Niche versus Neutrality: A Dynamical Analysis

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abstract: Understanding the forces shaping ecological communities is of crucial importance for basic science and conservation. After 50 years in which ecological theory has focused on either stable communities driven by niche-based forces or nonstable "neutral" communities driven by demographic stochasticity, contemporary theories suggest that ecological communities are driven by the simultaneous effects of both types of mechanisms. Here we examine this paradigm using the longest available records for the dynamics of tropical trees and breeding birds. Applying a macroecological approach and fluctuation analysis techniques borrowed from statistical physics, we show that both stabilizing mechanisms and demographic stochasticity fail to play a dominant role in shaping assemblages over time. Rather, community dynamics in these two very different systems is predominantly driven by environmental stochasticity. Clearly, the current melding of niche and neutral theories cannot account for such dynamics. Our results highlight the need for a new theory of community dynamics integrating environmental stochasticity with weak stabilizing forces and suggest that such theory may better describe the dynamics of ecological communities than current neutral theories, deterministic niche-based theories, or recent hybrids.

Keywords: neutral theory, environmental stochasticity, demographic stochasticity, density dependence, Barro Colorado Island (BCI), Breeding Bird Survey (BBS).

Introduction

Understanding the complex processes that determine the dynamics of ecological communities is one of the oldest and most formidable challenges in ecology. Roughly, from the 1960s to the 1990s, most ecological theories focused on stable communities in which species composition and abundance were thought to be determined by functional trade-offs and stabilizing niche differentiation (Tilman 1982; Purves and Turnbull 2010). This "niche perspective" was challenged by the gradual emergence of an alternative viewpoint, with Hubbell's "Unified Neutral Theory of Biodiversity and Biogeography" at its forefront, emphasizing the unstable nature of ecological communities and the role of demographic stochasticity ("ecological drift") as a major determinant of species composition and abundance (Chesson 2000; Hubbell 2001). These contradicting views are currently being merged into a "continuum" perspective (Gravel et al. 2006), where ecological communities are shaped by a combination of niche mechanisms acting as stabilizing forces and demographic stochasticity acting as a destabilizing force (Chesson 2000; Tilman 2004; Gravel et al. 2006; Kadmon and Allouche 2007; Allouche and Kadmon 2009). However, this reasoning has rarely been put to explicit empirical tests, which limits our ability to assess its applicability to natural communities.

Another limitation of the current "continuum" perspective is that it ignores environmental stochasticity. This is a major drawback of continuum theories since variability in both abiotic and biotic components of the environment is one of the most fundamental characteristics of natural ecosystems.

The idea of environmental stochasticity is related to the concept of a species-specific niche, as it relies on the assumption that all individuals of a certain species in the community react, on average, in a similar way to the variability in (abiotic or biotic) components of the environment. Consequently, the environment may have two opposing effects on the dynamics of populations and communities. On the one hand, environmental fluctuations may act to destabilize populations. On the other hand, as emphasized in many niche-partitioning-based theories (Tilman 1982; Chesson 2000; Purves and Turnbull 2010), the sensitivity of a certain species to environmental constraints, like resource availability, acts to regulate population size and to diminish the magnitude of fluctuations around some equilibrium point.

The aim of this article, therefore, is to examine two

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fundamental aspects of contemporary theories of community dynamics: the nature of the destabilizing mechanisms and their relative strength with respect to the stabilizing forces. To achieve this goal, we propose a novel approach for analyzing the dynamics of ecological communities and use the proposed approach to test the basic premise of the "continuum" perspective, namely, that the dynamics of ecological communities is determined by the simultaneous effects of niche theoretic stabilizing forces and destabilizing mechanisms, attributed to demographic stochasticity (Tilman 2004; Gravel et al. 2006; Allouche and Kadmon 2009). Our methodology is capable of distinguishing stabilizing from destabilizing forces, demographic from environmental stochasticity, and process noise (real fluctuations in abundance) from sampling errors. In contrast to previous techniques (Dennis et al. 2006; Mutshinda et al. 2009; Knape et al. 2011; Knape and De Valpine 2012), our approach is model independent and does not require any assumptions about the underlying mechanisms of the dynamics.

