

LETTER

Setting the absolute tempo of biodiversity dynamics

Andrew P. Allen^{1*} andVan M. Savage²¹National Center for Ecological Analysis and Synthesis, 735 State St, Suite 300, Santa Barbara, CA 93101, USA²Department of System Biology, Harvard Medical School, 200 Longwood Ave., Boston, MA 02115, USA

*Correspondence: E-mail: drewa@nceas.ucsb.edu

Abstract

Neutral biodiversity theory has the potential to contribute to our understanding of how macroevolutionary dynamics influence contemporary biodiversity, but there are issues regarding its dynamical predictions that must first be resolved. Here we address these issues by extending the theory in two ways using a novel analytical approach: (1) we set the absolute tempo of biodiversity dynamics by explicitly incorporating population-level stochasticity in abundance; (2) we allow new species to arise with more than one individual. Setting the absolute tempo yields quantitative predictions on biodiversity dynamics that can be tested using contemporary and fossil data. Allowing incipient-species abundances greater than one individual yields predictions on how these dynamics, and the form of the species-abundance distribution, are affected by multiple speciation modes. We apply this new model to contemporary and fossil data that encompass 30 Myr of macroevolution for planktonic foraminifera. By synthesizing the model with these empirical data, we present evidence that dynamical issues with neutral biodiversity theory may be resolved by incorporating the effects of environmental stochasticity and incipient-species abundance on biodiversity dynamics.

Keywords

Demographic stochasticity, environmental stochasticity, extinction, macroevolution, neutral biodiversity theory, population dynamics, speciation.

Ecology Letters (2007) 10: 637–646

INTRODUCTION

Neutral biodiversity theory (NBT) represents an initial attempt to quantitatively incorporate the process of speciation into community ecology (Hubbell 2001). Extensions of NBT may therefore contribute to our understanding of how macroevolutionary dynamics influence contemporary biodiversity. NBT is derived using parameters that, in principle, reflect how rates of birth, death, dispersal and speciation combine to determine biodiversity (Hubbell 2001; Volkov *et al.* 2003, 2005). In particular, the NBT biodiversity parameter, $\theta = 2J_M\nu$, is equal to the product of ‘metacommunity’ abundance, J_M and a per-capita speciation parameter, ν (Hubbell 2001).

The time units of, θ , J_M , and ν have been debated (Hubbell 2003; Ricklefs 2003), in part reflecting unresolved issues regarding the dynamical predictions of NBT (Lande *et al.* 2003; Ricklefs 2003; Nee 2005; Ricklefs 2006). To highlight these issues, we will assume here that θ is dimensionless, and that J_M is in units of individuals. Adopting this convention, ν has no time units; instead it is the per-capita probability of speciation (individuals⁻¹)

during a time interval that entails a stochastic abundance change of one individual. This general definition for ν is consistent with the mathematical assumptions of previous NBT derivations (Hubbell 2001; Volkov *et al.* 2003, 2005).

The dynamical issues with NBT have been attributed to two biological assumptions. First, it is often assumed that stochastic population dynamics in NBT models are governed entirely by ‘demographic stochasticity’ (Ricklefs 2003; Hu *et al.* 2006). This type of stochasticity is coupled to the individual generation time, g , because it reflects intrinsic differences among individuals in their rates of survival and reproduction (Lande *et al.* 2003). By contrast, the other type of stochasticity – ‘environmental stochasticity’ – reflects the extrinsic effects of abiotic and biotic environmental variables on all individuals comprising populations (Engen *et al.* 1998). Theory and data indicate that environmental stochasticity is the primary determinant of stochastic population dynamics for species that are not rare (Lande *et al.* 2003). Consequently, demographic stochasticity yields expected times to extinction that are too long for abundant species (Lande *et al.* 2003; Ricklefs 2006). For example, a tree species comprised of $N_i \approx 10^8$ individuals, with a

generation time of $g = 30$ years individual⁻¹, would take $c. N_i g \approx 10^9$ years to go extinct via demographic stochasticity (Nee 2005). This estimate exceeds the age of the angiosperms by over 800 Myr (Sun *et al.* 1998).

Second, published analytical derivations of NBT assume that new species form via a ‘point-mutation’ mode of speciation, with an incipient-species abundance of $J_S = 1$ individual species⁻¹ (Volkov *et al.* 2003, 2005). Combining this assumption with the demographic stochasticity assumption yields an expression for the absolute per-capita rate of speciation (species individual⁻¹ Myr⁻¹): $v_\tau = v/J_S g$. If both assumptions are upheld, v can alternatively be defined as having time units (i.e. species individual⁻¹ generation⁻¹, Ricklefs 2003), making our three-parameter expression for v_τ unnecessary. However, neither assumption will hold true in general.

In particular, incipient-species abundances can be much greater than one individual (e.g. $J_S \approx 10^6$ individuals species⁻¹ for geminate shrimp species, Hickerson *et al.* 2003), which can greatly extend species longevities, as demonstrated by the computer simulations of Hubbell & Lake (2003). Consequently, longevities calculated by assuming a point-mutation mode of speciation are generally too short (Ricklefs 2003). For example, given that $\theta \approx 10^2$ for tropical tree communities (Hubbell 2001), the average longevity, $\langle l_S \rangle$, for a tree species formed via the point-mutation mode (i.e. $J_S = 1$ individual species⁻¹) in a metacommunity comprised of $J_M \approx 10^{10}$ individuals (Ricklefs 2003) and $S_M \approx \theta \ln(J_M/\theta) \approx 10^3$ species (Hubbell 2001) would only be $c. 10^3$ years ($= S_M/J_M v_\tau = 2S_M J_S g/\theta$). This estimate is three orders of magnitude lower than estimates obtained from the fossil record (~ 3.5 Myr, Niklas *et al.* 1983). As the above-mentioned examples demonstrate, resolving the dynamical issues with NBT is of fundamental importance for assessing factors that govern biodiversity dynamics.

Here we address these issues using a synthesis of theory and empirical data. In the *Model derivation* section, we present a model that incorporates four fundamental assumptions of NBT, but differs from previous NBT derivations in two ways. First, we incorporate a stochasticity parameter, s , that characterizes the combined effects of demographic and environmental variables on population abundance. Second, we allow new species to enter the metacommunity with incipient-species abundances, J_S , greater than 1 individual species⁻¹. In the *Results* section, we evaluate this new model using empirical data compiled for planktonic foraminifera from oceans around the world. Foraminifera are ideal for this task because it is possible to estimate *all* of the model parameters using contemporary data on abundance (Allen *et al.* 2006) and biodiversity (Prell *et al.* 1999), and fossil data on speciation rates (Allen *et al.* 2006) and population dynamics (McIntyre *et al.* 1989; Imbrie *et al.* 1992). Finally, in the *Discussion* section we assess whether the absolute

tempo of biodiversity dynamics is consistent with the assumption of neutrality for foraminifera.

MODEL DERIVATION

Our model derivation invokes four fundamental assumptions of NBT. First, the ‘zero-sum’ assumption is that there exists a ‘metacommunity’ whose total abundance, J_M (individuals), fluctuates about a constant average value (Volkov *et al.* 2003, 2005). Second, the ‘dynamic-equilibrium’ assumption is that the total speciation rate in the metacommunity, V_M (species Myr⁻¹), equals the total extinction rate, E_M :

$$V_M = J_M v_\tau = E_M \quad (1)$$

Equation 1 implies that total metacommunity richness, S_M (species), fluctuates about a constant average value. The metacommunity will eventually reach this dynamic equilibrium, given sufficient time, because increasing v_τ , while holding J_M constant, reduces the average population size, resulting in higher extinction rates (Levinton 1979; Hubbell 2001). For planktonic foraminifera, we can directly evaluate the dynamic-equilibrium assumption by applying new methods of analysis (Allen & Gillooly 2006) to data compiled in the Neptune fossil database (Spencer-Cervato 1999). Our analysis indicates that this assumption is reasonable for the past 15–20 Myr (Fig. 1), consistent with the work of Wei & Kennett (1986) and Patterson *et al.* (2004).

Third, the ‘demographic-equivalence’ assumption is that different species comprising the metacommunity have similar per-capita rates of speciation, v_τ (species individual⁻¹ Myr⁻¹, Allen *et al.* 2006), and stochastic abundance change, regardless of population size (Volkov *et al.* 2003). In our model, this stochasticity is attributable to the combined effects of demographic and environmental variables. Fourth, the ‘large-metacommunity’ assumption is that the metacommunity is sufficiently large to be treated as effectively infinite for modelling purposes, i.e. $J_M \gg 1$ individual. For planktonic foraminifera, this assumption is supported by a global abundance estimate of $J_M \approx 5.6 \times 10^{17}$ individuals. Metacommunity abundance was estimated by applying a function calibrated with plankton-tow data (Allen *et al.* 2006) to a global coverage of sea-surface temperature data (Casey & Cornillon 1999).

The structure and dynamics of our model follow directly from these four NBT assumptions. Following the demographic-equivalence assumption, we characterize metacommunity dynamics based on changes in total population abundance, N_i (individuals), for a single focal species i (McKane *et al.* 2000). Following the large-metacommunity assumption, we model abundance as a continuous variable using the Kolmogorov backward equation of diffusion theory (Maruyama 1977; Karlin & Taylor 1981; Ewens 2004;

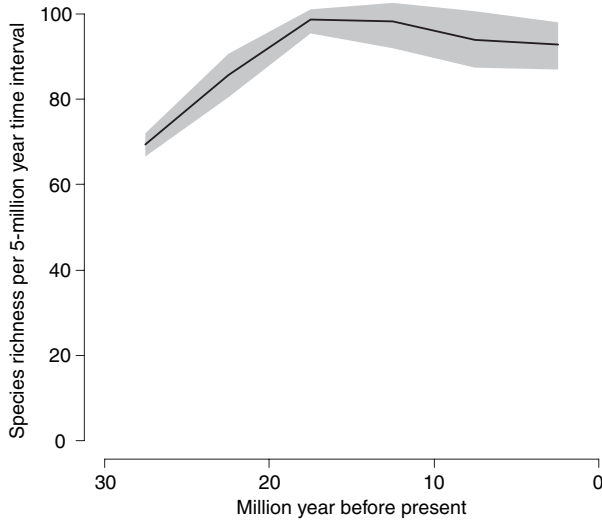


Figure 1 Changes in species richness (number observed per 5-Myr time interval) over the past 30 Myr for the global metacommunity of planktonic foraminifera. Averages (lines) and 95% confidence intervals (shaded areas) were generated as described by Allen & Gillooly (2006) using data compiled in the Neptune fossil database (Spencer-Cervato 1999). The data are in reasonable agreement with the dynamic-equilibrium assumption of the model for the past 15–20 Myr (eqn 1).

