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Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments

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ABSTRACT: Independent species fluctuations are commonly used as a null hypothesis to test the role of competition and niche differences between species in community stability. This hypothesis, however, is unrealistic because it ignores the forces that contribute to synchronization of population dynamics. Here we present a mechanistic neutral model that describes the dynamics of a community of equivalent species under the joint influence of density dependence, environmental forcing, and demographic stochasticity. We also introduce a new standardized measure of species synchrony in multispecies communities. We show that the per capita population growth rates of equivalent species are strongly synchronized, especially when endogenous population dynamics are cyclic or chaotic, while their long-term fluctuations in population sizes are desynchronized by ecological drift. We then generalize our model to nonneutral dynamics by incorporating temporal and nontemporal forms of niche differentiation. Niche differentiation consistently decreases the synchrony of species per capita population growth rates, while its effects on the synchrony of population sizes are more complex. Comparing the observed synchrony of species per capita population growth rates with that predicted by the neutral model potentially provides a simple test of deterministic asynchrony in a community.

Keywords: environmental variability, stochastic population dynamics, species synchrony, neutral theory, niche differentiation, interspecific competition.

Temporal fluctuations in populations and in their environment are ubiquitous in natural ecosystems. These fluctuations are thought to play a significant part in the co-

existence of species (Levins 1979; Armstrong and McGehee 1980; Chesson 2000) and in the stability of aggregate community or ecosystem properties (McNaughton 1977; Yachi and Loreau 1999; Loreau 2000; McCann 2000; Loreau et al. 2001; Hooper et al. 2005). Both species coexistence and ecosystem stability require some form of temporal niche differentiation by which different species respond differently to variations in their environment, such that their fluctuations are asynchronous and may compensate for each other through time.

Defining and measuring species asynchrony in multispecies communities, however, has proved difficult for at least two reasons. First, there are strong mathematical constraints on negative covariations between species, which makes it difficult to distinguish a species-rich community in which species show strongly asynchronous fluctuations from one in which species show stochastic independent fluctuations on the basis of pairwise measures such as species covariances and correlations alone (Brown et al. 2004). Second, the null hypothesis against which species asynchrony should be defined is unclear. The traditional null hypothesis that most previous studies have used is, implicitly or explicitly, one in which species fluctuate independently of each other (Doak et al. 1998; Tilman 1999; Ernest and Brown 2001; Houlahan et al. 2007; Vasseur and Gaedke 2007). This hypothesis, however, is biologically unrealistic because it ignores the forces that contribute to synchronization of population dynamics.

What is the expected level of species synchrony under the null hypothesis of no niche differentiation between species? Does niche differentiation have a consistent signature on species synchrony, given the potentially complex dynamics generated by density dependence and environmental forcing? Does interspecific competition desynchronize the population dynamics of coexisting species, as is often assumed (e.g., Tilman 1999; Houlahan et al. 2007)? These are fundamental questions that remain, to a large extent, unanswered by existing theories and that we examine in this article. Niche theory (Levins 1979; Armstrong and McGehee 1980; Chesson 2000) provides key insights into the conditions for species coexistence in tem-

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porally varying environments, but it has not yet produced quantitative predictions for species synchrony in multi-species communities. Neutral theory (Hubbell 2001) provides elegant predictions for species abundance patterns and fluctuations in saturated, space-limited communities of equivalent species, but it considers only population fluctuations driven by demographic stochasticity and ignores fluctuations driven by density dependence and environmental forcing, which are ubiquitous in natural communities. The theory of stochastic population dynamics (Lande et al. 2003) provides some solid foundations for exploring the causes and consequences of species synchrony, but it has so far been applied mainly to the population dynamics of single species. Therefore, there is a need for new theory that links population dynamics and community stability.