Our article has two parts. In the first part, we describe our theoretical approach and the manner by which it can be applied to empirical data. In the second part, we apply the proposed approach to data sets from two systems that differ considerably in their ecological characteristics: a tropical rainforest in Panama and breeding birds in North America. For both systems, the results allow us to rule out (within the timeframe of the empirical observations) the effect of stabilizing forces, demographic stochasticity, or a combination of both as major drivers of community dynamics. We conclude that the dynamics of these communities does not fit the predictions of the continuum perspective and suggest an alternative perspective based on environmental stochasticity as a more realistic framework for understanding the dynamics of ecological communities.

Theoretical Analysis

Demographic stochasticity ("ecological drift") represents random events affecting the reproductive success and survival of single individuals independently of each other. In general, a birth-death process may be described using P_n, the probability of an individual producing n offspring within a certain time period, causing the expected growth rate to be $\lambda = \Sigma n P_n$. The stochasticity is purely demographic if λ is independent of time. In such a case, the per-generation stochastic fluctuations of population size (around its average value), $N_{t+1} - N_t$, is proportional to $N_t^{0.5}$ (Lande et al. 2003). Alternatively, if environmental variation affects all the individuals within a population in a correlated manner, λ itself varies in time. When the environment is stochastic, λ_t is picked at random at every time step, and the per-generation stochastic fluctuations scale with N_t, not with its square root. Here we use these scaling laws to discern the two processes.

Our method is a revised version of the "variance-time lag" technique (Keitt and Stanley 1998; Holmes 2001). It is based on the calculation of two measures of population change during time lag Δt:

$$D_{\Delta t} = \frac{N_{t+\Delta t} - N_t}{\sqrt{N_t}} \tag{1}$$

and

$$E_{\Delta t} = \ln\left(\frac{N_{t+\Delta t}}{N_t}\right). \tag{2}$$

The population change expressed by D (eq. [1]) is normalized by $N_t^{0.5}$, which is the typical scale of changes in population size if the underlying process is pure demographic stochasticity. In contrast, the change (on the logarithmic scale; all logarithms used here are natural unless otherwise stated) expressed by E (eq. [2]) is normalized by N_t, which is the typical scale of changes assuming the underlying process is pure environmental stochasticity (see appendix, available online).

Stochastic dynamics causes variable changes in populations, making population size diverge from some initial size differently in different realizations. This phenomenon can be explored by looking at the variance of population changes at increasing time lags. For a selected set of populations (e.g., all species in a given community or all populations of all species in a given region), a plot of the variances of D and E against time lag (Δt) provides information on the effects of demographic stochasticity, environmental stochasticity, sampling error, and stabilizing forces on the dynamics of the relevant populations. Such an analysis of simulated data is depicted in figure 1 (for a comprehensive theoretical analysis, see appendix and supplement 1; supplements available online).

Specifically, if the populations are driven by pure demographic stochasticity, Var(D) will grow linearly with Δt with the slope independent on initial population size N_t (fig. 1*A*), while the slope of Var(E) will decrease like $1/N_t$ (fig. 1*B*). The slope of Var(D) here represents the variance in the number of offspring per individual (Lande et al. 2003; Maruvka et al. 2010). On the other hand, if the process is pure environmental stochasticity, the slope of Var(D) will increase linearly with N_t (fig. 1*C*), while the slope of Var(E) versus Δt will be independent of population size (fig. 1*D*), representing the strength of the environmental noise in terms of the variance of population changes due to this process (Lande et al. 2003).

