

LETTERS

Dynamical evolution of ecosystems

Sandro Azae¹, Simone Pigolotti², Jayanth R. Banavar³ & Amos Maritan¹

The assembly of an ecosystem such as a tropical forest depends crucially on the species interaction network, and the deduction of its rules is a formidably complex problem¹. In spite of this, many recent studies^{2–16} using Hubbell's neutral theory of biodiversity and biogeography² have demonstrated that the resulting emergent macroscopic behaviour of the ecosystem at or near a stationary state shows a surprising simplicity reminiscent of many physical systems¹⁷. Indeed the symmetry postulate², that the effective birth and death rates are species-independent within a single trophic level, allows one to make analytical predictions for various static distributions such as the relative species abundance^{3–12}, β -diversity^{13–15} and the species–area relationship¹⁶. In contrast, there have only been a few studies of the dynamics and stability of tropical rain forests^{18–20}. Here we consider the dynamical behaviour of a community, and benchmark it against the exact predictions of a neutral model near or at stationarity. In addition to providing a description of the relative species abundance, our analysis leads to a quantitative understanding of the species turnover distribution and extinction times, and a measure of the temporal scales of neutral evolution. Our model gives a very good description of the large quantity of data collected in Barro Colorado Island in Panama in the period 1990–2000 with just three ecologically relevant parameters and predicts the dynamics of extinction of the existing species.

We present an analytical model that allows one to probe the characteristic timescales of evolving tropical forests and to evaluate the consequences of anthropogenic processes. Our approach is valid for an ecosystem at or near stationarity; indeed, one would expect important deviations from our predictions when the stationarity assumption is not valid (see, for example, ref. 21). Using a neutral model, we have obtained exact solutions for the probability distribution, $P(x,t)$, that a species has a population x at time t for arbitrary initial and boundary conditions (see Supplementary Information for details). The species are assumed to be non-interacting and are characterized by effective birth and death rates given by $b(x) = b_1x + b_0$ and $d(x) = d_1x + d_0$ respectively, where b_1 and d_1 are the per-capita rates and the constants b_0 and d_0 incorporate density dependence and result in a rare species advantage when $b_0 > d_0$ (ref. 9). To simplify the analytical treatment and for parsimony we have chosen $b_0 = -d_0$ in our analysis.

There are three biological parameters in our framework, namely τ , b and D : τ is the characteristic timescale associated with species turnover in neutral evolution—an ecosystem close to the stationary state is able to recover from a perturbation on a timescale of order τ and its inverse is simply the difference between d_1 and b_1 ; $b = 2b_0$ takes into account density dependence effects⁹ arising from immigration²² and/or speciation, for example; and D accounts for demographic stochasticity and is given by $(b_1 + d_1)/2$.

The steady-state solution, which is independent of initial conditions, provides an exact expression for the relative species abundance (RSA),

$$P_{\text{RSA}}(x) = \frac{(D\tau)^{-b/D}}{\Gamma(b/D)} x^{b/D-1} e^{-x/D\tau} \quad (1)$$

($\Gamma(x)$ is the gamma function²³), which is in good accord with RSA data for various censuses of the Barro Colorado Island (BCI) forest (Center for Tropical Forest Science website, <http://ctfs.si.edu>), and for several other tropical forests with the use of the data presented in the Supplementary Information of ref. 9. These fits allow us to estimate two combinations, b/D and $D\tau$ (see Fig. 1 and Supplementary Tables 1 and 2), of the three parameters.

The time-dependent species turnover distribution (STD), defined as the probability $P_{\text{STD}}(\lambda, t)$ that the ratio of the populations of a species separated by a time interval t , $x(t)/x(0)$, is equal to λ , is found under stationary conditions to be

$$P_{\text{STD}}(\lambda, t) = A \frac{(\lambda + 1)}{\lambda} \frac{(e^{t/\tau})^{b/2D}}{1 - e^{-t/\tau}} \left(\frac{\sinh(t/2\tau)}{\lambda} \right)^{b/D+1} \left(\frac{4\lambda^2}{(\lambda + 1)^2 e^{t/\tau} - 4\lambda} \right)^{b/D + \frac{1}{2}} \quad (2)$$

where A is the normalization constant. P_{STD} depends only on b/D and τ . The above result, derived for reflecting boundary conditions at