In this article, we seek to contribute to reaching this goal in three ways. We first present a neutral model that describes the dynamics of a community of equivalent species. Our neutral model makes the same assumption as Hubbell's (2001) that species are demographically equivalent, but it includes three main forces that drive population dynamics, that is, intra- and interspecific density dependence, environmental forcing, and demographic stochasticity. We use this model to derive quantitative predictions of species synchrony in the absence of niche differentiation. These predictions provide an appropriate null hypothesis to test for the effects of niche differentiation on species synchrony and ecosystem properties. Second, we present a new measure of community-wide species synchrony that avoids some of the drawbacks of previous measures and allows quantitative comparisons among communities with different species numbers. Finally, we develop a nonneutral version of our dynamical model and use our new measure of synchrony to analyze the effects of temporal niche differentiation and interspecific competition on species synchrony. The effects of temporal niche differentiation and interspecific competition on the stability of community properties will be examined in another contribution (M. Loreau and C. de Mazancourt, unpublished manuscript).

A Neutral Model of Community Dynamics in Fluctuating Environments

In this section, we build a neutral model that describes the stochastic population dynamics of equivalent species in fluctuating environments. We use this model to predict the level of species synchrony to be expected in the absence of niche differences between species.

Assume a set of S equivalent species that are limited by a common limiting factor and that respond identically to environmental fluctuations. Let $N_i(t)$ be the population

size or abundance of species i at time t and $r_i(t) = \ln N_i(t+1) - \ln N_i(t)$ be its instantaneous per capita population growth rate at time t . The theory of stochastic population dynamics predicts that, to a first-order approximation, the conditional variance of the per capita population growth rate driven by environmental and demographic stochasticity is

$$\text{Var}(r_i(t)|N_i(t)) = \sigma_e^2 + \frac{\sigma_d^2}{N_i(t)}, \quad (1)$$

where σ_e^2 and σ_d^2 are the environmental and demographic variances, respectively (Lande et al. 2003). Further assume that community size, $N_T(t) = \sum_{i=1}^S N_i(t)$, is regulated according to a simple discrete-time logistic equation with intrinsic rate of natural increase r_m and carrying capacity K . The population dynamics of each species then obeys the equation

$$\begin{aligned} r_i(t) &= \ln N_i(t+1) - \ln N_i(t) \\ &= r_m \left[1 - \frac{N_T(t)}{K} \right] + \sigma_e U_e(t) + \frac{\sigma_d U_{di}(t)}{\sqrt{N_i(t)}}, \end{aligned} \quad (2)$$

where $U_e(t)$ and $U_{di}(t)$ are independent normal variables with zero mean and unit variance (Lande et al. 2003; Engen et al. 2005).

Density dependence in the form represented in model (2) yields a wide range of endogenous dynamical behaviors for a single population (May and Oster 1976). The deterministic dynamical attractors vary from a stable equilibrium point when $0 < r_m < 2$ to limit cycles when $2 < r_m < 2.692$ and chaos when $r_m > 2.692$ (fig. 1). Community size in model (2) is regulated and has the same deterministic attractors, on which the effects of environmental forcing and demographic stochasticity are superimposed. In addition, population sizes of individual species drift because of demographic stochasticity, as in neutral theory (Hubbell 2001). For species that do not become extinct, however, the expected temporal variances, covariances, and correlations of their per capita population growth rates can be calculated (app. A). These are, respectively,