Furthermore, an extrapolation of these patterns to $\Delta t = 0$ might show an intercept, that is, a positive variance

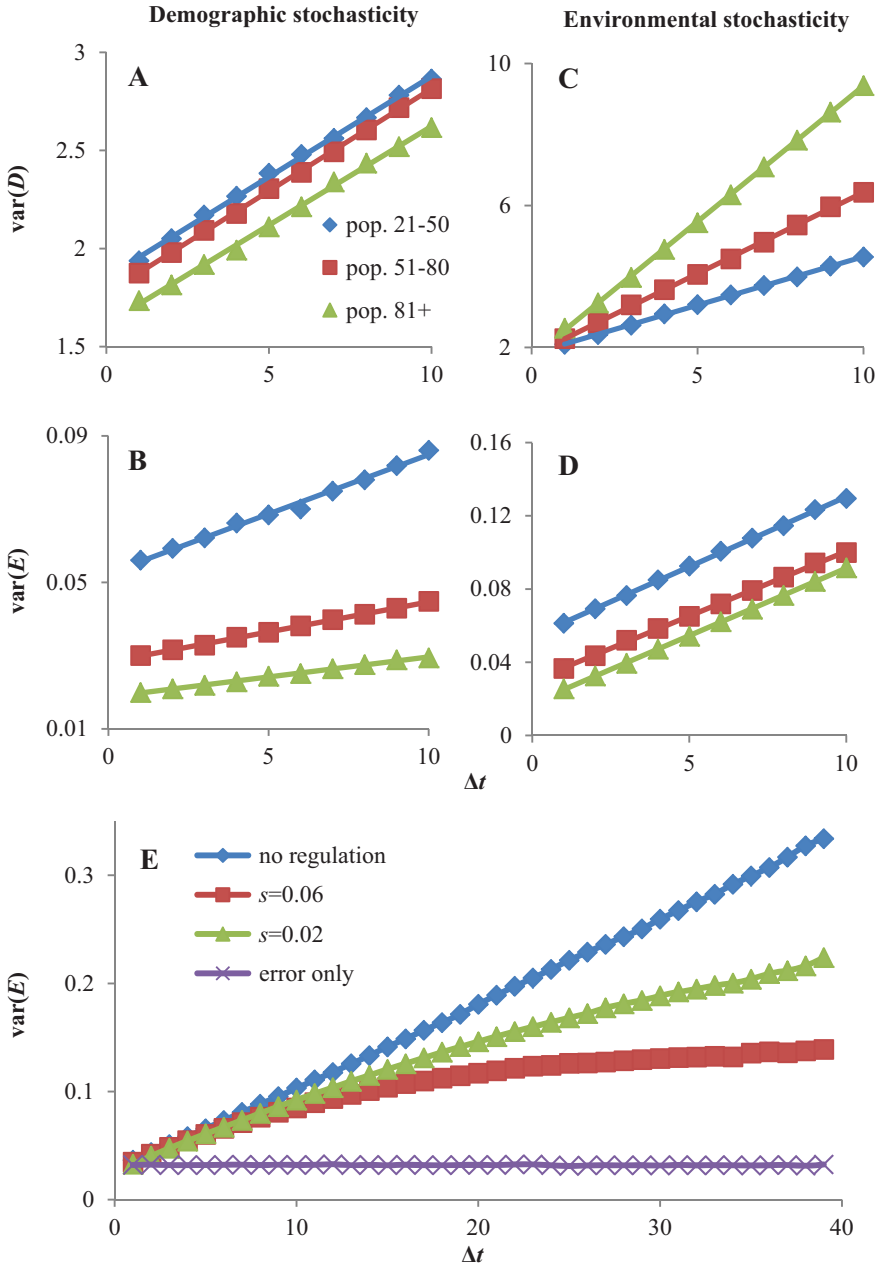

Figure 1: Variance-time lag plots for simulated data. To investigate the properties of D and E metrics, we analyze their variance at different time lags Δt. Under pure demographic stochasticity (A and B) the growth of Var(D) is independent of N_t, while the slope of Var(E) decreases with N_t. In contrast, under pure environmental stochasticity (C and D) the Var(D) slope increases with N_t, while the growth of Var(E) is independent of population size. E, Decrease of the slope under population regulation affecting mean growth rate $\lambda = 1 - s \ln(N_t/N_{\text{equilibrium}})$, where $N_{\text{equilibrium}}$ is equilibrium population size, and a scenario of pure sampling errors. See appendix and supplement 1, available online.

