals experience random events of death and recruitment irrespective of the species, so that community size remains constant. Hence, the species composition fluctuates due to stochastic drift only. In addition, Hubbell (2001) assumed that this local community is connected to a regional pool via migration, so that a fraction m of recruits is drawn from the regional pool rather than from local offspring. The local community hence reaches a dynamic equilibrium between stochastic local extinction and the immigration of new species, while in the regional pool, diversity is maintained by speciation. This speciation is modeled at the individual level simply by assuming that each new recruit has a small probability ν of yielding a new species, so that θ new species appear in the system on average per generation (where $\theta = \nu \times J_M$ with J_M the

number of individuals in the regional pool). This parameter θ can be estimated from species abundance data following a procedure first described by Hubbell (2001) and formalized by Etienne (2005). A more detailed description of Hubbell's model is provided in "Nonneutral Model."

Hubbell's model offers a number of advantages compared to previous theoretical models of community dynamics. First, it addresses whether the neutral approximation is sufficient to explain empirical patterns such as species abundance distributions or species-area relationships (McGill et al. 2006). Hence, the neutral model may serve as a null model of community structure and dynamics (Leigh 2007). Second, Hubbell's model offers a simple way to incorporate basic features of metacommunity dynamics (Holyoak et al. 2005). Third, it is also "tractable" in the sense that a mathematical analysis of the model enables an exact computation of the expected species abundance distribution (Vallade and Houchmandzadeh 2003; Volkov et al. 2003) and, even more remarkably, of a sampling formula $P(\{n_i\} \mid \{p_j\})$, the probability of a given species abundance distribution $\{n_i\}$ in a sample, given the model parameters $\{p_j\}$ (Etienne 2005; Etienne and Alonso 2005). Through this formula, ecologists may infer the two parameters θ and m of Hubbell's neutral model from species abundance data based on likelihood maximization.

With Hubbell's neutral model and its associated method of statistical inference, it has been possible to move beyond qualitative comparisons of models of species coexistence (Chave et al. 2002). It has also facilitated discussions on issues that have traditionally remained outside of the realm of classical community ecology. For instance, Latimer et al. (2005) explained the diversity patterns in the South African fynbos by the high diversification rate (high θ) and the dispersal characteristics (low m) of the plants of this biome; Jabot and Chave (2009) showed that empirical phylogenetic tree shapes could be used to better infer the neutral parameters. But the real strength of this inferential framework is to make possible a direct quantitative comparison between neutral models and nonneutral ones [q1] (Etienne and Olff 2005; Chave et al. 2006). In this regard, Hubbell's neutral model should be seen as the first step toward more complex models that encapsulate more biology, and several authors have proposed such extensions (Tilman 2004; Gravel et al. 2006; Adler et al. 2007). Yet it is critical to realize that while the goodness of fit of the neutral model may be estimated, more complex models are not so easily compared against empirical data. For instance, Volkov et al. (2005) extended the neutral model to account for negative density-dependent effects, but this came at the cost of ignoring dispersal limitation, an integral feature of Hubbell's model. Moreover, the likelihoods of alternative models were not compared, as is customary in model comparison procedures (Chave et al. 2006). Thus, in spite of the already large literature on this topic, nonneutral dynamic community models that could be quantitatively fitted to species abundance data are sorely lacking (but see Engen et al. 2002).

Before constructing complex nonneutral models, an important step is to check whether neutrality may be rejected using a quantitative test for the system under study. Here, we propose a novel test of neutrality based on species abundance, inspired by Watterson's homozygosity test in population genetics (Watterson 1978). We then present a nonneutral dynamical model that generalizes Hubbell's two-parameter dispersal-limited neutral model by adding a nonneutral parameter δ. The δ parameter quantifies the degree of conspecific frequency dependence in mortality rates. This new parameter is then inferred from species abundance distributions using an approximate Bayesian computation (ABC) method (Beaumont et al. 2002; Jabot and Chave 2009). Applying these two methods to empirical species abundance data from permanent tropical forest tree plots, we explore whether and how frequently a significant deviation from neutrality is detected. We also explore which ecological mechanisms are consistent with the observed deviation from neutrality and how this deviation depends on the spatial extent of the plots. Finally we discuss the biological and theoretical implications of our findings. The programs described in this article can be freely downloaded at http://www.edb.ups-tlse.fr/equipe1/chave/parthy.htm. [q2]

Benchmark Data

The methods developed below were benchmarked against two empirical rain forest tree diversity data sets. Both data sets are maintained by the Smithsonian Tropical Research Institute Center for Tropical Forest Science (CTFS; Losos and Leigh 2004; Condit et al. 2002, 2006).

The first data set consists of 10 large tropical tree plots of the CTFS (20–52 ha in area) with a worldwide distribution (table 1; data from Condit et al. 2006, supplementary information). In each plot, trees greater than 10 cm diameter at breast height were tagged, mapped, and identified as to species. For one of these large plots, Barro Colorado Island (BCI), Panama, we also had access to the abundance data in the 50 1-ha subplots (data from Condit et al. 2002, supplementary information). In one analysis reported below, we studied how neutrality varied with spatial scale. We performed this test using the BCI data set by assembling the 1-ha plots into larger subplots of 4 and 10 ha.