$$\sigma_{r_i}^2 = \sigma_e^2 + \sigma_d^2 + \frac{\sigma_d^2}{N_i}, \quad (3)$$

$$\text{Cov}(r_i, r_j) = \sigma_e^2 + \sigma_e^2, \quad (4)$$

and

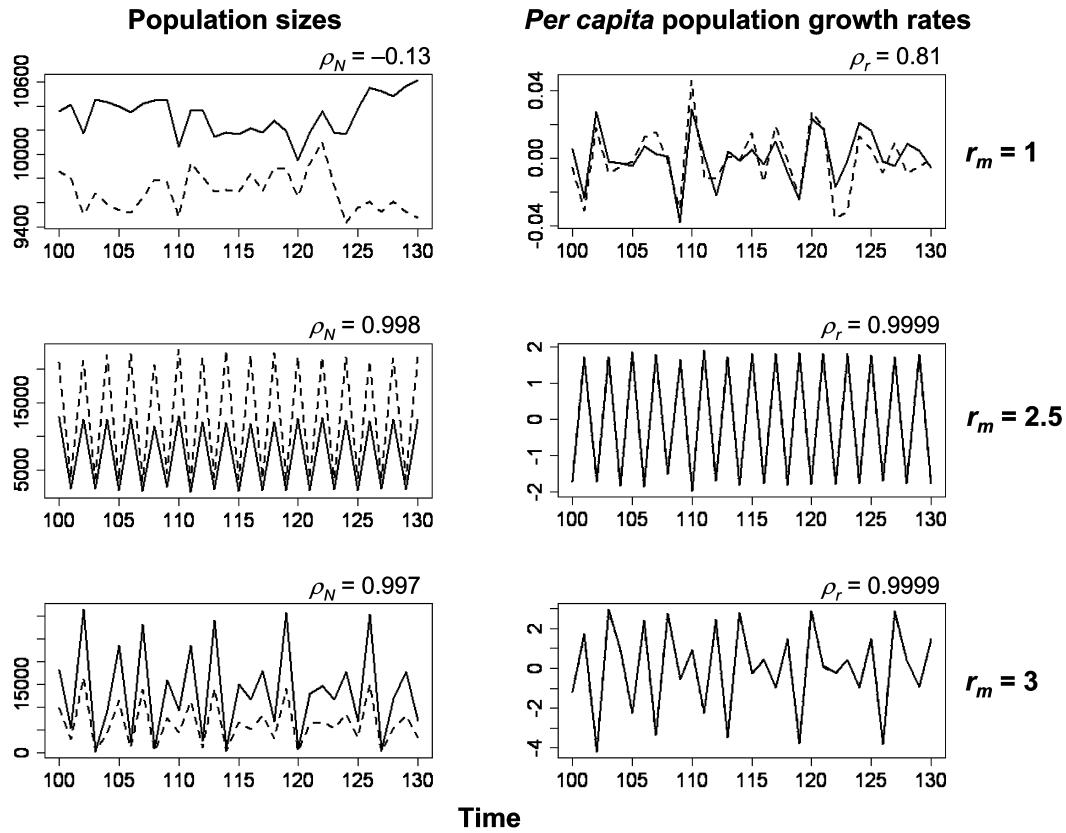


Figure 1: Fluctuations in population sizes (left) and per capita population growth rates (right) in two-species neutral communities. Community size fluctuates as a result of the combined effects of density dependence, environmental forcing, and demographic stochasticity. Population sizes of individual species also drift because of demographic stochasticity. Density dependence drives community size toward a stable equilibrium (top), a stable limit cycle (middle), or a chaotic attractor (bottom), depending on the value of the intrinsic rate of natural increase, r_m . The higher the intrinsic rate of natural increase, the larger the population fluctuations, the stronger the density dependence, and the more synchronous the population fluctuations. The synchrony of per capita population growth rates (measured by the correlation coefficient ρ_r , right) is always higher than that of population sizes (measured by the correlation coefficient ρ_N , left) because per capita population growth rates capture the short-term effects of the forces that govern population dynamics, while fluctuations in population sizes are also affected by long-term ecological drift. Synchrony is so high in some plots that the lines for the two species are superimposed. These time series were obtained using the Poisson version (see app. D) of the neutral model with $K = 20,000$, $\sigma_e = 0.01$, $\alpha = 1$, and $\varphi_c = 1$. Time is measured as the number of generations (time steps) after the start of the simulation run.