of population change at zero time. Such a positive intercept, if it exists, represents sampling error, which does not change the variance growth with the lag. Thus, our variance-time lag analysis separates the error noise from the process noise (Holmes 2001; Thompson 2010). Finally, the time dependence might not be linear, due to temporal correlations in population changes caused by density regulation, correlated environmental changes, or population trends (fig. 1*E*; Keitt and Stanley 1998). The level and temporal scale of the deviation from linearity indicate the

strength and temporal scale at which these forces act, respectively.

Empirical Analysis

Empirical Data

We applied our technique to time series of species abundance from two systems that have previously been used as benchmarks for testing theories of community dynamics: the Barro Colorado Island tree community in Panama (BCI; Hubbell 2001; McGill 2003; Feeley et al. 2011); and the Breeding Bird Survey in North America (BBS; Keitt and Stanley 1998; McGill 2003).

BCI Data. The BCI data set includes abundance data for ~300 species of trees and understory plants within a 500 × 1,000-m rectangle over six different censuses. The first census was conducted during 1982–1983, with subsequent censuses completed in 1985, 1990, 1995, 2000, and 2005. In order to analyze the dynamics of species in constant time lags, we excluded the 1982–1983 survey from our analysis and counted only the main stem of trees. We took the species list from http://www.ctfs.si.edu/site/Barro+Colorado+Island/abundance (Hubbell et al. 2005). This data set has previously been considered an example for neutral dynamics driven by demographic stochasticity (Condit 1998; Hubbell et al. 1999, 2005).

BBS Data. The North American Breeding Birds Survey is the largest collection of time series available for a particular system in the world. Here we used annual counts of 624 species at 4,528 sites censused at least twice during the period 1966–2010, which provided us with more than 100,000 time series longer than 13 years. To prepare the data for analysis, we downloaded all records for the years 1966–2010 (Sauer et al. 2012). Only the runs that were certified as standard according to the BBS survey protocol (in terms of weather conditions, time of the day, and time of the year) were analyzed. We also reconciled BBS species codes according to the American Ornithologists' Union taxonomy (AOU 1998; lumping infraspecies to the species level and dropping unidentified species). Finally, in cases where multiple surveys of the same route were performed during the same year, we used only the first.

Since both D and E are normalized, we were able to pool all population changes measured in each system (as in Keitt and Stanley 1998), grouping them by initial population size, thus obtaining the most general picture with maximal statistical power.

Results

The two systems exhibited remarkably similar patterns. For BCI, and for the BBS data when examined over a relatively short timescale ($\Delta t \leq 10$ years), both Var(D) and Var(E) increase approximately linearly with Δt (fig. 2*A*–2*D*). However, in contrast to expectations based on the current "continuum" perspective, for both data sets the slope of Var(E) was independent of initial population size (BBS: $F_{1,2} = 0.028$, $P = .882$; BCI: $F_{1,2} = 0.389$, $P = .597$; fig. 2*B*, 2*D*), while the slope of Var(D) showed a linear increase with population size (BBS: $F_{1,2} = 150$, $P < .01$; BCI: $F_{1,2} = 151$, $P < .01$, fig. 2*A*, 2*C*, and figs. S3, S4 in supplement 5). These results indicate that in both systems the main driving force is environmental stochasticity, while demographic stochasticity may be significant only for very small populations (see also supplement 2). The finding that the dynamics of the BCI tree community is dominated by environmental rather than demographic stochasticity is particularly interesting because the BCI system is a widely cited example for neutral dynamics driven by demographic stochasticity.