Rice 2004) (see Online Supplement S1). This same theoretical framework has been used to characterize neutral dynamics of local communities at ecological time scales (Azaele *et al.* 2006). In our model, changes in population abundance are controlled by two distinct dynamical processes. The first process is governed by speciation. Despite the fact that individuals may be chosen at random to form new species, this first process is ‘deterministic’ because creating a new species always entails removing individuals from a pre-existing species. By contrast, the second process is ‘stochastic’ because it may result in abundance increase or decrease.

The deterministic rate of change in population abundance, $M(N_i)$ (individuals Myr^{-1}), is always negative due to the NBT assumptions, and reflects the effects of speciation. To show this, we first note that the rate of change in the total average abundance of a metacommunity, dJ_M/dt , comprised of S_M species and $J_M = \sum_{i=1}^{S_M} N_i$ individuals is equal to

$$\frac{dJ_M}{dt} = V_M J_S + \sum_{i=1}^{S_M} M(N_i) = v_\tau J_S \sum_{i=1}^{S_M} N_i + \sum_{i=1}^{S_M} M(N_i) \quad (2)$$

Here $V_M = J_M v_\tau$ is the total rate of speciation in the metacommunity (species Myr^{-1}) (eqn 1), J_S is the incipient-species abundance (individuals species $^{-1}$), $V_M J_S = J_M v_\tau J_S$ is the total rate of introduction of new individuals into the

metacommunity through speciation (individuals Myr^{-1}), and $\sum_{i=1}^{S_M} M(N_i)$ is the total rate of change in the abundances of pre-existing species in the metacommunity. Given the zero-sum assumption ($dJ_M/dt=0$), the dynamic-equilibrium assumption ($dS_M/dt=0$), and the demographic-equivalence assumption, we can equate the corresponding terms in eqn 2 to show that $M(N_i)$ is negatively and directly coupled to v_τ , J_S , and N_i :

$$M(N_i) = -v_\tau J_S N_i \quad (3)$$

This coupling exists because a speciation event entails a loss of J_S individuals from a pre-existing species, and because the rate of speciation per species ($=v_\tau N_i$ species Myr^{-1}) increases linearly with total population abundance, N_i due to the demographic-equivalence assumption.

Stochastic abundance changes, $V(N_i)$ (individuals 2 Myr^{-1}), may be positive or negative, and reflect the combined effects of demographic and environmental variables. The demographic-equivalence assumption implies that all species experience the same per-capita stochasticity, s (individuals Myr^{-1}), regardless of total abundance, N_i . This assumption implies that demographic stochasticity, $s_d N_i$, and environmental stochasticity, $s_e N_i$, both increase proportionally with abundance, N_i ,

$$V(N_i) = s_d N_i + s_e N_i = s N_i \quad (4)$$

where $s = s_d + s_e$. Three features of eqn 4 are noteworthy. First, there is no density-dependent term because long-term environmental changes are known to alter the carrying capacities of species (Lande *et al.* 2003). Thus, at macroevolutionary time scales, variance cannot readily be assigned to density-dependent mechanisms. Second, the variance increases monotonically with population abundance, rather than approaching zero as N_i approaches J_M . Consequently, metacommunity abundance, J_M , is not a fixed quantity, but rather fluctuates about a constant average value, as in the derivations of Volkov *et al.* (2003, 2005).

Third, environmental stochasticity increases proportionally with abundance, and not with the square of abundance (i.e. $\propto N_i^2$), as assumed when modelling the dynamics of a local population (Lande *et al.* 2003). Abundance-squared scaling is only expected if all individuals experience identical environmental changes (Engen *et al.* 1998). This assumption is violated at broad spatial scales because environmental changes are spatially heterogeneous. Consequently, subpopulations that are widely separated in space tend to exhibit statistically independent dynamics (Keeling 2000; Lande *et al.* 2003), which results in pronounced deviations from abundance-squared scaling at regional to global scales (e.g. Keitt *et al.* 2002). Here we will assume that environmental stochasticity scales proportionally with population abundance, as in eqn 4, because foraminifera have geographic ranges that are often global in extent (Prell *et al.* 1999). This

scaling is justified by the central limit theorem if the number of statistically independent subpopulations increases linearly with N_i (Keitt *et al.* 2002). We will return to this assumption in the *Discussion* section.

In principle, the demographic and environmental stochasticity can be modelled separately (Engen *et al.* 1998), but this is not recommended in practice (see Lande *et al.* 2003, p. 18–20). Instead, environmental stochasticity is inferred from the total variance by subtracting the estimated demographic stochasticity (i.e. $s_e = s - s_d$ in eqn 4), which is governed by the individual generation time (i.e. $s_d \approx 1/g$, following eqn 5). Thus, if environmental stochasticity is the primary determinant of stochastic population dynamics, the total per-capita stochasticity should be much greater in magnitude than the inverse of the individual generation time (i.e. $s \gg 1/g$). The magnitude of s can be estimated from empirical data:

$$s \approx \frac{\langle (N_i - N_0)^2 \rangle_t}{N_0 t} \tag{5}$$

Here N_i and N_0 are the abundances of species i at times t and 0, respectively, and $\langle (N_i - N_0)^2 \rangle_t$ is the expectation for the mean-squared deviation in abundance over this time interval (see Online Supplement S2). We divide $\langle (N_i - N_0)^2 \rangle_t$ by t to calculate s because s characterizes the rate of increase in the mean-squared deviation with time.

Combining eqns 3 and 4 with the Kolmogorov backward equation (see Online Supplement S1) yields an expression, $\phi(J_S, N_i) dN_i$, that characterizes the total amount of time (in Myr) that the focal species i spends, on average, in each abundance interval $(N_i - dN_i/2, N_i + dN_i/2)$ from its time of formation at abundance J_S to its time of extinction (see Online Supplement S3):

$$\begin{aligned} &\phi(J_S, N_i) dN_i \\ &= \begin{cases} [1 - \exp(-\frac{2v_\tau J_S}{s} N_i)] \left(\frac{1}{J_S v_\tau N_i}\right) dN_i, & N_i < J_S, \\ \left[\exp\left(\frac{2v_\tau J_S^2}{s}\right) - 1\right] \exp\left(-\frac{2v_\tau J_S}{s} N_i\right) \left(\frac{1}{J_S v_\tau N_i}\right) dN_i & N_i \geq J_S \end{cases} \end{aligned} \tag{6}$$

Here $\exp(-2v_\tau J_S N_i/s)$ is an exponential function. Integrating this expression yields the average species longevity

$$\begin{aligned} \langle k \rangle &= \int_0^\infty \phi(J_S, N_i) dN_i \\ &= \frac{\gamma + \exp(2J_S^2 v_\tau/s) E_1(2J_S^2 v_\tau/s) + \ln(2J_S^2 v_\tau/s)}{J_S v_\tau} \end{aligned} \tag{7}$$

where γ is Euler’s constant (~ 0.577216) and $E_1(2J_S^2 v_\tau/s)$ is an exponential integral function.

Equations 6 and 7 yield expressions for steady-state biodiversity in the metacommunity. Species richness is equal to

$$S_M = V_M \langle k \rangle = J_M v_\tau \langle k \rangle \tag{8}$$

because V_M speciation events and V_M extinction events occur per unit time, following the dynamic-equilibrium assumption (eqn 1, Fig. 1). The frequency distribution of species abundance is similarly calculated. Specifically, $V_M \langle \phi(J_S, N_i) \rangle dN_i$ is the expected number of species in the abundance interval $(N_i - dN_i/2, N_i + dN_i/2)$ (Maruyama 1977; Engen & Lande 1996). Here $\langle \phi(J_S, N_i) \rangle$ is used to denote an average across species because our model can accommodate variation among taxa in J_S , v_τ , and s (see Engen & Lande 1996 for theoretical justification). Performing a change of variables in this expression ($N_i \rightarrow P_i J_M$, $J_S \rightarrow P_S J_M$) yields the probability, $f(P_i) dP_i$, that the proportional abundance of a species is in the interval $(P_i - dP_i/2, P_i + dP_i/2)$:

$$\begin{aligned} f(P_i) dP_i &= \frac{V_M \langle \phi(J_M P_S, J_M P_i) \rangle}{S_M} d(J_M P_i) \\ &= \frac{\langle \phi(J_M P_S, J_M P_i) \rangle}{\langle k \rangle} d(J_M P_i) \\ &= \begin{cases} \left\langle \frac{1 - \exp(-\theta P_i)}{[\gamma + \exp(\theta P_S) E_1(\theta P_S) + \ln(\theta P_S)] P_i} \right\rangle dP_i & P_i < P_S \\ \left\langle \frac{[\exp(\theta P_S) - 1] \exp(-\theta P_i)}{[\gamma + \exp(\theta P_S) E_1(\theta P_S) + \ln(\theta P_S)] P_i} \right\rangle dP_i & P_i \geq P_S \end{cases} \end{aligned} \tag{9}$$

where

$$\theta = \frac{2J_M v_\tau J_S}{s} = \frac{2S_M J_S}{s \langle k \rangle} = \frac{2V_M P_S J_M}{s} \tag{10}$$

and P_S is the incipient-species proportion ($= J_S/J_M$).

The dimensionless parameter in eqn 10 is denoted by θ because it is equivalent to the NBT biodiversity parameter of Volkov *et al.* (2003, 2005) (see Online Supplement S4). Specifically, our model and those of Volkov *et al.* (2003, 2005) yield species frequencies that asymptotically approach Fisher’s log-series distribution (Fisher *et al.* 1943), characterized by θ , as $P_i \rightarrow 1$. Consequently, frequencies of abundant species are governed largely by θ , as noted by McGill *et al.* (2006). Combining eqn 10 with Hubbell’s (2001) original expression for θ ($= 2J_M v$) yields

$$v = \frac{v_\tau J_S}{s} \tag{11}$$

Thus, v is interpreted as a per-capita probability of speciation (individuals⁻¹) in our model, consistent with how the parameter was defined in *Introduction*.