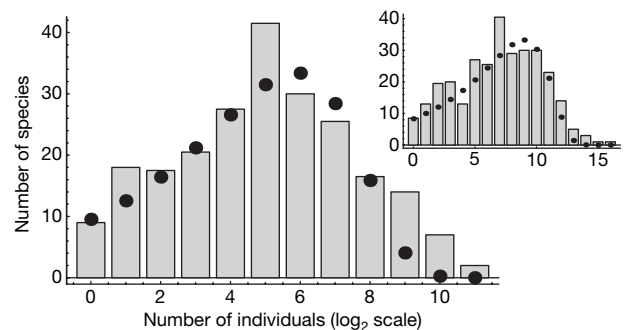


Figure 1 | Relative species abundance plot in the BCI forest from the 1990 census (Center for Tropical Forest Science website). The individuals of more than 10 cm d.b.h. in this tropical forest are binned with the method of refs 7, 29. The inset shows the same histogram for the individuals of more than 1 cm d.b.h. for the same forest and yields consistent estimates of the model parameters and temporal scales within the error bars. The estimated parameters are robust within error bars on changing the nature of binning of the empirical data to non-overlapping bins. The points are the best fits to the mean number of species with population between 2^{n-1} and 2^n , as given by equation (1). The fit for large x is readily improved at the cost of introducing an additional parameter (see Supplementary Information for error analysis and other details). Note that the RSA plot for individuals of more than 10 cm d.b.h. is smoother at low abundance than the plot for individuals of more than 1 cm d.b.h. This is to be expected because younger populations are subject to larger fluctuations than older ones.

¹Dipartimento di Fisica 'G. Galilei', Università di Padova, via Marzolo 8, 35131 Padova, Italy. ²The Niels Bohr Institute, Blegdamsvej 17, 2100 Copenhagen, Denmark. ³Department of Physics, The Pennsylvania State University, 104 Davey Laboratory, University Park, Pennsylvania 16802, USA.

$x = 0$, is essentially independent of the specific boundary conditions for the relatively short time interval of 5–10 years for which the dynamical data exists. The histograms in Fig. 2 are fitted with equation (2), with τ as a free parameter (see Supplementary Tables 1 and 2). We find τ , the characteristic timescale for the BCI forest, to be about $3,500 \pm 1,000$ years (for trees of more than 10 cm stem diameter at breast height (d.b.h.)) and $2,900 \pm 1,100$ years (for trees of more than 1 cm d.b.h.), where the broad uncertainty is due to the fact that the data are sampled at relatively short time intervals. Long-term vegetation studies of a *Tsuga*-dominated forest in New England²⁴ reveal a recovery time for the *Tsuga canadensis* that is of the same order of magnitude (roughly 1,500 years) in spite of being quite different from the BCI forest. Studies of Pleistocene forest dynamics²⁵ are also in good agreement with our estimate. The exact analytic expression permits the prediction of a characteristic timescale more than two orders of magnitude larger than the time interval of measurement, reminiscent of the classic example of the prediction of the half-lives of radioactive isotopes, which are often many times the age of the Universe. The estimate of the timescale becomes asymptotically exact as the number of species or nuclei increases. The BCI data analysis for trees of more than 10 cm d.b.h. yields $b = 0.02 \pm 0.01$ and $D = 0.04 \pm 0.02$ (both in units of individuals per year), leading to an effective per-capita death rate $d_1 = (1/\tau + 2D)/2 \approx D$, which is consistent with the estimate given in ref. 19.

One can obtain a measure of the mean lifetime of a species, $\langle t \rangle = -\tau[\gamma + \psi(1 - b/D)]$, where the Euler constant $\gamma = 0.577\dots$, $\psi(z) = \Gamma'(z)/\Gamma(z)$ and $\Gamma(z)$ is the gamma function²³, yielding $\langle t \rangle = 3,400 \pm 1,000$ years, of the same order as τ . This timescale is in accord with the estimates of extinction times given in ref. 26. $\langle t \rangle/\tau$ depends only on b/D , which can be calculated from the steady-state RSA without the need for dynamical data. We have used equation (1) to fit the RSA of various tropical forests, yielding $\langle t \rangle/\tau = 1.94, 1.67, 0.67, 0.95$ and 1.38 for Yasuni, Lambir, Sinharaja, Korup and Pasoh, respectively (see Supplementary Information). The similarity of the two timescales $\langle t \rangle$ and τ is not mandated by the theory because the function $\psi(1 - b/D)$ diverges as b/D approaches 1. Were $\tau \gg \langle t \rangle$, one would obtain a contradiction because the ecosystem would not reach a steady state: extinction would be much faster than recovery. In contrast, $\tau \ll \langle t \rangle$ would lead to a very robust and essentially unchanging ecosystem, rapidly recovering (with respect to the extinction time) from disturbances and with little room for evolution. Our result suggests that ecosystems at stationarity are marginally