The length of the time series available for the BBS data set allowed us to test for the existence of stabilizing forces over longer timescales. This analysis showed that the increase in Var(E) with Δt almost perfectly fits a sublinear power law with power 0.66 (fig. 2*E*), indicating that, at least at the scale for which data are available, the variance does not approach a saturation point. Apparently, breeding bird populations in North America are subject to only weak stabilizing forces that operate at relatively long temporal scales. In fact, the lack of saturation indicates that the populations are probably not attracted to any specific equilibrium (Murdoch 1994). Qualitatively similar results were obtained in an analysis of individual bird species that are relatively common (see figs. S1, S2 in supplement 2).

As stated above, the growth of the variance with the time lag reflects the real process, and the effect of sampling errors determines only the intercept with the Y-axis (Holmes 2001; Thompson et al. 2010). It turns out that the BCI data set is almost free of error (intercept close to 0), as expected, while in the BBS data set, sampling error accounts for about 80% of the yearly variance in population abundance. Interestingly, this value is close to a previous estimate (~70%) based on BBS data (for a single species) using a different methodology (Dennis et al. 2006).

To better understand the dynamics of the system, it is very informative to know not only the variance of environmental stochasticity but also the nature of its distribution. The vast amount of data we have for the BBS allows us to suggest, via analysis of higher moments, a distribution for both the real yearly fluctuations in the