RESULTS

Equations 1–11 link the absolute tempo of biodiversity dynamics in the metacommunity (eqns 1, 2, 6, 7) to steady-state biodiversity (eqns 8–11) based on the deterministic effects of speciation (eqn 3), and the stochasticity effects of

Table 1 Compilation of empirical data for the global metacommunity of planktonic foraminifera

Parameter	Empirical data	
	Estimate	Timespan of data (source of data)
J_M	5.6×10^{17} individuals	Contemporary (Allen <i>et al.</i> 2006)
S_M	32 species	Contemporary (Fig. 4)
θ	5.3	Contemporary (Fig. 4)
P_S	6.8×10^{-4} species $^{-1}$	Contemporary (Fig. 4)
V_M	4.7 species Myr $^{-1}$	30-Myr average (Allen <i>et al.</i> 2006)
$\langle l_S \rangle$	6.6 Myr	30-Myr average (Stewart & Pearson 2000)

Sources and timespans of data used to obtain the estimates are listed.

demographic and environmental variables (eqns 4 and 5), on population abundance. Combining these equations with contemporary and fossil data for planktonic foraminifera (Table 1) yields the following four italicized statements.

(1) *The incipient-species abundance, the per-capita speciation rate and the population-level stochasticity combine to determine species longevity and richness in ways that are explicitly quantified by the model.* We explore the dynamics of the model for 10-fold ranges of parameter values that are centred on empirical estimates of J_S , v_τ , and s (closed circles in Figs 2 and 3) for planktonic foraminifera (see Table 1 and calculations below). The average species longevity, $\langle l_S \rangle$ (eqn 7), increases with the incipient-species abundance (Fig. 2a), J_S , indicating that macroevolutionary dynamics are sensitive to the mode of speciation. Longevity declines with increases in the per-capita speciation rate, v_τ (Fig. 2b), because macroevolutionary-scale changes in abundance are negatively and directly coupled to speciation rates (eqns 2 and 3). Both of these findings are consistent with the computer simulations of Hubbell & Lake (2003). Here we build on this work by using

well-established mathematical techniques (see Online Supplements 1–4) to derive analytical expressions that characterize the absolute tempo of these dynamics (eqns 6 and 7), and their effects on the species-abundance distribution (eqns 8–11). Because these expressions have absolute time units, we obtain the additional insight that longevity is particularly sensitive to the per-capita stochasticity, s (Fig. 2c) for this range of parameter values. Thus, the demographic and environmental processes that control stochastic population dynamics are also primary determinants of macroevolutionary extinction rates.

Because of its relationship to longevity, species richness, S_M (eqn 8), is also sensitive to these three variables (Fig. 3). In particular, species richness increases with the speciation rate (Fig. 3b), in agreement with recent empirical work (Allen & Gillooly 2006), but declines with increasing stochasticity (Fig. 3c). The latter finding accords with intuition that greater population-level stochasticity should increase the susceptibility of species to extinction, thereby resulting in fewer species when metacommunity size, J_M ,

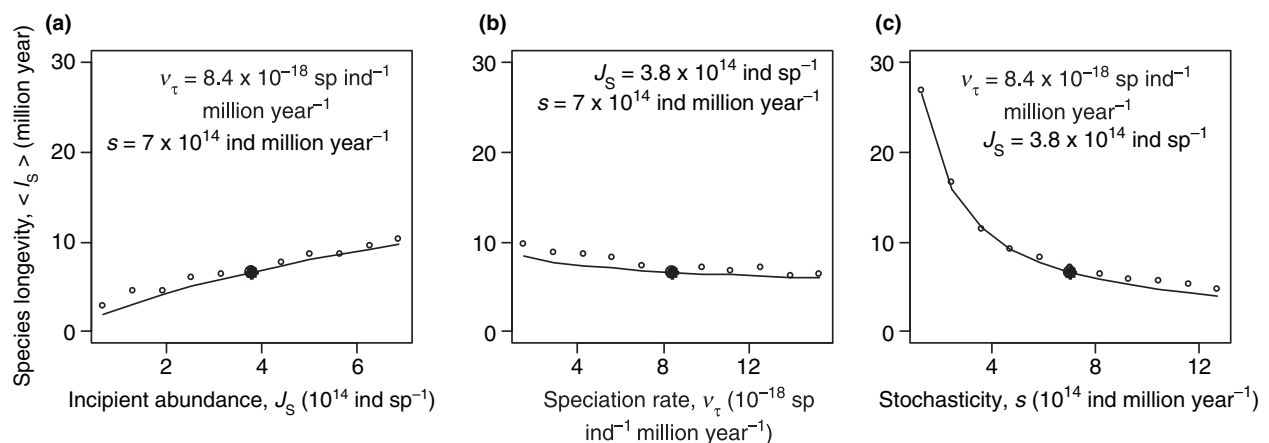


Figure 2 Relationship of the average species longevity, $\langle l_S \rangle$ (Myr), to each of following three variables, holding the others constant: (a) incipient-species abundance, J_S (individuals species $^{-1}$); (b) per-capita speciation rate, v_τ (species individual $^{-1}$ Myr $^{-1}$); and (c) abundance stochasticity, s (individuals Myr $^{-1}$). The lines are analytical predictions from eqn 7. Each open circle represents an average of 10 000 computer-simulation trials that enforce integer abundances for species at discrete 0.1-Myr time steps (see Online Supplement S5). Closed circles correspond to empirical estimates of the model parameters for planktonic foraminifera (Table 1).

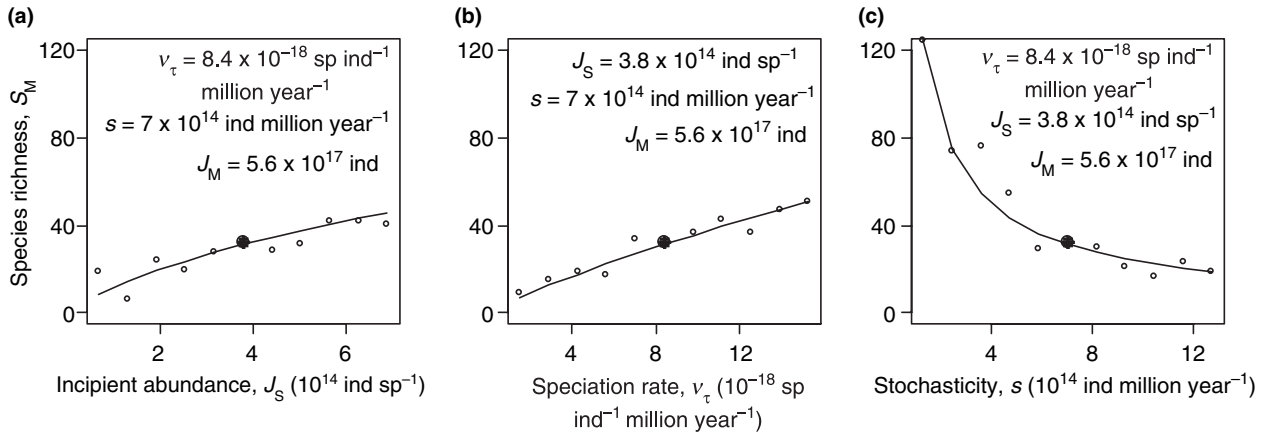


Figure 3 Relationship of species richness, S_M , to each of the following three variables, holding the others constant: (a) incipient-species abundance, J_S (individuals species $^{-1}$); (b) per-capita speciation rate, v_τ (species individual $^{-1}$ Myr $^{-1}$); and (c) abundance stochasticity, s (individuals Myr $^{-1}$). The lines are analytical predictions from eqns 7 and 8. Each open circle represents an average of 10 000 computer-simulation trials that enforce integer abundances for species at discrete 0.1-Myr time steps (see Online Supplement S5). Closed circles correspond to empirical estimates of the model parameters for planktonic foraminifera (Table 1).

and speciation rate, V_M , are held constant. In general, we note excellent agreement between analytical predictions of the model (lines in Figs 2 and 3), which treats abundance as a continuous variable, and computer simulations (open circles), which enforce integer abundances for species at discrete time steps (see Online Supplement S5).

(2) *Metacommunity-level data indicate that the incipient-species abundance is orders of magnitude greater than a single individual.* Using eqn 9, we can estimate the incipient-species abundance from the species-abundance distribution. We do so by combining the estimated metacommunity abundance ($J_M \approx 5.6 \times 10^{17}$ individuals, Table 1) with estimates of proportional abundance, P_i , for contemporary taxa comprising the global metacommunity of planktonic foraminifera (Prell *et al.* 1999). Submitting these data to maximum-likelihood analyses (see Online Supplement S6) yields estimates for the biodiversity parameter ($\hat{\theta} = 5.3$; 95% CI 1.6–12.2) and the incipient-species proportion ($\hat{P}_S = 6.8 \times 10^{-4}$ species $^{-1}$; 95% CI 1.6×10^{-4} – 4.4×10^{-3}) (Fig. 4). The latter estimate implies that the average incipient-species abundance is extremely high: $J_S = \hat{P}_S J_M = 3.8 \times 10^{14}$ individuals species $^{-1}$. Qualitatively, this finding is consistent with molecular and fossil evidence indicating that foraminifera speciation often entails genetic divergence among large, regionally distributed populations (Wei & Kennett 1988; Lazarus *et al.* 1995; Spencer-Cervato & Thierstein 1997; de Vargas *et al.* 1999; Darling *et al.* 2004). Quantitatively, this finding is consistent with the high stochasticity observed for population-level data, as discussed below in relation to statement (4).