$$\begin{aligned} \rho_{r_i r_j} &= \frac{\text{Cov}(r_i, r_j)}{\sigma_{r_i} \sigma_{r_j}} \\ &= \frac{1}{\sqrt{1 + \sigma_d^2 / [(\sigma_c^2 + \sigma_e^2) \tilde{N}_i]} \sqrt{1 + \sigma_d^2 / [(\sigma_c^2 + \sigma_e^2) \tilde{N}_j]}}, \quad (5) \end{aligned}$$

where \tilde{N}_i is the harmonic temporal mean of species i 's population size, and $\sigma_c^2 = (r_m^2 / K^2) \sigma_{N_T}^2$ is the community response variance, defined as the temporal variance of per capita population growth rates due to regulation of community size. Since the various species are equivalent, density-dependent regulation takes place at the aggregate community level as though there were a single population. The community response variance quantifies the effects of

these community-level variations on per capita population growth rates. For values of the intrinsic rate of natural increase that lead to a stable equilibrium of community size ($0 < r_m < 2$), the variance of community size is, to a first-order approximation (app. B),

$$\sigma_{N_T}^2 \approx \frac{K^2 (\sigma_e^2 + \sigma_d^2 / K)}{r_m (2 - r_m)}, \quad (6)$$

and hence the community response variance is approximately

$$\sigma_c^2 \approx \frac{r_m (\sigma_e^2 + \sigma_d^2 / K)}{2 - r_m}. \quad (7)$$

From equation (7), we can see that the community response variance is driven by environmental forcing and demographic stochasticity, but their effects are amplified or reduced by density dependence, the strength of which is controlled by parameter r_m . The number of species in the community affects neither the covariances of per capita population growth rates (eq. [4]) nor the variance of community size (eq. [6]). This is logical since the number of species should have no effect on the properties of the community as a whole under the hypothesis of equivalence; species are then arbitrary groupings of equivalent individuals.

Equations (3) and (4) show that there are three additive components to the temporal variances and covariances of the per capita population growth rates of equivalent species: (1) a component due to endogenous regulation of community size, (2) a component due to exogenous environmental forcing, and (3) a component due to demographic stochasticity. The first two components are shared by all species according to the hypothesis of equivalence; therefore, they are independent of population size, appear in both variances and covariances, and contribute to the synchronization of population dynamics. In contrast, demographic stochasticity operates mostly at small population sizes and independently in different species; therefore, it does not appear in covariances, and it contributes to the desynchronization of population dynamics. When demographic stochasticity is weak compared with community regulation and environmental forcing ($\sigma_e^2 + \sigma_c^2 \gg \sigma_d^2/\tilde{N}_i$), species are expected to fluctuate synchronously ($\rho_{r_f} \approx 1$; eq. [5]). In contrast, when community regulation and environmental forcing are weak compared with demographic stochasticity ($\sigma_e^2 + \sigma_c^2 \ll \sigma_d^2/\tilde{N}_i$), species are expected to fluctuate independently ($\rho_{r_f} \approx 0$). Considerable fluctuations in community size when the deterministic attractors are cyclic or chaotic result in strongly synchronous population fluctuations (fig. 1).

The covariances of the per capita population growth rates of all species pairs are expected to be positive and identical under the hypothesis of equivalence (eq. [4]). This is in contrast to Hubbell's (2001) neutral model, which predicts negative covariances, on average. The difference between the two models comes from the fact that total community size is constant in Hubbell's, forcing species abundances to compensate instantaneously for each other. By contrast, ours allows for changes in community size driven by density dependence and environmental stochasticity. These changes affect all species simultaneously and hence tend to synchronize their dynamics.

In contrast to changes in absolute log abundances (i.e., per capita population growth rates), which co-vary positively, changes in relative log abundances co-vary negatively overall, and their variations are entirely driven by

demographic stochasticity (app. A). Thus, relative log abundances in our model play the same role as do absolute abundances in Hubbell's (2001): they obey the same zero-sum-game constraint. Changes in community size driven by density dependence and environmental forcing generate positive correlations between per capita population growth rates, while demographic stochasticity generates negative correlations between changes in relative log abundances.