The second data set contains 50 plots between 0.36 and 1 ha in size that were established across the Panama Canal Zone (which extends between the Pacific and the Atlantic

Table 1: Neutrality test in the large plots (20–52 ha, including all trees >10 cm in trunk diameter) of the Smithsonian Tropical Research Institute Center for Tropical Forest Science

Location, site	Area (ha)	J	S	H	δ	P value
Panama:						
BCI (1982)	50	20,788	236	4.29	.06	.103
BCI (1985)	50	20,640	235	4.28	.09	.095
BCI (1990)	50	21,176	227	4.27	.04	.097
BCI (1995)	50	21,404	225	4.26	.04	.107
BCI (2000)	50	21,148	225	4.26	.07	.083
Ecuador:						
Yasuni	50	16,804	828	5.47	.40	**<.001**
Colombia:						
La Planada	25	14,103	167	3.98	.03	.37
Dem. Rep. Congo:						
Edoro	20	8,684	208	3.67	.56	**<.001**
Lenda	20	7,107	212	2.71	.80	**<.001**
India:						
Mudumala (1988)	50	15,033	62	2.51	.33	.089
Mudumalai (1992)	50	14,028	63	2.47	.40	.062
Mudumalai (1996)	50	13,070	63	2.39	.46	**.04**
Sri Lanka:						
Sinharaja	25	16,838	171	3.83	.19	.224
Thailand:						
Huai Kha Khaeng	50	21,446	240	3.80	.45	**.001**
Malaysia:						
Pasoh (1987)	50	26,550	678	5.65	−.10	.273
Pasoh (1990)	50	27,659	666	5.65	−.17	.382
Pasoh (1995)	50	29,257	674	5.66	−.16	.379
Lambir	52	29,890	990	5.94	.05	**<.001**

Note: J is the total number of trees in the census, S the number of species, H the empirical evenness, δ the value of the nonneutral parameter as inferred by the approximate Bayesian computation method (see main text), and P value the significance of the neutrality test (see main text). Bold numbers indicate P values under .05.

oceans) using the same sampling procedure (Condit et al. 2002, supplementary information; see also Pyke et al. 2001; Engelbrecht et al. 2007). These 50 plots contained a total of 20,231 individuals belonging to 781 tree species (Condit et al. 2002).

Neutrality Test

Methods

Previous neutrality tests based on species abundance distributions have consisted of comparing the neutral fit to the prediction of alternative phenomenological models such as the lognormal distribution (McGill et al. 2006). Such procedures do not evaluate the ability of the neutral model to reproduce observed data: the fact that a neutral model is a better or a worse fit than a lognormal model says little about the ability of both models to reproduce field data satisfactorily. An exception is the test devised by Etienne (2007), which is designed for the particular case where several sampling sites within the same region are available.

Here we build on Watterson's homozygosity test of neutrality in molecular evolution to design such a test (Watterson 1978). We first fitted the neutral parameters θ and m by maximum likelihood based on the entire species abundance distribution (Etienne 2005). Parameter estimation was performed using the freeware TeTame (Jabot et al. 2008, http://www.edb.ups-tlse.fr/equipe1/chave/tetame.htm). These neutral parameters are then used to simulate 1,000 neutral species abundance distributions for each study plot, fixing the numbers J of individuals and S of species to their observed value in any given plot. We use the algorithm of Etienne (2005) to simulate neutral communities and retain only the simulated communities in which the number of species equals S. In each simulated neutral community, we compute Shannon's entropy H (also called evenness), which is defined by
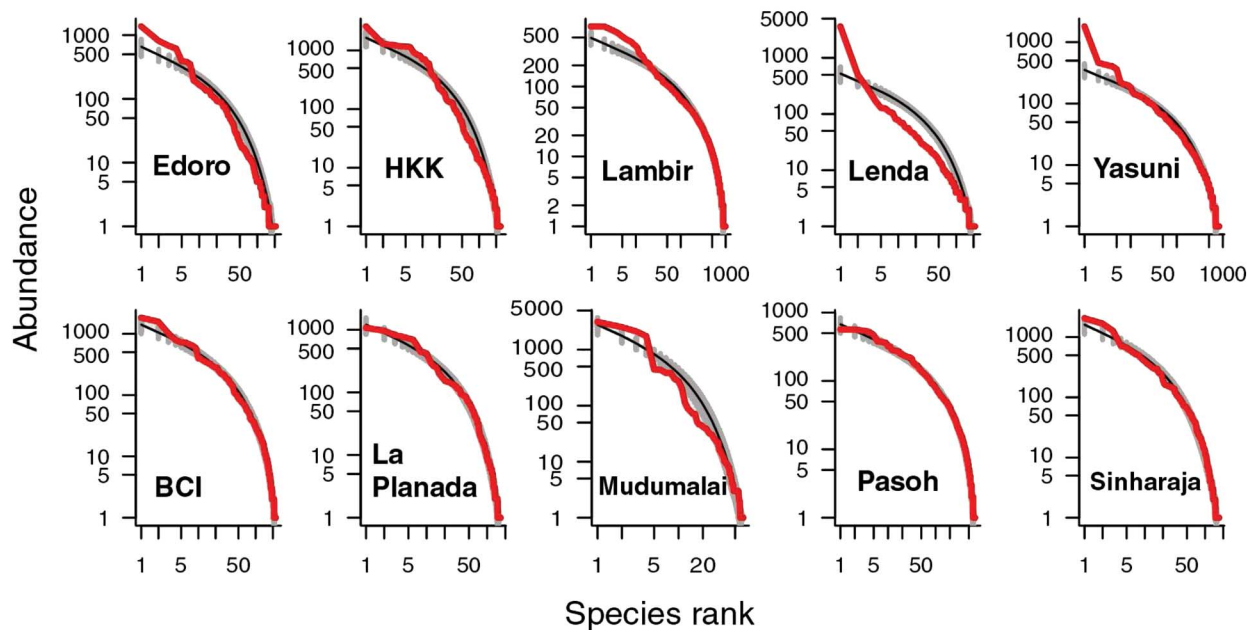
$$H = -\sum_i p_i \ln(p_i). \tag{1}$$