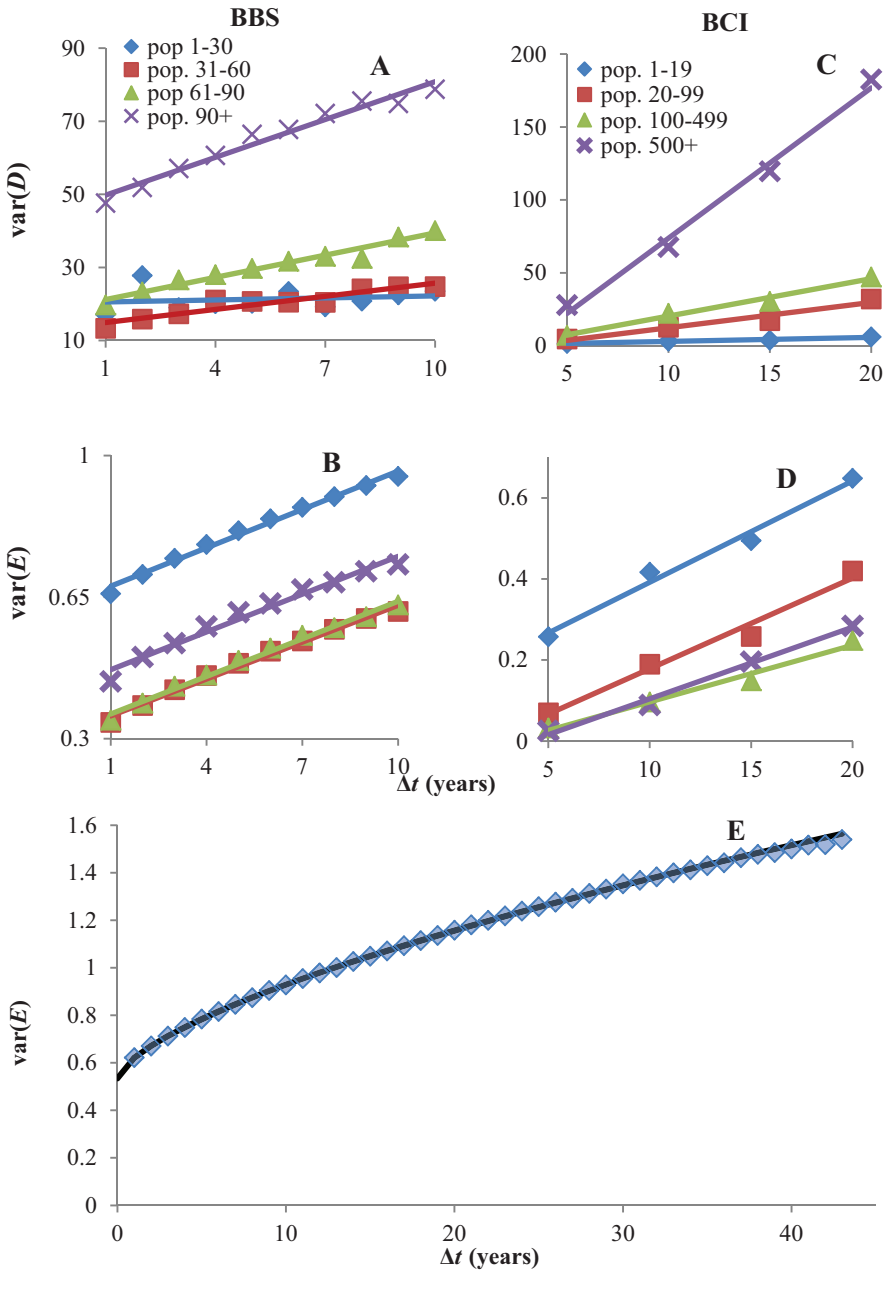

Figure 2: Variance-time lag plots for empirical data. An investigation of the short-term dynamics in the Breeding Bird Survey (BBS; *A*, *B*) and Barro Colorado Island (*C*, *D*) by analyzing Var(E) and Var(D) in short time lags Δt, calculated separately for different initial population size groups (supplement 1, available online). *E*, Var(E) versus time lag in the BBS for time lags up to 43 years and fit with a power function $\mathrm{Var}(E) = 0.515 + 0.107 \cdot \Delta t^{0.66}$ (adjusted $R^2 = 0.9999$).

population growth rate (expressed by the logarithm of annual changes; eq. [2]) and the sampling error (supplement 3). The distribution of the growth rates on the logarithmic scale appears to be symmetric, much wider than expected for a normal distribution but narrower than a power law, with a reasonable fit to a symmetric Weibull distribution with a stretched exponential tail (Laherrere and Sornette 1998; see fig. 3*A* for a comparison of the fits of different distributions to the empirical moments):

$$f(r) = \frac{k}{2l}\left(\frac{|r|}{l}\right)^{k-1} \exp\left(-\left[\frac{|r|}{l}\right]^{k}\right), \tag{3}$$