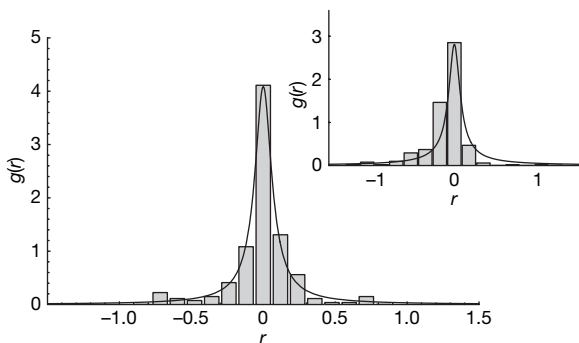


Figure 2 | STD for the interval 1990–95 in the BCI forest. The main panel shows results for individuals of more than 10 cm d.b.h., and the inset results for individuals of more than 1 cm d.b.h. (Center for Tropical Forest Science website). We have defined the new variable $r = \log(\lambda)$, which is distributed as $g(r) = e^r P_{STD}(e^r, t)$, where $P_{STD}(\lambda, t)$ is given by equation (2). Data are plotted with a linear binning in the $r = \log(\lambda)$ axis and fitted to $g(r)$. b/D is obtained from fitting the RSA data in 1990 (see Fig. 1). The best-fit parameter is found to be $\tau \sim 4,400$ years for individuals of more than 10 cm d.b.h., and $\tau \sim 3,900$ years for individuals of more than 1 cm d.b.h. The fits of both RSA (see Fig. 1) and STD for individuals of more than 10 cm d.b.h. are systematically better than those for individuals of more than 1 cm d.b.h.

stable—not so stable that they are frozen in time and not so fragile that they are prone to extinction.

One may also study the time correlation function $\kappa(t) = \langle x(t)x(0) \rangle - \langle x(t) \rangle \langle x(0) \rangle$, where the averages are taken over the species. For neutral dynamics, we find that $\kappa(t) = bD\tau^2 e^{-t/\tau}$. Physically, the time correlation function approaches zero in an exponential fashion, with τ as the characteristic relaxation time. Although the currently available data for the BCI forest are not sufficient for analysis, a study of the time correlation function provides a simple yet powerful probe for obtaining the timescale τ as well as for probing departures from neutrality.

We turn now to a prediction of a quantity that we call the restricted relative species abundance, $q(x, t)$, which is a measure of the relative species abundance of just the species present in the forest at initial time denoted by $t = 0$. Unlike the RSA, the restricted relative species abundance does not consider any new species or any species reintroduced after its original extinction. One finds that

$$q(x, t) = \frac{\alpha^\beta x^{\beta-1} e^{-\alpha x}}{\Gamma(\beta)\Gamma(1-\beta)} \gamma\left(1-\beta, \frac{\alpha x}{e^{t/\tau}-1}\right) \quad (3)$$

where $\Gamma(x)$ is the gamma function and $\gamma(a, z) = \int_0^z t^{a-1} e^{-t} dt$ (see ref. 23), $\beta = b/D$, and $\alpha = 1/D\tau$. Figure 3 depicts the inexorable march to extinction of the species, with the rare species being more prone to extinction. Note that, unlike the RSA and STD, the fitting of restricted relative species abundance, when the data become available, can be employed to determine all three parameters of the model simultaneously. Unfortunately, with just one set of data (RSA or STD), it is not possible to determine the parameters and predict the behaviour of the other in a manner similar to the treatment in ref. 27.

We conclude by noting that different choices of b_0 and d_0 have also been shown to lead to very good fits of the RSA of various tropical forests, but the analytical treatment for the dynamics is much more involved. Indeed, the predicted macroscopic properties of the ecosystem at or near stationarity are not very sensitive to specific choices of the model parameters but rather depend on the key assumptions; that is, the symmetry (or neutrality) principle and the independent individual effective dynamics. Our approach represents a complete description of an ecosystem undergoing neutral dynamics that can be solved analytically. The goodness of the fits of both RSA and STD does not imply that neutrality is a valid description of how nature operates. Rather, the analytical expressions for various measurable

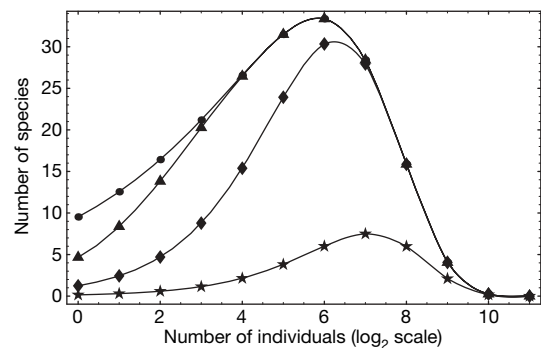


Figure 3 | Restricted relative species abundance. Plot of the mean number of species originally present in an ecosystem with population between 2^{n-1} and 2^n after time t has evolved, as given by equation (3). The circles denote the steady state at $t = 0$, namely the standard RSA; the triangles correspond to $t = 100$ years; the diamonds to $t = 1,000$ years; and the stars to $t = 10,000$ years. The parameters are those deduced from the RSA of the BCI plot in 1990 for more than 10 cm d.b.h. (see Supplementary Table 1). Note the shift of the maximum of the curve to the right and that rare species are more prone to extinction.

quantities will allow one not only to estimate the relevant timescales but also to look for deviations from the idealized theory. It yields good fits of both RSA and STD, it provides estimates of timescales that are in accord with previous analysis and it also predicts the extinction-time distribution. The issue of model selection²⁸ is beyond the scope of our current analysis and will become increasingly important as other models with exact solutions for the dynamics are developed. Our model is an ideal starting point for the incorporation of features such as non-neutral dynamics and time-dependent environmental and spatial effects including heterogeneities.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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