Figure 1: Deviation from neutrality in the Smithsonian Tropical Research Institute Center for Tropical Forest Science plots. The upper five panels deviate significantly from neutrality, while the lower five do not. The black lines represent neutral species rank abundance curves averaged over 1,000 simulations with best-fit neutral parameters (see "Methods"), gray bars indicate standard deviations, and the red lines indicate observed rank abundance curves.

The evenness is bounded by 0 and ln (S). This set of 1,000 values for H computed from communities simulated with Hubbell's neutral model form a null distribution against which the empirical observation may be compared (appendix). If the observed H value falls outside of the null distribution, we conclude that the neutral model is unable to model the shape of the species abundance distribution. This test detects deviations from neutrality since the range of H values found in communities simulated with Hubbell's neutral model is much smaller than [0; ln (S)] (see fig. A1; Jabot and Chave 2009). By constraining the simulated samples to have the same richness S, the test does not assess the ability of the neutral model to reproduce S. This is because any value of S may be obtained by tuning the parameters of a neutral model (Hubbell 2001).

Results

When applied to the large (20–52 ha) plots, our test detected significant deviations from neutrality in half of the plots. In these nonneutral plots, best-fit neutral communities had a significantly higher evenness than the observed value. When several censuses of the same plot were available, the deviations were consistent across years (table 1). In the plots where significant deviations from neutrality

could be detected, a few species were overabundant compared with the neutral expectation (fig. 1). These overabundant species caused a decrease in community evenness that our neutrality test detected. When applied to the network of small (0.36–1 ha) plots, half of the plots were again significantly nonneutral according to our test (table A1).

Finally, we tested whether the spatial size of the plots had an influence on our test of neutrality. In the 50-ha BCI plot, nonneutrality was detected in 36% of the 1-ha subplots, in 30% of the 4-ha subplots, and in 20% of the 10-ha subplots (1 out of 5), while in the full 50-ha BCI plot, the deviation from neutrality was no longer significant.

Nonneutral Model

Model Description

In the previous section we showed that Hubbell's neutral model is unable to fit species abundance data for half of the rain forests data sets that we included in our analysis. This was the primary motivation for building a simple nonneutral extension of Hubbell's model to assess the potential role of one ecological mechanism likely to produce this deviation from neutrality. In Hubbell's neutral model,

one individual dies per time step, and this individual is immediately replaced by an offspring coming from a regional species pool of size J_M (probability m) or from the surviving residents (probability $1 - m$). The probability that species i gains 1 individual while species j loses 1 individual (with $i \neq j$) is given by the state transition

$$P_{ji} = \frac{N_j^{(t)}}{J} \times \left[(1 - m) \frac{N_i^{(t)}}{J - 1} + m\chi_i^{(t)} \right], \qquad (2)$$

where $N_i^{(t)}$ is the abundance of species i at time t, J is the local community size, m is the immigration rate, and $\chi_i^{(t)}$ is the regional relative abundance of species i at time t. In the regional species pool, the dynamics is panmictic and neutral. Individuals die sequentially as in the local community, they are replaced by the offspring of randomly drawn surviving individuals, and the newly recruited individuals belong to an altogether new species with a small probability ν, so that θ new species appear in the system on average per generation. Etienne (2005) derived a likelihood formula based on species abundance data for the parameters θ and m and showed that a more rigorous definition for θ was

$$\theta = \frac{\nu \times (J_M - 1)}{1 - \nu} \approx \nu \times J_M. \qquad (3)$$

Our nonneutral generalization of Hubbell's neutral model is as follows. At each time step, we let an individual from species j die with probability q_j:

$$q_j = \frac{(N_j^{(t)})^{1-\delta}}{\sum_{k=1}^{S} (N_k^{(t)})^{1-\delta}}, \qquad (4)$$

where δ is a new parameter. Here again, a vacant site is immediately filled by the offspring of a randomly chosen individual in the local community (with probability $1 - m$) or from the regional pool (with probability m). Equation (2) is then replaced by

$$P_{ji} = \frac{(N_j^{(t)})^{1-\delta}}{\sum_{k=1}^{S} (N_k^{(t)})^{1-\delta}} \times \left[(1 - m) \frac{N_i^{(t)}}{J - 1} + m\chi_i^{(t)} \right]. \qquad (5)$$

When $\delta = 0$, equations (2) and (5) are equal. For instance, when δ is negative, individuals of abundant species face increased mortality rates compared with individuals of rare species (negative frequency dependence). When δ is positive, individuals of rare species face increased mortality rates compared with those of abundant species (positive frequency dependence).