(3) *Metacommunity-level data indicate that environmental stochasticity is the primary determinant of stochastic population dynamics.* Using eqn 10, we can infer the per-capita stochasticity, s ,

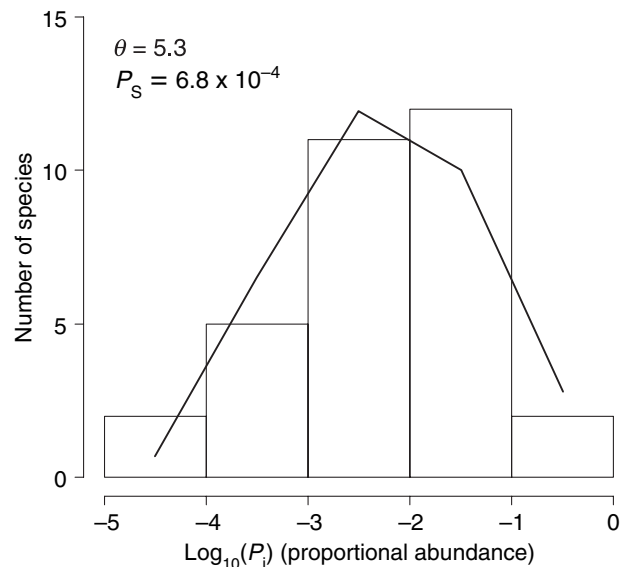


Figure 4 Species-abundance distribution for the global metacommunity of planktonic foraminifera. Estimates of the biodiversity parameter, θ (eqn 10), and the incipient-species proportion, P_S , were obtained by fitting the species-abundance distribution of our model (lines, eqn 9) to empirical data (bars) using the method of maximum likelihood (see Online Supplement S6). The species-abundance distribution was estimated by taking arithmetic averages of morphospecies-level data for a global compilation of 1265 local community samples in the Brown University Foraminiferal Database (Prell *et al.* 1999). Data were aggregated for the *Globorotalia menardii* complex due to variation among samples in taxonomic resolution.

from metacommunity-level data. To do so, we combine our contemporary estimates of S_M , θ and P_S (Fig. 4) with fossil estimates of metacommunity dynamics (Table 1). These

data yield two estimates for the stochasticity parameter: $s = 2V_M P_S / \theta = 6.8 \times 10^{14}$ individuals Myr^{-1} (95% CI 6.8×10^{13} – 1.5×10^{16}), and $s = 2S_M P_S / \langle l_s \rangle \theta = 7.0 \times 10^{14}$ individuals Myr^{-1} (95% CI 7.0×10^{13} – 1.6×10^{16}). The consistency of these estimates implies that the dynamic-equilibrium assumption is a reasonable first approximation for foraminifera (Fig. 1), meaning that $S_M \approx V_M \langle l_s \rangle$ (eqn 8).

Using eqns 4 and 5, we can infer the contribution of environmental stochasticity, s_e , to the total per-capita stochasticity, s , by estimating the expected demographic stochasticity, s_d . Given that foraminifera have generation times, g , of *c.* 1 month to 1 year (Hemleben *et al.* 1989), the expected contribution of demographic stochasticity is $s_d \approx 1/g \approx 10^6$ – 10^7 individuals Myr^{-1} (following eqn 5). This expectation is about eight orders of magnitude lower than the total per-capita stochasticity, s , inferred from metacommunity-level data. These findings indicate that environmental stochasticity is the primary determinant of stochastic population dynamics (i.e. $s_d \ll s_e \approx s$ in eqn 4). This conclusion is consistent with previous NBT studies, which demonstrate that demographic stochasticity alone cannot account for the metacommunity dynamics observed in nature (Leigh 1981; Clark & McLachlan 2003; Lande *et al.* 2003; Ricklefs 2003; McGill *et al.* 2005; Nee 2005; Ricklefs 2006).

(4) *Population-level data support statements (2) and (3) that environmental stochasticity is the primary determinant of stochastic population dynamics, and that the incipient-species abundance is orders of magnitude greater than 1 individual species⁻¹.* We can obtain approximate estimates for the per-capita stochasticity, s , using population-level data in the Specmap database (McIntyre *et al.* 1989; Imbrie *et al.* 1992). This database is remarkable in terms of its time span (the last 240 000 years), resolution (5000 years) and spatial extent (seven sites in the Atlantic Ocean spanning 37.27° S to 18.43° N). Analysing these data as described in Online Supplement S7 yields s values that range from 6.3×10^{14} to 6.1×10^{16} individuals Myr^{-1} (Fig. 5). These direct estimates of population-level stochasticity are similar in magnitude to the values inferred from metacommunity-level data, and are again much greater in magnitude than the expected demographic stochasticity ($\sim 10^6$ – 10^7 individuals Myr^{-1}). These findings serve to reinforce the importance of environmental stochasticity, consistent with statement (3).

This high population-level stochasticity implies that the incipient-species abundance is orders of magnitude greater than a single individual, consistent with statement (2). For example, taking s to be 7.0×10^{14} individuals Myr^{-1} , V_M to be 4.7 species Myr^{-1} , and v_t to be $V_M/J_M = 8.4 \times 10^{-18}$ species individual⁻¹ Myr^{-1} (Table 1), species richness would be negligible if the incipient-species abundance were $J_s = 1$ individual species⁻¹ (following eqns 7 and 8). Richness

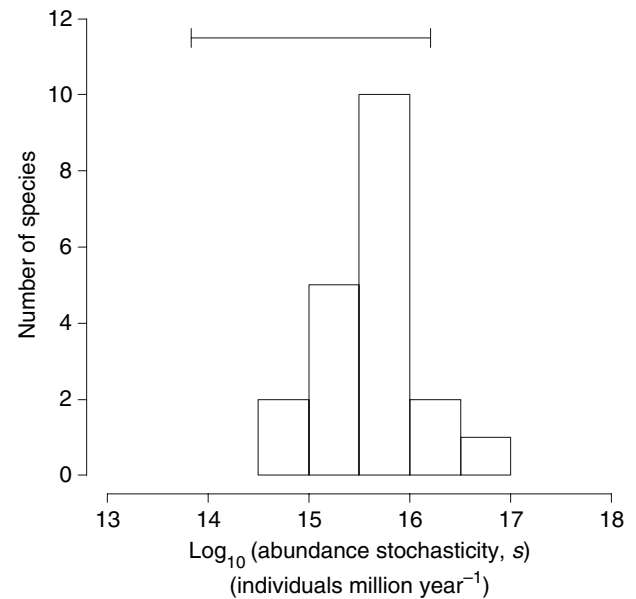


Figure 5 Frequency distribution of per-capita stochasticity estimates, s (eqn 5), derived from time-series data for 20 morphospecies of planktonic foraminifera. Estimates were derived as described in Online Supplement S7 using 240 000 years of population-level data (McIntyre *et al.* 1989; Imbrie *et al.* 1992). The bar above the histogram represents a 95% confidence interval for s , which was independently inferred from metacommunity-level data as described in statement (3) of the *Results* section.

would, in fact, still be negligible if the incipient-species abundance were ‘only’ $J_s = 10^{10}$ individuals species⁻¹ because the species longevity would only be $\langle l_s \rangle = 775$ years, and not 6.6 Myr, as observed empirically (Table 1). As this example demonstrates, to reconcile contemporary biodiversity with macroevolutionary dynamics (Table 1) we must invoke high incipient-species abundance to account for the species-abundance distribution of the metacommunity (Fig. 4).

DISCUSSION

Our synthesis of theory with empirical data provides the first evidence that the two dynamical issues with NBT (highlighted in *Introduction*) may be resolved by incorporating the effects of environmental stochasticity and incipient-species abundance on the absolute tempo of biodiversity dynamics. With respect to the first issue, incorporating environmental stochasticity reduces the longevities of abundant species, as hypothesized by Ricklefs (2006). With respect to the second issue, the model derivation demonstrates that the average species longevities increase with J_s (Fig. 2a), and that $\theta \propto J_s$ (eqn 10). Thus, the speciation rate, V_M , required to maintain a given amount of biodiversity in

the metacommunity can be reduced by increasing the incipient-species abundance, as noted by Hubbell (2005). The model and foraminifera data indicate that θ is of moderate magnitude (5.3; Fig. 4), despite a low speciation rate ($V_M \approx 4.7$ species Myr⁻¹; Table 1) and high population-level stochasticity ($s \approx 10^{15}$ individuals Myr⁻¹; Fig. 5), because incipient-species abundances are very large ($J_S = P_S J_M \approx 3.8 \times 10^{14}$ individuals species⁻¹; Fig. 4, Table 1). These parameter values yield an estimate of average species longevity that is consistent with empirical data.

These findings contrast with those of Lande *et al.* (2003), who conclude that realistic estimates of demographic and environmental stochasticity yield species longevities that are orders of magnitude too long for abundant species. Our theory and data differ from those considered by Lande *et al.* (2003) in two important ways. First, with respect to the theory, Lande *et al.* (2003) assume constant (i.e. stationary) carrying capacities for species populations when calculating expected times to extinction. Lande *et al.* (2003) note, however, that 'real environments over very long time scales are actually non-stationary because of long-term climate change and extremely rare catastrophes, both of which are well documented in paleoclimatology' (p. 46). Our model addresses the issue of non-stationary carrying capacities indirectly, at the metacommunity level, by imposing the zero-sum assumption, which dynamically links speciation to changes in population abundance (eqn 3). This dynamic coupling reduces the expected time to extinction (Fig. 2b). Second, with respect to the data, Lande *et al.*'s (2003) estimates of environmental stochasticity were obtained using ecological-scale time series (i.e. 10⁰–10² years in length). By contrast, our estimates encompass long-term climatic changes (i.e. 10³–10⁵ years), and therefore are likely of greater magnitude, which also reduces the expected time to extinction (Fig. 2c). The general consistency of our direct estimates of stochasticity with those inferred from metacommunity-level data suggests that our model characterizes linkages between contemporary biodiversity, population dynamics and metacommunity dynamics. In interpreting these findings, it is important to note, however, that the stochasticity estimates are approximate (see Online Supplement S7) and vary by several orders of magnitude.

We consider two limitations of the model presented here to highlight areas for future research. First, the model does not explicitly account for variation in the incipient-species abundances, J_S , although it can accommodate such variation by averaging over a range of J_S values (eqn 9). Consequently, our maximum-likelihood estimate for J_S represents an average, and the extent to which J_S varies remains an open question. Ideally, one would hope to predict the frequency distribution of J_S values based on dynamical mechanisms. These mechanisms will likely vary considerably among taxa

depending upon their particular speciation modes (Coyne & Orr 2004).