Correlations between population sizes are intermediate between these two extremes. Per capita population growth rates are always more strongly synchronized than population sizes (fig. 1) because their fluctuations capture the short-term effects of the forces that govern population dynamics from one generation to the next, including the synchronizing effects of community regulation and environmental forcing. Long-term fluctuations in population sizes are affected by ecological drift, which plays a prominent role when species are equivalent. Together with regulation of community size, ecological drift results in species abundances compensating for each other, thereby desynchronizing their fluctuations in the long term.

A New Measure of Community-Wide Synchrony

In the previous section, we used the temporal correlation coefficient as a standardized measure of synchrony between two species. Although the average correlation coefficient has also been used commonly to measure species synchrony at the community level (Bjørnstad et al. 1999), this pairwise measure has limitations because the lower bound on the average correlation coefficient increases from -1 when there are two species to 0 when there are many species (app. C). This mathematical property makes comparisons between communities with different numbers of species difficult. Here we present a new standardized measure of community-wide synchrony that makes such quantitative comparisons possible.

The variance of a community-level variable is directly related to the synchrony of the corresponding population-level variables. This variance drops to 0 when there is perfect asynchrony between species (or no population fluctuations). Its upper bound is determined by the variances of individual species. Let $x_i(t)$ denote any population-level temporal variable of interest for species i , $x_T(t) = \sum_{i=1}^S x_i(t)$ the equivalent aggregate community-level variable, and $\sigma_{x_i}^2$ and $\sigma_{x_T}^2$ their respective temporal variances. The variance of the community-level variable is maximal when the population-level variables of all species are perfectly correlated through time ($\rho_{x_i x_j} = 1$ for all species i and j). In this case, since the variance of a sum of variables is the sum of the variances and covariances of these variables,

$$\begin{aligned}\sigma_{x_{\text{rmax}}}^2 &= \sum_i \sigma_{x_i}^2 + \sum_i \sum_{j \neq i} \sigma_{x_i} \sigma_{x_j} \\ &= \sum_i \sigma_{x_i} \sum_j \sigma_{x_j} = \left(\sum_i \sigma_{x_i} \right)^2.\end{aligned}\quad (8)$$

Therefore, we propose the following statistic to measure community-wide synchrony:

$$\varphi_x = \frac{\sigma_{x_{\text{r}}}^2}{(\sum_i \sigma_{x_i})^2}. \quad (9)$$

This statistic is standardized between 0 (perfect asynchrony) and 1 (perfect synchrony), just like the variance ratio recently proposed by Vasseur and Gaedke (2007). Its additional advantage is that it is readily applied to empirical data because it is particularly simple and makes no specific assumption about the magnitude and distribution of species abundances and variances.

In the special case where all species variances are equal, the dependence of our statistic on species richness, S , and the average temporal correlation coefficient between species, $\bar{\rho}_x$, can be made explicit:

$$\varphi_x = \frac{S\sigma_{x_i}^2 + S(S-1)\bar{\rho}_x\sigma_{x_i}^2}{S^2\sigma_{x_i}^2} = \frac{1 + (S-1)\bar{\rho}_x}{S}. \quad (10)$$

This equation shows that community-wide synchrony, as measured by φ_x , increases with the average temporal correlation between species, which is intuitively satisfactory. It stays constant at its minimum value of 0 when the average correlation is at its minimum value, $\bar{\rho}_x = -1/(S-1)$ (app. C) and stays constant at its maximum value of 1 when the average correlation is also maximum ($\bar{\rho}_x = 1$). But it decreases with species richness for any intermediate value of the average correlation when the latter is kept constant. In particular, it declines as $1/S$ in the special case where species fluctuate independently ($\bar{\rho}_x = 0$). This occurs because our synchrony measure compares the observed community-level variance (numerator of eq. [9]), which is reduced by imperfect correlations between species, with its maximum value when species are perfectly synchronized (denominator of eq. [9]). Since the number of covariance terms that contribute to community-level variance is $S(S-1)$ while the number of variance terms is only S , imperfect correlations between species play an ever-increasing role as species richness S increases, which makes community-wide synchrony decline. Note, however, that the average temporal correlation between species need not stay constant as species richness varies. Since the minimum value of the average temporal correlation approaches 0 as species richness increases, any

initially negative value is bound to increase with species richness (app. C).