When nonzero values for δ are selected , the simulated communities may have an evenness H that falls outside the range typically produced by Hubbell's neutral model (fig. A1): with positive values of δ, the evenness will be

lower than in neutral communities, while with negative values it will be higher. This model is nonneutral in a particular sense: species with different abundances have different demographic rates. However, any two species with exactly the same abundance are strictly equivalent demographically. The model is thus symmetric sensu Alonso et al. (2008). A symmetric model is a natural first generalization of Hubbell's model when species-specific data are unavailable (see also Volkov et al. 2005).

Fitting the Nonneutral Model by ABC Inference

Approximate Bayesian computation (Beaumont et al. 2002) is a method of statistical inference that may be used to assess the goodness of fit of even complex models. We use ABC to infer δ from species abundance distributions. Specifically, we simulate a large number of communities with the three model parameters θ, m, and δ drawn from prior distributions. Each simulated community is used to compute a set of two summary statistics—the species richness S and Shannon's entropy H (see Jabot and Chave 2009)—and the quality of the fit is assessed by computing a distance between the summary statistics of the simulated community (S_{sim}, H_{sim}) and that of the empirical data (S_{data}, H_{data}). More precisely, we computed the Euclidean distance d after having normalized each statistics by its variance, as recommended by Beaumont et al. (2002):

$$d = \sqrt{\frac{(S_{sim} - S_{data})^2}{\text{Var}(S_{sim})} + \frac{(H_{sim} - H_{data})^2}{\text{Var}(H_{sim})}}, \qquad (6)$$

where $\text{Var}(S_{sim})$ and $\text{Var}(H_{sim})$ are the variances of S_{sim} and H_{sim} among the simulated communities. Only a fraction of the simulations, the ones closest to the empirical observations, were retained (lowest d values), and the parameters corresponding to these retained simulations were used to compute an approximate posterior distribution for the parameters. Since our goal is to estimate solely the marginal posterior distribution on δ, two summary statistics were found to be sufficient (appendix).

As mentioned above, the ABC method is based on simulating the model for a wide array of parameter values. Further details on the algorithms used in the simulations may be found in the appendix. Here we briefly explain the major steps. To simulate the nonneutral model, we proceed in two steps. First, we simulate by coalescence a large neutral regional species pool of size J_n with neutral parameters $\ln(\theta)$ and $\ln(I)$ drawn from a flat prior on [0; 10], where I is related to m by (Etienne 2005)

$$I = \frac{m \times (J_n - 1)}{1 - m}. \qquad (7)$$

The choice of the prior for $\ln(\theta)$ and $\ln(I)$ is based on

our empirical knowledge of the data and should be reappraised on a case-by-case basis. We henceforth use the scaled immigration rate I instead of m because I has comparable statistical properties to θ (Etienne 2005). We defined prior distributions on $\ln(\theta)$ and $\ln(I)$ instead of θ and I because the summary statistics such as richness and evenness respond to variations in order of magnitudes of θ and I (Hubbell 2001; fig. 1 in Jabot and Chave 2009). The boundaries of the priors were chosen to encompass previously empirically estimated parameter values.

A local community of size J is then drawn from the regional pool, where J is the size of the real sampled community, such that $J_n \gg J$. This local community is used as an initial condition, from which the nonneutral dynamics starts. The nonneutral dynamics cannot be simulated by coalescence, since the symmetry among individuals no longer exists (Ewens 2004). We therefore use a forward-in-time algorithm run until a dynamic equilibrium is reached. For this simulation step, we use a parameter δ drawn from a flat prior distribution on $[-1; 1]$. This prior explores a wide range of situations. When δ equals 1, individuals of abundant species have such a low death probability compared with those of rare species that death rates at the species level are independent of species abundances. When δ equals -1, death rates of individuals of rare species are considerably lower than those of individuals of abundant species. We chose to model nonneutrality during the mortality phase for the sake of simplicity (see also Chave et al. 2002). We also studied a model where frequency dependence is acting at the recruitment phase and obtained similar results.

For each plot of the benchmark data set, we simulated a total of 200,000 communities and retained the 1,000 communities that had the smallest distance d to empirical data (eq. [6]). We then computed the approximate posterior parameters distribution from the distribution of the 1,000 best-match parameters in the parameter space. To smooth the distribution, we used the routine "density" in R, with a bandwidth equal to 0.2 (R Development Core Team 2009). This bandwidth was chosen based on simulated data sets. We then inferred the value of δ from the mode of the marginal posterior δ distribution.