Second, the model presented here assumes that environmental stochasticity scales proportionally with population abundance (eqn 4), and that population dynamics follow simple diffusion (eqn 5). In reality, however, population dynamics may be correlated over broad spatial and temporal scales (Lande *et al.* 1999). For example, population dynamics of some foraminifera taxa have exhibited significant periodicity in response to glacial–interglacial cycles (McIntyre *et al.* 1989; Imbrie *et al.* 1992), which encompass only about the last 2 Myr of evolutionary history. Our modelling framework could be extended to encompass broad-scale correlated behaviour by introducing additional parameters into eqn 4. The population-level data analysed here are only regional in extent, and therefore cannot be used to evaluate such extensions of the model. However, in future work, it may be possible to determine whether additional parameters are necessary by analysing frequency distributions of species longevities. Such analyses will require longevity data of high quality (Pigolotti *et al.* 2005).

These two limitations highlight the challenges involved in formulating and testing biodiversity theory. Nevertheless, even if refinements of the model are required, we expect statements (1)–(4) to remain true for two reasons. First, population-level stochasticity is far greater than can be accounted for by demographic processes for foraminifera (Fig. 5). Second, given this high stochasticity, incipient-species abundances must be orders of magnitude greater than a single individual to reconcile contemporary biodiversity with speciation rates in the fossil record (Table 1), as highlighted above in relation to statement (4).

We conclude by considering whether our model and results support the assumption of 'neutrality'. Using the strictest definition of the term, the answer is clearly no because we must invoke environmental stochasticity as a driver of metacommunity dynamics. In doing so, we also implicitly invoke niche differences among species. For example, laboratory experiments demonstrate that foraminifera taxa vary considerably in their temperature tolerances (Hemleben *et al.* 1989), and previous Specmap studies demonstrate that cold-adapted taxa have generally maintained higher relative abundances during glacial periods (McIntyre *et al.* 1989; Imbrie *et al.* 1992). The population-level stochasticity we observe for foraminifera (Fig. 5) is thus partly a consequence of niche-related differences in how taxa respond to changes in climate. In short, if environmental stochasticity matters, so do species' niches. Therefore, we propose that a primary effect of niche differences among species is to rescale the absolute tempo of biodiversity dynamics in an ever-changing abiotic and biotic environment.

Despite these complications, biodiversity dynamics may adhere to the ‘neutrality’ assumption if the term is much more broadly defined to mean that the per-capita rates of abundance increase and decrease (characterized by s and v , see Online Supplement S4) are largely independent of species identity and age at macroevolutionary time scales (Volkov *et al.* 2005). This macroevolutionary-scale definition can encompass environmental stochasticity, and hence niche differences among species. Intriguingly, this definition is also consistent with the Red Queen hypothesis, which explicitly invokes species differences in support of the proposition that the ‘environment of any homogenous group of organisms deteriorates at a stochastically constant rate’ (Van Valen 1973). If deterioration of the environment is viewed in terms of per-capita losses of individuals, this rate is precisely what is characterized by eqn 3 of our model.

ACKNOWLEDGEMENTS

APA was supported as a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by National Science Foundation Grant DEB-0072909, and the University of California, Santa Barbara. VMS thanks Walter Fontana’s laboratory in the Systems Biology Department at Harvard Medical School for support and enlightening conversations. We thank Jérôme Chave, James Gillooly, Stephen Hubbell, Allen Hurlbert, Pablo Marquet, Carlos Melián, John Orrock, Pippi Ruskin and two anonymous referees for helpful comments on the manuscript.

REFERENCES

- Allen, A.P. & Gillooly, J.F. (2006). Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.*, *9*, 947–954.
- Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *PNAS*, *103*, 9130–9135.
- Azaele, S., Pigolotti, S., Banavar, J.R. & Maritan, A. (2006). Dynamical evolution of ecosystems. *Nature*, *444*, 926–928.
- Casey, K.S. & Cornillon, P. (1999). A comparison of satellite and *in situ*-based sea surface temperature climatologies. *J. Clim.*, *12*, 1848–1863.
- Clark, J.S. & McLachlan, J.S. (2003). Stability of forest biodiversity. *Nature*, *423*, 635–638.
- Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinaur Associates, Sunderland, MA.
- Darling, K.F., Kucera, M., Pudsey, C.J. & Wade, C.M. (2004). Molecular evidence links cryptic diversification in polar planktonic protists to quaternary climate dynamics. *PNAS*, *101*, 7657–7662.
- Engen, S. & Lande, R. (1996). Population dynamic models generating the lognormal species abundance distribution. *Math. Biosci.*, *132*, 169.
- Engen, S., Bakke, O. & Islam, A. (1998). Demographic and environmental stochasticity – concepts and definitions. *Biometrics*, *54*, 840–846.
- Ewens, W.J. (2004). *Mathematical Population Genetics I. Theoretical Introduction*. Springer-Verlag, New York.
- Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.*, *12*, 42–58.
- Hemleben, C., Spindler, M. & Andersen, O.R. (1989). *Modern Planktonic Foraminifera*. Springer-Verlag, New York.
- Hickerson, M.J., Gilchrist, M.A. & Takebayashi, N. (2003). Calibrating a molecular clock from phylogeographic data: moments and likelihood estimators. *Evolution*, *57*, 2216–2225.
- Hu, X.S., He, F. & Hubbell, S.P. (2006). Neutral theory in macroecology and population genetics. *Oikos*, *113*, 548–556.
- Hubbell, S.P. (2001). *A Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hubbell, S.P. (2003). Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs. *Oikos*, *100*, 193–199.
- Hubbell, S.P. (2005). The neutral theory of biodiversity and biogeography and Stephen Jay Gould. *Paleobiology*, *31*, 122–132.
- Hubbell, S.P. & Lake, J.K. (2003). The neutral theory of biodiversity and biogeography, and beyond. In: *Macroecology: Patterns and Processes* (eds. Blackburn, T.M. & Gaston, K.J.). Blackwell, Oxford.
- Imbrie, J., Boyle, E.A., Clemens, S.C., Duffy, A., Howard, W.R.K., Kutzbach, J. *et al.* (1992). On the structure and origin of major glaciation cycles. 1. Linear responses to Milankovitch forcing. *Paleoceanography*, *7*, 701–738.
- Karlin, S. & Taylor, H.M. (1981). *A Second Course in Stochastic Processes*. Academic Press, New York.
- Keeling, M.J. (2000). Simple stochastic models and their power-law type behaviour. *Theor. Pop. Biol.*, *58*, 21–31.
- Keitt, T.H., Amaral, L.A.N., Buldyrev, S.V. & Stanley, H.E. (2002). Scaling in the growth of geographically subdivided populations: invariant patterns from a continent-wide biological survey. *Philos. Trans. R. Soc. Lond.*, *357*, 627–633.
- Lande, R., Engen, S. & Saether, B.E. (1999). Spatial scale of population synchrony: environmental correlation vs. dispersal and density regulation. *Am. Nat.*, *154*, 271–281.
- Lande, R., Engen, S. & Saether, B.E. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, UK.
- Lazarus, D., Hilbrecht, H., Spencer-Cervato, C. & Thierstein, H. (1995). Sympatric speciation and phyletic change in Globorotalia truncatulinoides. *Paleobiology*, *21*, 28–51.
- Leigh, E.G. (1981). The average lifetime of a population in a varying environment. *J. Theor. Biol.*, *90*, 213–239.
- Levinton, J.S. (1979). Theory of diversity equilibrium and morphological evolution. *Science*, *204*, 335–336.
- Maruyama, T. (1977). *Stochastic Problems in Population Genetics*. Springer-Verlag, New York.
- McGill, B.J., Hadly, E.A. & Maurer, B.A. (2005). Community inertia of quaternary small mammal assemblages in North America. *PNAS*, *102*, 16701–16706.
- McGill, B.J., Maurer, B.A. & Weiser, M.D. (2006). Empirical evaluation of neutral theory. *Ecology*, *87*, 1411–1423.

- McIntyre, A., Ruddiman, W.F., Karlin, K. & Mix, A.C. (1989). Surface water response of the equatorial Atlantic ocean to orbital forcing. *Paleoceanography*, 4, 19–55.
- McKane, A., Alonso, D. & Sole, R.V. (2000). Mean-field stochastic theory for species-rich assembled communities. *Phys. Rev. E*, 62, 8466–8484.
- Nee, S. (2005). The neutral theory of biodiversity: do the numbers add up? *Funct. Ecol.*, 19, 173–176.
- Niklas, K.J., Tiffney, B.H. & Knoll, A.H. (1983). Patterns in vascular land plant diversification. *Nature*, 303, 614.
- Patterson, R.T., Fowler, A.D. & Huber, B.T. (2004). Evidence of hierarchical organization in the planktic foraminiferal evolutionary record. *J. Foramin. Res.*, 34, 85–95.
- Pigolotti, S., Flammini, A., Marsili, M. & Maritan, A. (2005). Species lifetime distribution for simple models of ecologies. *PNAS*, 102, 15747–15751.
- Prell, W., Martin, A., Cullen, J. & Trend, M. (1999). *Brown University Foraminiferal Database*. NOAA/NGDC Paleoclimatology Program, Boulder, CO.
- Rice, S.H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sinauer Associates, Sunderland, MA.
- Ricklefs, R.E. (2003). A comment on Hubbell's zero-sum ecological drift model. *Oikos*, 100, 185–192.
- Ricklefs, R.E. (2006). The unified neutral theory of biodiversity: do the numbers add up? *Ecology*, 87, 1424–1431.
- Spencer-Cervato, C. (1999). The Cenozoic deep sea microfossil record: explorations of the DSDP/ODP sample set using the Neptune Database. *Palaeont. Electron.*, 2, 4.
- Spencer-Cervato, C. & Thierstein, H.R. (1997). First appearance of Globorotalia truncatulinoides: cladogenesis and immigration. *Mar. Micropaleontol.*, 30, 267–291.
- Stewart, D.R.M. & Pearson, P.N. (2000). *PLANKRANGE: A Database of Planktonic Foraminiferal Ranges*. Available at: <http://palaeo.gly.bris.ac.uk/Data/plankrange.html>, accessed 12/1/2002.
- Sun, G., Dilcher, D.L., Zheng, S. & Zhou, Z. (1998). In search of the first flower: a Jurassic angiosperm, *Archaeofructus*, from northeast China. *Science*, 282, 1692–1695.
- Van Valen, L. (1973). A new evolutionary law. *Evol. Theory*, 1, 1–30.
- de Vargas, C., Norris, R., Zaninetti, L., Gibb, S.W. & Pawlowski, J. (1999). Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces. *PNAS*, 96, 2864–2868.
- Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in Ecology. *Nature*, 424, 1035–1037.
- Volkov, I., Banavar, J.R., He, F., Hubbell, S.P. & Maritan, A. (2005). Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, 438, 658.
- Wei, K.Y. & Kennett, J.P. (1986). Taxonomic evolution of neogene planktonic foraminifera and paleoceanographic relations. *Paleoceanography*, 1, 67–84.
- Wei, K.-Y. & Kennett, J.P. (1988). Phyletic gradualism and punctuated equilibrium in the Late Neogene planktonic foraminiferal clade *Globoconella*. *Paleobiology*, 14, 345.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 A pdf-file consisting of the following:

- **S1** The Kolmogorov Backward Equation (Eqs 3, 4)
- **S2** Approximation for the variance terms s (Eq. 5).
- **S3** Green's Function Solution to the Kolmogorov Backward Equation (Eq. 6)
- **S4** Relationship of our model to those of Volkov *et al.* (2003, 2005) (Eqs 9–10)
- **S5** Computer simulation trials (Figs. 2–3)
- **S6** Maximum-likelihood estimation of θ and P_s (Fig. 4)
- **S7** Obtaining approximate estimates of s using the Specmap data (Fig. 5)
- **References**

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01057.x>

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, Jérôme Chave

Manuscript received 29 August 2006

First decision made 3 October 2006

Second decision made 12 January 2007

Manuscript accepted 18 April 2007

1 **S1. The Kolmogorov Backward Equation (Eqs. 3, 4)**

2 The Kolmogorov backward equation is derived in standard textbooks on stochastic
 3 processes (e.g. Maruyama 1977; Karlin & Taylor 1981; Ewens 2004; Rice 2004). Here,
 4 following Rice (2004), we provide a simple derivation of this equation to aid the reader in
 5 its interpretation. Let $p(N_i, t | N_0)$ be the probability density that the abundance of a
 6 given species i is equal to N_i at time t given that its abundance was equal to N_0 at time
 7 0. And let $g(N_0 + \varepsilon, \Delta t | N_0)$ be the probability that abundance changes from N_0 to
 8 $N_0 + \varepsilon$ over some other time interval Δt . We obtain an integro-equation for
 9 $p(N_i, t | N_0)$ by observing that

$$10 \quad p(N_i, t + \Delta t | N_0) = \int_{-N_0}^{\infty} p(N_i, t | N_0 + \varepsilon) g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon \quad (\text{A1})$$

11 This equation states that the probability of going from N_0 to N_i in time $t + \Delta t$ is equal to
 12 the probability of going from N_0 to $N_0 + \varepsilon$ in time Δt multiplied by the probability of
 13 going from $N_0 + \varepsilon$ to N_i in time t . By integrating over all possible values of ε , Eq. A1
 14 encompasses all paths from N_0 to N_i .

15 To derive the Kolmogorov backward equation from Eq. A1, we first perform a
 16 Taylor expansion of $p(N_i, t | y)$ about the point $y = N_0$ to obtain the following
 17 expression:

$$18 \quad p(N_i, t | N_0 + \varepsilon) = p(N_i, t | N_0) + \varepsilon \frac{\delta p(N_i, t | N_0)}{\delta N_0} + \frac{\varepsilon^2}{2} \frac{\delta^2 p(N_i, t | N_0)}{\delta N_0^2} + O(\varepsilon^3) \quad (\text{A2})$$

19 Combining Eqs. A1 and A2 yields

$$\begin{aligned}
& p(N_i, t + \Delta t | N_0) = \\
& \int_{-N_0}^{\infty} \left[p(N_i, t | N_0) + \varepsilon \frac{\partial p(N_i, t | N_0)}{\partial N_0} + \frac{\varepsilon^2}{2} \frac{\partial^2 p(N_i, t | N_0)}{\partial N_0^2} \right] g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon = \\
1 \quad & \int_{-N_0}^{\infty} p(N_i, t | N_0) g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon + \int_{-N_0}^{\infty} \varepsilon \frac{\partial p(N_i, t | N_0)}{\partial N_0} g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon \quad (A3) \\
& + \frac{1}{2} \int_{-N_0}^{\infty} \varepsilon^2 \frac{\partial^2 p(N_i, t | N_0)}{\partial N_0^2} g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon
\end{aligned}$$

2 We can take $p(N_i, t | N_0)$ and its partial derivatives outside of the integrals because they
3 do not depend on ε . After noting that $\int_{-N_0}^{\infty} g(N_0 + \varepsilon, \Delta t | N_0) d\varepsilon = 1$ because we are
4 integrating over all values of ε , we can rearrange terms in Eq. A3, and then take the limit
5 as $\Delta t \rightarrow 0$, to obtain the Kolmogorov backward equation

$$6 \quad \frac{\partial p(N_i, t | N_0)}{\partial t} = M(N_0) \frac{\partial p(N_i, t | N_0)}{\partial N_0} + \frac{V(N_0)}{2} \frac{\partial^2 p(N_i, t | N_0)}{\partial N_0^2} \quad (A4)$$

7 where

$$8 \quad M(N_0) = \lim_{\Delta t \rightarrow 0} \frac{\int_{-N_0}^{\infty} g(N_0 + \varepsilon, \Delta t | N_0) \varepsilon d\varepsilon}{\Delta t} \quad (A5)$$

9 and

$$10 \quad V(N_0) = \lim_{\Delta t \rightarrow 0} \frac{\int_{-N_0}^{\infty} g(N_0 + \varepsilon, \Delta t | N_0) \varepsilon^2 d\varepsilon}{\Delta t} \quad (A6)$$

11 are the first and second moments for the instantaneous rate of change in abundance. In
12 the parlance of diffusion theory, $M(N_0)$ and $V(N_0)$ respectively represent the
13 deterministic drift coefficient and the stochastic diffusion coefficient of a one-
14 dimensional diffusion process.

1 As demonstrated by the derivation above, the Kolmogorov backward equation
 2 starts with the state of the system at time t , and then evolves backwards in time towards
 3 the initial state. Since each step backwards is contingent on this initial state, the backward
 4 equation characterizes the entire history of the system. This equation is perhaps less
 5 intuitive than the corresponding Kolmogorov forward equation (Eq. A7 below), which
 6 has a straightforward mapping onto the actual dynamics of a system. Nevertheless, it is
 7 frequently used in population genetics (Maruyama 1977; Karlin & Taylor 1981; Ewens
 8 2004; Rice 2004) because it yields predictions for many quantities of interest (e.g.
 9 lifetimes, abundances) using a straightforward approach involving Green's functions (see
 10 section S3 below).

11

12 **S2. Approximation for the variance term s (Eq. 5)**

13 Equation 5 is derived using the Kolmogorov forward equation:

$$14 \quad \frac{\partial p(N_i, t | N_0)}{\partial t} = -\frac{\partial}{\partial N_i} \{M(N_i)p(N_i, t | N_0)\} + \frac{\partial^2}{\partial N_i^2} \left\{ \frac{V(N_i)}{2} p(N_i, t | N_0) \right\} \quad (\text{A7})$$

15 which can also be obtained from Eq. A1 using a Taylor expansion (Karlin & Taylor
 16 1981; Ewens 2004; Rice 2004). In contrast with Eq. A4, Eq. A7 describes how the
 17 probability density function evolves forward in time t . Consequently, the first term in Eq.

18 A7, $-\frac{\partial}{\partial N_i} \{M(N_i)p(N_i, t | N_0)\}$, differs in sign from the first term in Eq. A4,

19 $M(N_0) \frac{\partial p(N_i, t | N_0)}{\partial N_0}$, and the drift and diffusion coefficients, $M(N_i)$ and $V(N_i)$, both

20 occur inside the partial derivatives.

1 Combining Eq. A7 with our expressions for $M(N_i)$ (Eq. 3) and $V(N_i)$ (Eq. 4)
 2 demonstrates that our model is a special case of Feller's equation (Feller 1951), which
 3 has been thoroughly analyzed (e.g. Feller 1951, 1952; Lehnigk 1993). In particular, we
 4 can obtain an analytical expression for $p(N_i, t | N_0)$ by combining Eqs. 3, 4, and A7 with
 5 Eq. 8.1.2 of Lehnigk (1993):

$$6 \quad p(N_i, t | N_0) = \sqrt{\frac{N_0}{N_i}} \left(\frac{2J_s v_\tau}{s} \right) \exp\left(- \left(\frac{2J_s v_\tau}{s} \right) \frac{(N_i + N_0 \exp(-J_s v_\tau t))}{(1 - \exp(-J_s v_\tau t))} \right) \times \quad (A8)$$

$$\left(\frac{\exp(-J_s v_\tau t / 2)}{(1 - \exp(-J_s v_\tau t))} \right) I_1 \left(2\sqrt{N_0 N_i} \left(\frac{2J_s v_\tau}{s} \right) \left(\frac{\exp(-J_s v_\tau t / 2)}{(1 - \exp(-J_s v_\tau t))} \right) \right)$$

7 Here $I_1(\)$ is a modified Bessel function of the first kind and order 1. For small values of
 8 t , such that $J_s v_\tau t \ll 1$, $(1 - \exp(-J_s v_\tau t)) \approx J_s v_\tau t$, and $\exp(-J_s v_\tau t) \approx 1$, Eq. A8 reduces
 9 to

$$10 \quad p(N_i, t | N_0) \approx \tilde{p}(N_i, t | N_0) = \left(\frac{2}{st} \right) \sqrt{\frac{N_0}{N_i}} \exp\left(- \left(\frac{2}{st} \right) (N_i + N_0) \right) I_1 \left(\left(\frac{4}{st} \right) \sqrt{N_0 N_i} \right) \quad (A9)$$

11 Equation A9 applies when the effects of speciation on changes in species abundance are
 12 negligible, relative to stochasticity, over the time interval 0 to t . The mean of this
 13 probability density function is equal to

$$14 \quad \int_0^\infty \tilde{p}(N_i, t | N_0) N_i dN_i = N_0 \quad (A10)$$

15 which is independent of time t , and therefore equal to the initial abundance, N_0 . The
 16 mean-squared displacement is therefore

$$17 \quad \langle (N_i - N_0)^2 \rangle_t = \int_0^\infty \tilde{p}(N_i, t | N_0) (N_i - N_0)^2 dN_i = N_0 st \quad (A11)$$

1 where N_i is the abundance of the given species i at time t . Integration of Eqs. A10-A11 is
 2 facilitated by noting that Eq. A9 can be converted to a non-central chi distribution in
 3 standard form by performing a substitution of variables. Rearranging the terms in Eq.
 4 A11 yields Eq. 5.