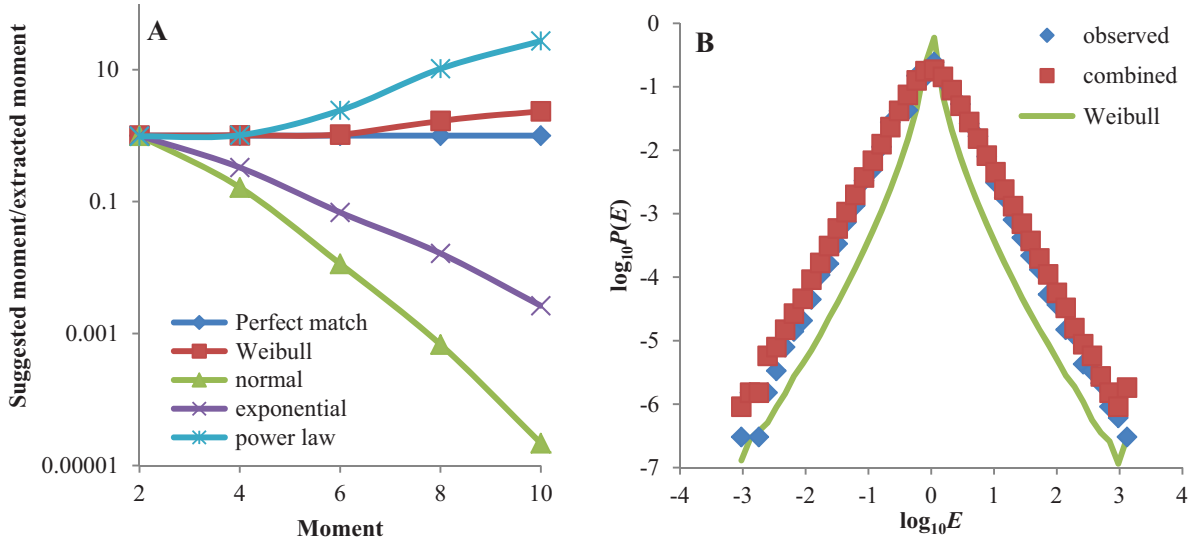

Figure 3: Analysis of moments for the yearly changes in the BBS. *A*, Comparison of the extracted moments of the real fluctuations to the moments of some suggested distributions. A ratio of 1 represents a perfect match to the empirically derived moments from the BBS analysis. Only the even moments are presented, as odd moments are very small, suggesting a symmetric distribution. It is evident that "compact" distributions (normal and exponential) are inadequate as their higher moments are too small, while a power law distribution is too wide (higher moments too large). Weibull statistics with stretched exponential tails fit the data well. *B*, Log_{10}-$\log_{10}$ histogram showing that a superposition of the extracted Weibull environmental stochasticity and sampling error recovers the observed power law fluctuations (Keitt and Stanley 1998). See also supplements 3–5, available online.

Here r is the logarithm of the growth rate λ, k is the shape parameter, which we found to be 0.68, and l is the scale parameter, which we found to be 0.14.

The corresponding moments of the sampling error fit those of a triangle distribution (supplements 4-5); that is, if the minimum number of individuals sampled is 0 and the maximum is N, the probability of sampling M individuals is

$$P(M) = \begin{cases} \dfrac{4M}{N^2} & M < N/2 \\ \dfrac{4(N-M)}{N^2} & M > N/2 \end{cases}. \tag{4}$$

Importantly, superimposing the triangular distribution obtained for the sampling error on the Weibull distribution of the real population fluctuations successfully recovers the original (uncorrected) distribution of population changes in our data (fig. 3*B*) and matches the power law distribution reported in a previous study that ignored the consequences of sampling error (Keitt and Stanley 1998). This confirms the reliability of our results, and demonstrates the importance of accounting for sampling errors in analyses of population changes (fig. 3*B*; supplement 4 and table S1).

Discussion

The finding that the logarithm of population fluctuations follows a symmetric heavy-tailed distribution (Keitt and Stanley 1998) has important implications for conservation in general and population viability analyses (PVA) in particular. Many PVAs assume that environmental fluctuations are lognormally distributed (Coulson et al. 2001; Holmes 2001; Lande et al. 2003), and some also incorporate additional catastrophic events (Lande 1993; Coulson 2001). Our results (fig. 3*B*) suggest that catastrophes (rare events resulting from the very wide "tails" of the distribution) might be roughly as common and intense as population outbreaks and may belong to the same statistical distribution as the "ordinary" fluctuations. This unification, gaining popularity in other fields (Stanley et al. 2006), can make analyses of extreme events in conservation planning more feasible (Coulson 2001) and is further justified by the fact that catastrophic events should not be universally treated as outliers. Rather, given sufficient data, their occurrence has been shown not to deviate from regular events if fit with the appropriate heavy-tailed distribution (Schoenberg et al. 2003; Wilson and Toumi 2005).