Test of the Method with Simulated Data

To assess the performance of the ABC method, we simulated artificial data sets with known model parameter values and evaluated the ability of our ABC method to recover these parameter values. Since the efficiency of the ABC inference is likely to depend on both sample size J and species richness S in the observed data, we repeated our test of inference efficiency for the different values of empirically observed J and S. For each of the 50 plots, we

recorded the empirical values of J and S. Then, for each (J, S), we simulated 100 communities with different δ values. Using ABC, we then inferred the δ values from each of these 100×50 simulated data sets, and we compared the input δ value to the one inferred in each of the plots (hence yielding 50 different R^2 values). The R^2 values were always greater than 0.55 (median = 0.77) except in one case (where $R^2 = 0.27$) for which J was small and S unusually large (appendix; fig. A2). The slopes of these regressions were close to 1, and the intercept was close to 0 (appendix). We further computed the percentage of simulations in which inferred δ had the same sign as the simulated one: it was always greater than 77% (median = 87%). Similar analyses were performed with (J, S) values corresponding to values in large plots and yielded similar results. Hence, our inference method infers δ with reasonable accuracy from tropical tree species abundance distributions.

Application to the Benchmark Data

We then estimated the parameters of our nonneutral model in the tropical forest tree plots. In all the large plots except in Pasoh, we found positive δ values (table 1). The fit provided by our nonneutral model for the entire species abundance distributions was also more satisfactory than the fit of the neutral model (fig. A3). Similarly, in the 1-ha plots of the Panama Canal watershed, inferred δ values were positive in the majority of the plots (fig. 2A). In the Panama Canal watershed plot network, we also found that δ values were negatively correlated with dry-season rainfall (fig. 2B; $n = 39$, $R^2 = 0.23$, $P = .002$; rainfall data from Pyke et al. 2001). In other terms, drier plots had larger δ values.

We also found that the size of the plots had an influence on measured deviations from neutrality: in the 50-ha BCI plot, the mean posterior distribution of δ was wider in small subplots than in large ones, and its mode decreased toward smaller δ values as plot size increased (fig. 3).

Discussion

Departure from Neutrality in Tropical Rain Forests

Hubbell's (2001) proposal that neutral theory adequately reproduces patterns of species abundance has generated a great deal of controversy (reviewed in McGill et al. 2006; Leigh 2007). Previous tests of neutrality have compared the fit of neutral models to that of alternative phenomenological models such as the lognormal model (McGill et al. 2006). These tests disregard the fact that the neutral model is not always capable of reproducing precisely the observed biodiversity patterns in terms of abundance
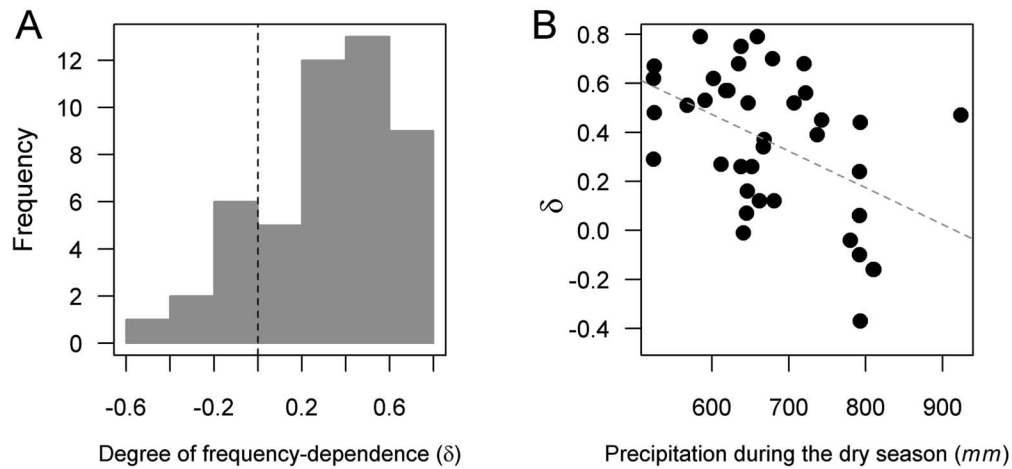
Figure 2: Deviation from neutrality and environmental filtering in the Panama Canal watershed (PCW). *A*, Estimated δ in the PCW tree plots ($n = 50$). Fifty percent of the forest plots have δ values significantly different from 0, all due to positive δ values. *B*, Correlation between δ and the amount of rainfall during the dry season (mm) in the PCW tree plots; $R^2 = 0.23$ ($P = .002$, $n = 39$).

evenness. Here we proposed a test based on Shannon's index H and found that neutrality could be rejected in half of the tropical forest tree plots we studied. This suggests that departures from neutrality may be more pervasive than previously reported in tropical forests.