Our measure of synchrony can be applied to any temporal variable of interest, including population size, per capita population growth rate, and species environmental response. When the temporal variable is population size, synchrony is simply a standardized measure of the variance of community size. In the above neutral model, the per capita population growth rate is a key temporal variable. The expected synchrony of per capita population growth rates can then be obtained using equations (3) and (4):

$$\varphi_r = \frac{\sigma_c^2 + \sigma_e^2 + \sigma_d^2/(S\tilde{N})}{[(1/S)(\sum_i \sqrt{\sigma_c^2 + \sigma_e^2 + \sigma_d^2/\tilde{N}_i})]^2}. \quad (11)$$

When demographic stochasticity is weak compared with community regulation and environmental forcing ($\sigma_c^2 + \sigma_e^2 \gg \sigma_d^2/\tilde{N}_i$), species are expected to fluctuate synchronously, and $\varphi_r \approx 1$. At the other extreme, when community regulation and environmental forcing are weak compared with demographic stochasticity ($\sigma_c^2 + \sigma_e^2 \ll \sigma_d^2/\tilde{N}_i$), species are expected to fluctuate independently, and $\varphi_r \approx 1/S$. Thus, even in the absence of any form of niche differentiation, species synchrony is expected to decline as species richness increases because of the desynchronizing effect of demographic stochasticity. This particular source of asynchrony, however, does not contribute to community stability. The variance of community size is independent of the number of species when these are equivalent, as equation (6) shows, because demographic stochasticity comes from stochastic variations among individuals, irrespective of species identity.

Species Synchrony under Nonneutral Dynamics

Model Formulation and Methods

Having defined a neutral model of community dynamics and an appropriate measure of community-wide synchrony, we are now ready to examine the deterministic effects of niche differentiation on species synchrony under nonneutral dynamics. Our neutral model can easily be generalized and incorporate niche differences between species by relaxing the hypothesis of species equivalence in two ways: (1) letting interspecific competition be smaller than intraspecific competition, which generates a nontemporal form of niche differentiation that decouples density dependence in the various species, and (2) allowing species to have different responses to environmental forcing, which generates temporal niche differentiation. These two factors constitute a deterministic source of asynchrony that

adds to the effects of demographic stochasticity. Our dynamical model then becomes

$$\begin{aligned} r_i(t) &= r_m \left[1 - \frac{N_i(t) + \alpha \sum_{j \neq i} N_j(t)}{K'} \right] + \varepsilon_i(t) + \frac{\sigma_d U_{di}(t)}{\sqrt{N_i(t)}} \\ &= r_m \left[1 - \frac{(1 - \alpha)N_i(t) + \alpha N_{\text{T}}(t)}{K'} \right] + \varepsilon_i(t) + \frac{\sigma_d U_{di}(t)}{\sqrt{N_i(t)}}. \end{aligned} \quad (12)$$

As in Ives et al. (1999), we assume for simplicity that all species have equal intrinsic rates of natural increase r_m , carrying capacities K' , and interspecific competition coefficients α ($0 \leq \alpha \leq 1$). We also remove the effect of community size on variability by standardizing species carrying capacities such that the carrying capacity of the whole community, K , is independent of α (Ives et al. 1999):

$$K' = \frac{1 + \alpha(S - 1)}{S} K. \quad (13)$$

These simplifying assumptions are made to explore the specific effect of incorporating niche differences between species into the neutral baseline scenario. Including differences among species in their intrinsic rate of natural increase, carrying capacity, or interspecific competition coefficients would undoubtedly be more realistic, but doing so would confound the effects of niche differentiation with those of differences in competitive ability.