Most previous attempts to evaluate the role of stabilizing and destabilizing forces using time series of population dynamics have assumed specific models of population dy-

namics and arbitrary distributions of environmental stochasticity, without testing the potential consequences of alternative assumptions (Knape et al. 2011; Knape and De Valpine 2012). Such models have led to variable and often conflicting results (such as Sibly et al. 2005; Knape and De Valpine 2012). Our approach is model independent, thus allowing us to evaluate the role of stabilizing versus destabilizing forces of population dynamics directly, making no assumptions about the mechanisms underlying the observed patterns. The fact that a "characteristic" population follows a very weakly stabilized dynamics supports previous suggestions that stabilizing forces might be much weaker in nature than has often been suggested (Mutshinda et al. 2009; Knape and De Valpine 2012). For example, if we model regulation as an effect on mean growth rate, $\lambda = 1 - s \cdot \ln(N_t/N_{\text{equilibrium}})$, when $N_{\text{equilibrium}}$ is equilibrium population size, s would have to be on the order of 0.03 to obtain a similarly weak response.

Moreover, a highly debated aspect of stabilization is whether populations are attracted to a specific equilibrium size, as most population dynamics models assume (e.g., Dennis et al. 2006; Mutshinda et al. 2009; Knape et al. 2011; Knape and De Valpine 2012). It has previously been proposed that the variance in the size of some populations increases without apparent bounds and that this property indicates that the underlying dynamics is nonequilibrial (Pimm and Redfearn 1988; Murdoch 1994). Our extensive analysis, spanning tens of thousands of long time series, fully supports this nonequilibrium view of populations.

It is clear from our analysis that neglecting the effect of sampling error (i.e., assuming zero intercept of Var(E) in fig. 2E) leads to an underestimate of the (sub)diffusion exponent, that is, to an overestimate of the strength of stabilizing mechanisms (Keitt and Stanley 1998). This fact was already pointed out in studies that implement state-space models (Knape et al. 2011; Knape and De Valpine 2012). Apparently, at least some of the contradictions observed in previous evaluations of stabilizing versus destabilizing forces of population dynamics are an artifact of mistreating sampling errors.

The above insights emphasize the strength of our model-independent macroecological approach, whose generality and simplicity allow one to analyze a large number of populations without going into a detailed description of each population, thereby providing an effective tool for analyses focusing on the community level. We believe that lack of appropriate tools is a major reason why such analyses have rarely been conducted.

While most traditional niche models of community dynamics predict stable coexistence and dynamics (Tilman 1982; Chesson 2000; Purves and Turnbull 2010), neutral theories and integrative "continuum" theories of community dynamics predict unstable coexistence and stochastic dynamics. Although such stochastic models are more realistic in terms of stability, it has been argued that they are still too stable (Ricklefs 2003; Leigh 2007) and cannot account for the magnitude and "directionality" of changes observed in natural communities (Feeley et al. 2011). Our results provide a possible explanation for this gap between theory and empirical data since environmental stochasticity is directional, unlike demographic stochasticity, and is considerably stronger in large populations.

Our results indicate that the communities we analyzed are best described by a model where populations are not attracted to any equilibrium (unstable), and the main destabilizing force is environmental stochasticity. A first step in that direction might be the development of a neutral community model driven by environmental rather than demographic stochasticity (Alonso et al. 2007). In addition to offering a solution to the problem of large fluctuations, a neutral model based on environmental stochasticity may provide a resolution to the niche-neutrality debate by integrating species responses to environmental variation (the missing element in neutral theories) with stochasticity (the missing element in classical niche theories). Importantly, in contrast to conventional wisdom in community ecology, the fundamental role of niche forces in such a model is to destabilize, rather than to stabilize communities.

Historically, community ecologists have evaluated their theories based on static patterns such as species abundance distributions and species-area curves (Hubbell 2001; McGill 2003; Allouche and Kadmon 2009; Rosindell and Cornell 2007). We believe that this practice must change to one focused on dynamics. A cardinal aspect of recent debates in community ecology is the degree of stability in species composition (Chesson 2000; Purves and Turnbull 2010)—an issue directly related to the stability of populations. The methodology presented here provides a strong tool for characterizing population and community dynamics, and the empirical results obtained with the BCI and BBS systems might be used as a yardstick that should be explained by future, mechanistic models of community dynamics.

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