In our worldwide comparison of the large CTFS plots, departures from neutrality, as measured by the community evenness H, could be explained by the overabundance of a limited number of species (fig. 1). Remarkably, there was no clear relation between the overabundance of a species and its relative abundance within the community. At Lambir, for instance, the canopy dipterocarp species *Dryobalanops aromatica*, representing only 2.4% of the stems, was overabundant while *Mesua nagassarium*, the first-ranking species in Sinharaja (12.2% of the stems, was not. This result suggests that the status of species overabundance should be gauged against the predictions of suitable null model, here Hubbell's neutral model.

This deviation from neutrality was then quantified mechanistically using a simple nonneutral generalization of Hubbell's model. We found that this model was better able to reproduce empirical patterns of species abundance than Hubbell's neutral model. In most of the cases, positive frequency dependence ($\delta > 0$) was found to better describe species abundance patterns than Hubbell's neutral model ($\delta = 0$). This is consistent with the reanalysis of Volkov et al.'s (2005) model, which showed that a model with negative density dependence performs worse than a neutral model in tropical tree plots (Chave et al. 2006). This combination of results may seem contradictory with the numerous studies attesting the prominent role of negative density and frequency dependence in the maintenance of

tropical tree diversity (Janzen 1970; Connell 1971; Harms et al. 2000; Wills et al. 2006; Comita et al. 2010; Gonzalez et al. 2010). From this contradiction, we can draw two insights. First, negative density dependence, although present, does not seem to have a detectable impact on the shape of the species abundance distribution in tropical tree communities we tested here, or more plausibly, its impact
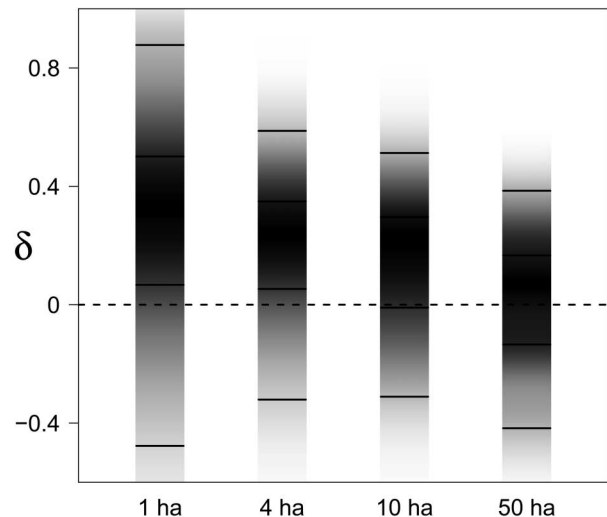

Figure 3: Variation of δ with sample size in the 50-ha BCI tree plot. For each area size, we summed the approximate posterior distribution of δ over the subplots (50 1-ha subplots, 10 4-ha subplots, and 5 10-ha subplots). The gray levels in the figure indicate the approximate posterior density distribution, and the black lines stand for percentiles 2.5, 25, 75, and 97.5 of the posterior distribution.

is counterbalanced by another process. Second, our model may provide good fits to species abundance distributions but for the wrong reason. Our nonneutral model with positive δ values outperforms Hubbell's neutral model because it yields less even abundance distributions, not because the system shows positive frequency-dependent dynamics. Any ecological mechanism other than positive frequency dependence, which would yield a decrease in abundance evenness, is consistent with our results. One such mechanism is environmental filtering.

Interpreting δ as a Measure of Environmental Filtering

The role of environmental filtering in the distribution and abundance of tropical tree species has been recurrently demonstrated from the seedling to the adult stage (Plotkin et al. 2000; Valencia et al. 2004; John et al. 2007; Norden et al. 2009). Species that show specific adaptations for local environmental conditions are likely to be more abundant in their preferred environment (Bazzaz 1991). Consequently, in environmentally filtered communities, species abundances should be less even than in neutral communities (Jabot 2010). Positive values of δ could thus be a signature of environmental filtering.

Consistent with our interpretation that positive δ values are a signature of environmental filtering, we observe that drier plots have larger δ values in Panama (fig. 2*B*). Engelbrecht et al. (2007; fig. 2*A*, 2*B*) showed empirically that drought-intolerant tree species tend to be excluded from drought-prone sites, while drought-tolerant tree species are less often excluded in humid sites. Hence, environmental filtering caused by drought is expected to be stronger in drier sites.

Similarly, observed departures from neutrality in the large CTFS plots are likely related, at least in part, to the occurrence of environmental stresses, in particular, drought events (Losos and Leigh 2004): Edoro, Huai Kha Khaeng, and even more Mudumalai all face relatively intense drought periods, and Lambir, although very wet, experiences brief and severe droughts due to shifts in monsoonal wind trades. In contrast, La Planada, Sinharaja, and Pasoh all experience very wet or only slightly seasonal climates, consistent with our finding that these plots do not depart from neutrality. The Mudumalai plot was somewhat of an outlier in this analysis. Indeed, in this site species abundances are also altered by elephant browsing and understory fires, yet patterns of tree species abundances were only marginally nonneutral.