5

6 **S3. Green's Function Solution to the Kolmogorov Backward Equation (Eq. 6)**

7 Given that all species eventually go extinct due to speciation and stochasticity (i.e.
 8 $p(N_i, \infty | N_0) = 0$), we obtain the following expression by integrating the Kolmogorov
 9 backward equation (Eq. A4) with respect to time:

$$10 \quad -p(N_i, 0 | N_0) = \int_0^{\infty} \hat{A} p(N_i, 0 | N_0) dt = \hat{A} \int_0^{\infty} p(N_i, 0 | N_0) dt \quad (\text{A12})$$

11 where $\hat{A} \equiv \left(M(N_0) \frac{\partial}{\partial N_0} + \frac{V(N_0)}{2} \frac{\partial^2}{\partial N_0^2} \right)$ is a differential operator that is not time-

12 dependent and can therefore be pulled outside of the integral. We demand that the initial
 13 abundance take the specific value $N_0 = J_S$, so $p(N_i, 0 | J_S) = \delta(N_i - J_S)$, where $\delta(\cdot)$ is
 14 the delta function, and

$$15 \quad \hat{A} \phi(J_S, N_i) + \delta(N_i - J_S) = 0 \quad (\text{A13})$$

16 where

$$17 \quad \phi(J_S, N_i) \equiv \int_0^{\infty} p(N_i, t | J_S) dt \quad (\text{A14})$$

18 Equations A13-A14 demonstrate that $\phi(J_S, N_i)$ is the Green's function to this system of
 19 equations.

1 The Green's function solution depends crucially on the boundary conditions
 2 constraining the dynamics of the system. Here $N_0 = 0$ individuals is an absorbing
 3 boundary because a species can never reenter the metacommunity after going extinct, and
 4 $N_0 = \infty$ individuals is a reflecting boundary because speciation and stochasticity prevent
 5 any species population from ever becoming infinitely large. The derivations of Volkov *et*
 6 *al.* (2003; 2005) invoke these same assumptions because there exists a direct
 7 correspondence between our model and theirs (see Section S4 below). Given these
 8 boundary conditions, Eqs. 3, 4, A13, and A14 yield Eq. 6 in the text. (For the general
 9 solution see, for example, Eq. 4.57 of Maruyama 1977). Since $p(N_i, t | J_S) dN_i$ is the
 10 dimensionless probability that the species is in the abundance interval $(N_i - dN_i/2, N_i +$
 11 $dN_i/2)$ at time t , and therefore $p(N_i, t | J_S) dN_i dt$ is in units of time, the integral of this
 12 expression over all time, $\phi(J_S, N_i) dN_i$ (Eqs. 6, A14), is the expectation for the total
 13 amount of time that the focal species i spends in each abundance interval $(N_i - dN_i/2, N_i +$
 14 $dN_i/2)$ from its time of formation through speciation at abundance J_S to its time of
 15 extinction.

16

17 **S4. Relationship of our model to those of Volkov *et al.* (2003, 2005) (Eqs. 9-10)**

18 Equations 9-10 yield species frequencies that asymptotically approach Fisher's logseries
 19 distribution (Fisher *et al.* 1943), characterized by θ , as $P_i \rightarrow 1$. To demonstrate this, we
 20 characterize our continuous distribution (Eqs. 9-10) in terms of integer values, n , by
 21 performing the following integration (see, for example, Eq. 7.2 of Lande *et al.* 2003):

$$\langle \phi_n \rangle \approx S_M \int_0^1 f(P) \exp\left(-\left(J_M/J_M^0\right)P\right) \frac{\left(\left(J_M/J_M^0\right)P\right)^n}{n!} dP =$$

$$1 \quad (1/P_S)(\exp(P_S\theta)-1)\Gamma\left(n, J_M/J_M^0 + \theta\right) \frac{x^n}{n} \quad (\text{A15})$$

$$- (1/P_S)(\exp(P_S\theta)x^n\Gamma\left(n, \left(J_M/J_M^0 + \theta\right)P_S\right) - \Gamma\left(n, \left(J_M/J_M^0\right)P_S\right)) \frac{1}{n}$$

2 Here $\langle \phi_n \rangle$ is the number of species expected to take abundance n , and $\Gamma\left(n, J_M/J_M^0 + \theta\right)$

3 is an incomplete gamma function ($= \frac{1}{(n-1)!} \int_0^{J_M/J_M^0 + \theta} t^{n-1} e^{-t} dt$). The parameters θ (Eq. 10)

4 and

$$5 \quad x = \frac{s/2}{s/2 + J_M^0 v_\tau J_S} = \frac{J_M}{J_M + J_M^0 \theta} \quad (\text{A16})$$

6 are both dimensionless, as is made explicit by introducing $J_M^0 = 1$ individual into Eqs.

7 A15 and A16. The need for the term, J_M^0 , is further emphasized below in Eq. A23. The

8 gamma functions in the second term of Eq. A15 rapidly approach 0 when

9 $n-1 - \sqrt{n} > \left(J_M/J_M^0 + \theta\right)P_S$ (Press *et al.* 1992). Consequently, for larger values of n , Eq.

10 A15 approaches

$$11 \quad \langle \phi_n \rangle \approx (1/P_S) (\exp(P_S\theta)-1)\Gamma\left(n, J_M/J_M^0 + \theta\right) \frac{x^n}{n} \approx \theta \frac{x^n}{n} \quad (\text{A17})$$

12 The final expression in Eq. A17 is Fisher's logseries distribution (Fisher *et al.* 1943).

13 This final expression follows from the biologically reasonable assumption that $P_S \ll 1$

14 species⁻¹, which implies that $(1/P_S)(\exp(P_S\theta)-1) \approx \theta$, and from the large-

15 metacommunity assumption, which implies that $\Gamma\left(n, J_M/J_M^0 + \theta\right) \approx 1$.

16 The NBT derivations of Volkov *et al.* (2003; 2005) yield Fisher's logseries

17 distribution for the metacommunity in the limit of large J_M when $J_S = 1$ individual

1 species⁻¹. Volkov *et al.* have proposed two local-scale, ecological mechanisms to account
 2 for deviations of species-abundance distributions from logseries expectations at a local
 3 scale – dispersal-limitation (Volkov *et al.* 2003) and density-dependent population
 4 regulation (Volkov *et al.* 2005) – both of which yield distributions that are essentially
 5 identical in form. The density-dependent mechanism yields the following species-
 6 abundance distribution:

$$7 \quad \langle \phi_n \rangle = \theta \frac{x^n}{n + c} \quad (\text{A18})$$

8 where c is a parameter that characterizes the strength of density dependence. Given that c
 9 is finite and constant for all n in Eq. A18, this distribution also asymptotically approaches
 10 Fisher’s logseries distribution as $n \rightarrow \infty$. Thus, our expression for θ is equivalent to the
 11 biodiversity parameter in the NBT derivations of Volkov *et al.* (2003; 2005). There is,
 12 however, an important biological distinction between these models. Whereas our model
 13 predicts deviations of species frequencies from the logseries distribution at the
 14 metacommunity level whenever the incipient-species abundance $J_S > 1$ individual
 15 species⁻¹, the models of Volkov *et al.* (2003; 2005) predict deviations from a logseries
 16 distribution at the local level due to dispersal limitation and/or density-dependent
 17 population regulation.

18 The fundamental connection between our model and the models of Volkov *et al.*
 19 (2003; 2005) is further emphasized by comparing our Kolmogorov forward equation (Eq.
 20 A7) to their master equation for the metacommunity (Eq. A22 below). To do so, we note
 21 that

$$\begin{aligned}
& \frac{\delta}{\delta N} \{M(N)p(N, t | N_0)\} = \\
& \lim_{\Delta N \rightarrow 0} \frac{M(N + \Delta N)p(N + \Delta N, t | N_0) - M(N)p(N, t | N_0)}{\Delta N}
\end{aligned} \tag{A19}$$

and that

$$\begin{aligned}
& \frac{\delta^2}{\delta N^2} \{V(N)p(N, t | N_0)\} = \\
& \lim_{\Delta N \rightarrow 0} \frac{V(N + \Delta N)p(N + \Delta N, t | N_0) - 2V(N)p(N, t | N_0) + V(N - \Delta N)p(N - \Delta N, t | N_0)}{(\Delta N)^2}
\end{aligned} \tag{A20}$$

We obtain the discrete approximation of our Kolmogorov forward equation by inserting Eqs. A19-A20 into Eq. A7, and then rearranging terms:

$$\begin{aligned}
& \frac{\partial p(N, t | N_0)}{\partial t} \approx p(N + \Delta N, t | N_0) \left(\frac{V(N + \Delta N)}{2(\Delta N)^2} - \frac{M(N + \Delta N)}{\Delta N} \right) \\
& + p(N - \Delta N, t | N_0) \left(\frac{V(N - \Delta N)}{2(\Delta N)^2} \right) - p(N, t | N_0) \left(\frac{V(N)}{(\Delta N)^2} - \frac{M(N)}{\Delta N} \right)
\end{aligned} \tag{A21}$$

The derivation of Volkov *et al.* (2003; 2005) yields the following master equation for the metacommunity

$$\frac{dP_N(T)}{dT} = P_{N+1}(T)d_{N+1} + P_{N-1}(T)b_{N-1} - P_N(b_N + d_N) \tag{A22}$$

where $P_N(T)$ is the probability that the focal species has N individuals at discrete time step T , and b_N and d_N represent the respective probabilities of a population of size N increasing or decreasing by $\Delta N = 1$ individual during a discrete time interval $\Delta T = 1$ (Volkov *et al.* 2003). In our model, if Δt (in Ma) is chosen such that $\Delta N = 1$ individual, then $P_{N+1}(T)\Delta T \cong p(N + 1, \Delta t | N)\Delta t$. Consequently, given that $b_N = bN$, $d_N = dN$

1 (Volkov *et al.* 2003), we can equate the corresponding terms in Eqs. A21 and A22 to
 2 obtain

$$3 \quad x = \frac{b_N}{d_N} = \frac{b}{d} = \frac{V(N)/2}{V(N)/2 - \Delta N M(N)} = \frac{s/2}{s/2 + \Delta N v_\tau J_S} \quad (\text{A23})$$

4 Given that $\Delta N = 1$ individual, the final expression in Eq. A23 is identical to Eq. A16. In
 5 our model, $x < 1$ because the per-capita rate of increase in abundance is governed entirely
 6 by stochasticity, $s/2$, whereas the per-capita rate of decrease is governed by the sum of
 7 the contributions from stochasticity, $s/2$, and speciation, $\Delta N v_\tau J_S$, following the zero-sum
 8 assumption (Eqs. 2-3). Thus, Eq. A23 is consistent with the assertions of Volkov *et al.*
 9 (2003) and Hubbell (2005) that b must be less than d to maintain a metacommunity of
 10 finite size due to speciation.