Abiotic environmental filtering was unlikely to be the unique cause of departure from neutrality. A few species rather seemed to be overabundant because of their intrinsic biology. The Lenda plot is dominated by the monodominant legume tree *Gilbertiodendron dewevrei*. In tropical forests, monodominance has been traditionally explained by various mechanisms of intraspecific facilitation, such as local modification of shading level, litter properties (Torti et al. 2001), or increased nutrient uptake through mycorrhizal networks (McGuire 2007). Local overabundance can also result from the species abundance structure at the regional scale. The two most abundant species in Yasuni, the palm *Iriartea deltoidea* and the tree *Eschweilera coriacea*, are members of the plant oligarchy that dominates vast expanses of the western Amazonian forest (Pitman et al. 2001). In Edoro, a similar pattern was observed, with *Cynometra alexandri*, *Diospyros bipidensis*, *Julbernardia seretii*, and *Pancovia harmsiana*, four overabundant species that were also overabundant in the Lenda plot, some 35 km away.

Dependence of the Neutrality Assumption with Spatial Scale

One troubling feature surrounding neutral theory is that while large samples may present neutral patterns of species abundances (e.g., Hubbell 2001), deviations from neutrality are observed when species distributions are explored at smaller spatial scales (e.g., John et al. 2007). Here, we were able to test whether deviations from neutrality were indeed scale dependent. If different environmental filtering processes operate across localized habitats, the overall filtering signal may be blurred in large samples. Confirming this prediction, we detected a nonneutral signal at fine spatial scales within the 50-ha plot on Barro Colorado Island, and this signal decreased as plot size increased. This provides evidence that even though Hubbell's neutral model suitably approximates species abundance distributions at a coarse-grained spatial scale, nonneutral processes are relevant to explaining plant species coexistence at a fine-grained scale, the scale that matters the most to individual performance (Plotkin et al. 2000; Tuomisto et al. 2003; Svenning et al. 2004; John et al. 2007). Consequently, the choice of sampling scale is crucial in the detection of ecological processes. In small and homogeneous plots, the species abundance distributions are more likely to deviate from neutrality than in large, heterogeneous ones.

Modeling Community Dynamics

We offered a simple nonneutral extension of Hubbell's dynamic model, which may be used to quantify potential deviations from neutrality. One of the main issues with previous models of community dynamics has been the difficulty in relating these dynamical models to static data. Numerous methods have been developed to extract relevant statistical information from ecological data sets (Su-

gihara and May 1990; Clark 2007), but they are mainly designed to analyze dynamical ecological data sets, so that the validity of the model assumptions may be directly compared to the observed dynamics. Such methods are difficult to extend to static data; they require the computation of a likelihood function, the probability of observing the static data (i.e., pattern) under the model assumption and for particular parameter values. This is a mathematical challenge in models of biodiversity, except in special cases (such as the neutral one; Etienne 2005). This limitation can be alleviated through computer-intensive techniques such as approximate Bayesian inference. Our study is one of the first applications of this type of inference in ecology. This method is flexible, and it is now commonplace in population genetics (Marjoram and Tavaré 2006; Csilléry et al. 2010). It should also be of great use in future ecological studies. We emphasize that in our use of the ABC method, we assumed a flat prior distribution for the parameters. In this sense, we really implemented an approximate maximum likelihood method and did not depart from the frequentist approach to statistical inference.

Here, we propose one possible model of nonneutrality. Despite its limitations, the advantage of our model is that it relaxes the demographic equivalence in a simple way and avoids a great inflation in the number of model parameters—a single new parameter is added. In addition, our model does not preclude a mechanistic interpretation of the results. Here, we were led to conclude that the tropical tree communities we analyzed were more likely shaped by environmental filtering than by positive frequency dependence. Additional data on species characteristics for entire communities will be critical to parameterize more-detailed community dynamic models, including ones that explicitly model environmental filtering (McGill et al. 2007; Jabot 2010).

Literature Cited

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Alonso, D., A. Ostling, and R. S. Etienne. 2008. The implicit assumption of symmetry and the species abundance distribution. Ecology Letters 11:93–105.

Bazzaz, F. A. 1991. Habitat selection in plants. American Naturalist 137(suppl.):S116–S130.

Beaumont, M. A., W. Y. Zhang, and D. J. Balding. 2002. Approximate Bayesian computation in population genetics. Genetics 162:2025–2035.

Bell, G. 2003. The interpretation of biological surveys. Proceedings of the Royal Society B: Biological Sciences 270:2531–2542.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago.

Chave, J., H. Muller-Landau, and S. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. American Naturalist 159:1–23.

Chave, J., D. Alonso, and R.S. Etienne. 2006. Theoretical biology: comparing models of species abundance. Nature 441:E1.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clark, J. S. 2007. Models for ecological data: an introduction. Princeton University Press, Princeton, NJ.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. Dispersal. Oxford University Press, Oxford.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. Science 329:330–332.

Condit, R., N. Pitman, E. G. Leigh Jr., J. Chave, J. Terborgh, R. B. Foster, P. Núñez, et al. 2002. Beta-diversity in tropical forest trees. Science 295:666–669.

Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, et al. 2006. The importance of demographic niches to tree diversity. Science 313:98–101.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 *in* P. J. den Boer, and G. Gradwell, eds. Dynamics of populations. Center for Agricultural Publishing and Documentation, Wageningen.