11

12 **S5. Computer simulation trials (Figs. 2-3)**

13 Computer simulation trials were conducted by modeling integer changes in abundance at
 14 discrete 0.1-Myr time intervals. For the first time step of each simulation trial, $T = 0$, the
 15 species is assigned the abundance $N(0) = J_S$. For subsequent time steps, the procedure
 16 used to determine $N(T + 1)$ varies depending upon $N(T)$ because speciation can only
 17 occur if $N(T)$ exceeds the incipient-species abundance, J_S . The probability of speciation
 18 during a 0.1-Myr time interval is equal to $0.1v_\tau J(T)$. Therefore, if $N(T) > J_S$, then with
 19 probability $0.1v_\tau J(T)$, let $N(T + 1) = N(T) + R(-J_S, 0.1sN(T))$. Here $R(-J_S, 0.1sN(T))$ is a
 20 discrete random variable of variance $0.1sN(T)$ and mean $-J_S$, which corresponds to the
 21 number of individuals lost during a speciation event. If speciation does not occur during
 22 the time interval, then let $N(T + 1) = N(T) + R(0, 0.1sN(T))$. This procedure is repeated

1 until the time of extinction when $N(T + 1) \leq 0$ individuals. Our continuous approximation
 2 of this discrete process (Eqs. 3, 4, A4) has negligible error, as demonstrated by the
 3 simulation results depicted in Figs. 2-3, because $s/J_S v_\tau \gg 1$ individual.

4

5 **S6. Maximum-likelihood estimation of θ and P_S (Fig. 4)**

6 The function $f(P_i)dP_i$ (Eq. 9) characterizes the probability that species i is in the
 7 proportional abundance interval $(P_i - dP_i/2, P_i + dP_i/2)$. Therefore, to estimate θ and P_S
 8 using the data depicted in Fig. 4, we take the likelihood function to be:

$$9 \quad l(P_1, P_2, \dots, P_{S_M} | \theta, P_S) \propto \prod_{i=1}^{S_M} f(P_i) \quad (A24)$$

10 where S_M is the number of species in the metacommunity. The maximum likelihood
 11 estimates of θ and P_S are those that maximize the likelihood function. In practice, when
 12 searching for the maximum, it is suggested that the negative of the logarithm of the
 13 likelihood function be used (Hilborn & Mangel 1997):

$$14 \quad L(P_1, P_2, \dots, P_{S_M} | \theta, P_S) = C - \sum_{i=1}^{S_M} \log f(P_i) \quad (A25)$$

15 The parameter C is an arbitrary constant. The minimum of this function yields maximum-
 16 likelihood estimates for θ and P_S , and its width yields confidence intervals for the
 17 estimates.

18

19 **S7. Obtaining approximate estimates of s using the Specmap data (Fig. 5)**

20 Analyses were conducted using the Specmap database (McIntyre *et al.* 1989; Imbrie *et al.*
 21 1992), which is comprised of proportional-abundance estimates, resolved to

1 morphospecies, for community samples of planktonic foraminifera taken at a series of
2 depths in 8 deep-sea drilling cores. Each core has an accompanying model, comprised of
3 age estimates at varying depths, that can be used to assign ages to community samples.
4 The timespans of these age models range from 146,000 yr to 785,000 yr. For this
5 analysis, we considered only the 7 cores with samples extending back over 235,000 years
6 (core IDs: RC12-294, RC13-228, RC24-16, V22-174, V25-56, V30-40, V30-49). These
7 cores span a broad range of latitudes (37.27°S to 18.43°N) in the Atlantic Ocean
8 (10.10°W to 35.23°W).

9 Preparing the Specmap data for analysis involved five steps. First, samples were
10 binned into 5,000 yr age classes because this corresponds to the estimated precision of
11 the Specmap age estimates (McIntyre *et al.* 1989). Second, if multiple samples occurred
12 in a particular core and age class, arithmetic averages of the morphospecies-level
13 proportional-abundance estimates were taken. Third, if no samples occurred in a
14 particular core and age class, morphospecies-level proportional-abundance estimates
15 were obtained using linear interpolation of values from adjacent samples. This
16 interpolation procedure was required for only about 2% of the proportional-abundance
17 estimates. Fourth, an arithmetic average of the proportional-abundance estimates in the
18 seven cores was taken for each age class and morphospecies. Finally, fifth, proportional-
19 abundances were converted to absolute abundances by taking the product of the
20 proportional abundance and the estimated total abundance of planktonic foraminifera in
21 the latitudinal band 37.27°S –18.43°N of the Atlantic Ocean (3.3×10^{16} individuals). This
22 regional-abundance estimate was obtained by combining sea-surface temperature data
23 (Casey & Cornillon 1999) with a function that was calibrated using plankton-tow data

1 (Allen *et al.* 2006). The same method was used to estimate global metacommunity
2 abundance J_M ($= 5.6 \times 10^{17}$ individuals, Table 1), so the values are directly comparable.

3 The fifth step entails two important assumptions. First, it is assumed that total
4 community abundance within this region has remained constant at 3.3×10^{16} individuals.
5 Second, in order to extrapolate the estimates of s derived from these data to the global
6 scale, it is assumed that population dynamics in this region are uncorrelated with the
7 dynamics in other regions. A positive correlation in the dynamics among regions would
8 imply that the Specmap data assay a community that is effectively larger than 3.3×10^{16}
9 individuals.

10 Using the transformed abundance data, values of s were calculated separately for
11 each morphospecies using Eq. 5. To ensure that the s estimates were robust, we only
12 analyzed data for the 20 morphospecies (out of 34) that had non-zero abundances in all
13 48 of the 5,000 year time intervals spanning the last 240,000 years. Furthermore, for each
14 of the 20 morphospecies, the overall estimate for s was calculated by taking the average
15 of the s estimates for all 1,128 ($=48 \times 47/2$) possible combinations of abundances and time
16 intervals. Due to the two assumptions above, the estimates of s obtained using this
17 procedure must be regarded as approximate. However, violating either assumption would
18 tend to bias the s estimates towards *lower* values. Thus, our conclusions in the text
19 regarding the importance of environmental stochasticity are robust to such violations.

20

1 **REFERENCES**

- 2 Allen A.P., Gillooly J.F., Savage V.M. & Brown J.H. (2006). Kinetic effects of
3 temperature on rates of genetic divergence and speciation. *PNAS*, 103, 9130-9135.
- 4 Casey K.S. & Cornillon P. (1999). A comparison of satellite and in situ-based sea surface
5 temperature climatologies. *J. Climate*, 12, 1848-1863.
- 6 Ewens W.J. (2004). *Mathematical Population Genetics I. Theoretical Introduction*.
7 Springer-Verlag, New York.
- 8 Feller W. (1951). Two Singular Diffusion Problems. *The Annals of Mathematics*, 54, 173.
- 9 Feller W. (1952). The Parabolic Differential Equations and the Associated Semi-Groups
10 of Transformations. *The Annals of Mathematics*, 55, 468.
- 11 Fisher R.A., Corbet A.S. & Williams C.B. (1943). The Relation Between the Number of
12 Species and the Number of Individuals in a Random Sample of an Animal
13 Population. *Journal of Animal Ecology*, 12, 42-58.
- 14 Hilborn R. & Mangel M. (1997). *The Ecological Detective: Confronting Models with*
15 *Data*. Princeton University Press, Princeton, NJ.
- 16 Hubbell S.P. (2005). The neutral theory of biodiversity and biogeography and Stephen
17 Jay Gould. *Paleobiol.*, 31, 122-132.
- 18 Imbrie J., Boyle E.A., Clemens S.C., Duffy A., Howard W.R.K., G., Kutzbach J.,
19 Martinson D.G., McIntyre A., Mix A.C., Molino B., Morley J.J., Peterson L.C.,
20 Pias N.G., Prell W.L., Raymo M.E., Shackleton N.J. & Toggweiler J.R. (1992).
21 On the Structure and Origin of Major Glaciation Cycles 1. Linear Responses to
22 Milankovitch Forcing. *Paleoceanogr.*, 7, 701-738.

- 1 Karlin S. & Taylor H.M. (1981). *A Second Course in Stochastic Processes*. Academic
2 Press, New York.
- 3 Lande R., Engen S. & Saether B.E. (2003). *Stochastic Population Dynamics in Ecology
4 and Conservation*. Oxford University Press, Oxford, UK.
- 5 Lehnigk S.H. (1993). *The Generalized Feller Equation and Related Topics*. Longman
6 Scientific & Technical, New York.
- 7 Maruyama T. (1977). *Stochastic Problems in Population Genetics*. Springer-Verlag, New
8 York.
- 9 McIntyre A., Ruddiman W.F., Karlin K. & Mix A.C. (1989). Surface water response of
10 the equatorial Atlantic ocean to orbital forcing. *Paleoceanogr.*, 4, 19-55.
- 11 Press W.H., Teukolsky S.A., Vetterling W.T. & Flannery B.P. (1992). *Numerical Recipes
12 in C*. Cambridge University Press, New York.
- 13 Rice S.H. (2004). *Evolutionary theory : mathematical and conceptual foundations*.
14 Sinauer Associates, Sunderland, MA.
- 15 Volkov I., Banavar J.R., He F., Hubbell S.P. & Maritan A. (2005). Density dependence
16 explains tree species abundance and diversity in tropical forests. *Nature*, 438, 658.
- 17 Volkov I., Banavar J.R., Hubbell S.P. & Maritan A. (2003). Neutral theory and relative
18 species abundance in Ecology. *Nature*, 424, 1035-1037.
- 19
- 20