Csilléry, K., M. G. B. Blum, O. E. Gaggiotti, and O. François. 2010. Approximate Bayesian computation (ABC) in practice. Trends in Ecology & Evolution 25:410–418.

Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody, and J. M. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, MA.

Engelbrecht, B. M. J., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.

Engen, S., R. Lande, T. Walla, and P. J. DeVries. 2002. Analyzing spatial structure of communities using the two-dimensional Poisson lognormal species abundance model. American Naturalist 160: 60–73.

Etienne, R. S. 2005. A new sampling formula for neutral biodiversity. Ecology Letters 8:253–260.

———. 2007. A neutral sampling formula for multiple samples and an "exact" test of neutrality. Ecology Letters 10:608–618.

Etienne, R. S., and D. Alonso. 2005. A dispersal-limited sampling theory for species and alleles. Ecology Letters 8:1147–1156.

Ewens, W. J. 2004. Mathematical population genetics. Springer, New York.

Gonzalez, M. A., E. A. Roger, E. A. Courtois, F. Jabot, N. Norden, C. E. T. Paine, C. Baraloto, et al. 2010. Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. Journal of Ecology 98:137–146.

Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9:399–409.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495.

Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, et al. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proceedings of the National Academy of Sciences of the USA 104:10904–10909.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Hubbell, S. P., F. He, R. Condit, L. Borda de Agua, J. Kellner, and H. ter Steege. 2008. How many tree species are there in the Amazon and how many of them will go extinct? Proceedings of the National Academy of Sciences of the USA 105:11498–11504.

Jabot, F. 2010. A stochastic dispersal-limited trait-based model of community dynamics. Journal of Theoretical Biology 262:650–661.

Jabot, F., and J. Chave. 2009. Inferring the parameters of the neutral theory of biodiversity using phylogenetic information, and implications for tropical forests. Ecology Letters 12:239–248.

Jabot, F., R. S. Etienne, and J. Chave. 2008. Reconciling neutral community models and environmental filtering: theory and an empirical test. Oikos 117:1308–1320.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, et al. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences of the USA 104:864–869.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Latimer, A. M., J. A. Silander, and R. M. Cowling. 2005. Neutral

ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. Science 309:1722–1725.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

Leigh, E. G., Jr. 2007. Neutral theory: a historical perspective. Journal of Evolutionary Biology 20:2075–2091.

Losos, E. C., and E. G. Leigh Jr. 2004. Tropical forest diversity and dynamism: findings from a large-scale plot network. University of Chicago Press, Chicago.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Princeton University Press, Princeton, NJ.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Marjoram, P., and S. Tavaré. 2006. Modern computational approaches for analyzing molecular genetic variation data. Nature Reviews Genetics 7:759–770.

McGill, B. J., B. A. Maurer, and M. D. Weiser. 2006. Empirical evaluation of neutral theory. Ecology 87:1411–1423.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. Kassa Benecha, M. Dornelas, et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

McGuire, K. L. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley, New York.

Norden, N., J. Chave, P. Belbenoit, A. Caubère, P. Châtelet, P.-M. Forget, B. Riéra, et al. 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. Journal of Ecology 97:186–197.

Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Núñez, D. A. Neill, C. E. Ceron, W. A. Palacios, et al. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82:2101–2117.

Plotkin, J. B., M. D. Potts, N. Leslie, N. Manokaran, J. LaFrankie, and P. S. Ashton. 2000. Species-area curves, spatial aggregation, and habitat specialization in tropical forests. Journal of Theoretical Biology 207:81–99.

Pyke, C. R., R. Condit, S. Aguilar, and S. Lao. 2001. Floristic composition across a climatic gradient in a Neotropical lowland forest. Journal of Vegetation Science 12:553–566.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Simberloff, D. 2004. Community ecology: is it time to move on? American Naturalist 163:787–799.

Sugihara, G., and R. M. May. 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. Nature 344:734–741.

Svenning, J. C., D. A. Kinner, R. F. Stallard, B. M. J. Engelbrecht, and S. J. Wright. 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85:2526–2538.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

———. 2004. Niche trade-offs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the USA 101:10854–10861.

Torti, S. D., P. D. Coley, and T. A. Kursar. 2001. Causes and consequences of monodominance in tropical lowland forests. American Naturalist 157:141–153.

Tuomisto, H., K. Ruokolainen, M. Aguilar, and A. Sarmiento. 2003. Floristic patterns along a 43-km long transect in an Amazonian rain forest. Journal of Ecology 91:743–756.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J.-C. Svenning, C. Hernandez, K. Romoleroux, et al. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92:214–229.

Vallade, M., and B. Houchmandzadeh. 2003. Analytical solution of a neutral model of biodiversity. Physical Review E 68:061902.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424:1035–1037.

Volkov, I., J. R. Banavar, F. L. He, S. P. Hubbell, and A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. Nature 438:658–661.

Watterson, G. A. 1978. Homozygosity test of neutrality. Genetics 88:405–417.

Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, et al. 2006. Nonrandom processes maintain diversity in tropical forests. Science 27:527–531.

Zobel, M. 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology & Evolution 12:266–269.

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