Environmental stochasticity is assumed to have the same variance σ_e^2 as before, but the species environmental responses $\varepsilon_i(t)$ can now have varying correlations. There are many different ways to incorporate differences in species environmental responses when these are negatively correlated. We chose two scenarios to generate them: (1) species are distributed into two response functional groups with synchronous fluctuations within groups and asynchronous fluctuations between groups, and (2) all species pairs have the same expected correlation between species environmental responses. The two scenarios provide similar results, but the results of the second are better behaved; therefore, we present only the latter here. In this scenario, the environmental response of species i is defined by

$$\varepsilon_i(t) = \beta u_{ei}(t) - \overline{u_{ei}(t)}, \quad (14)$$

where $u_{ei}(t)$ is an independent normal variable with 0 mean, $\overline{u_{ei}(t)}$ is the average of these variables across species, and β is a parameter that governs the synchrony of environmental responses. Since the environmental variance is assumed to be identical for all species, the synchrony of species environmental responses φ_e is related to their

average correlation by equation (10); that is, $\varphi_e = [1 + (S + 1)\rho_e]/S$. When $\beta = 0$, all species responses are perfectly synchronized ($\varphi_e = 1$); at the other extreme, when $\beta = 1$, species responses are maximally desynchronized ($\varphi_e = 0$). Parameter β and the variance of $u_{ei}(t)$, $\sigma_{u_{ei}}^2$, are adjusted so that the synchrony of environmental responses is equal to a chosen value φ_e and the variance of $\varepsilon_i(t)$ is equal to σ_e^2 irrespective of the number of species. Under these constraints,

$$\beta = \begin{cases} \frac{\varphi_e - 1 + \sqrt{\varphi_e(1 - \varphi_e)(S - 1)}}{S\varphi_e - 1} & \varphi_e \neq \frac{1}{S} \\ 0.5 & \varphi_e = \frac{1}{S} \end{cases}, \quad (15)$$

and

$$\sigma_{u_{ei}}^2 = \frac{\sigma_e^2}{\beta^2 + (1 - 2\beta)/S}. \quad (16)$$

We provide first-order analytical approximations of the synchrony of per capita population growth rates and of the synchrony of population sizes in appendix B. To be valid, however, these approximations require sufficiently small population fluctuations, in particular values of the intrinsic rate of natural increase that lead to a stable equilibrium of community size ($0 < r_m < 2$). The approximation of the synchrony of population sizes further requires that the interspecific competition coefficient be smaller than 1. When these conditions were met, we compared their predictions with simulated data. Although these approximations are fairly complex, in the limiting case when $\alpha = 0$ they reduce to the much simpler expression

$$\varphi_r|_{\alpha=0} \approx \varphi_N|_{\alpha=0} \approx \frac{\varphi_e \sigma_e^2 + \sigma_d^2/K}{\sigma_e^2 + \sigma_d^2 S/K}. \quad (17)$$

We analyzed numerically an equivalent model in which the normal approximation for demographic stochasticity was replaced with a Poisson process, which amounts to constraining the demographic variance to be roughly equal to 1, on average (app. D). Although our Poisson model constrains the value of the demographic variance, it incorporates demographic stochasticity in a more realistic way, especially at low population sizes where the normal approximation breaks down. Also, our results hinge mainly on the relative strength of demographic stochasticity compared with those of community regulation and environmental forcing, and this relative strength can be varied by simply changing the parameters that govern community regulation and environmental forcing. Therefore, we present only the results for the Poisson model below.

Using this model, we first checked that our analytical formulas for the neutral model correctly predicted simulated data, which they did. We then analyzed the effects of deterministic niche differentiation on the synchrony of both per capita population growth rates and population sizes, by decreasing the competition coefficient α (11 values, uniformly distributed between 0 and 1) and the synchrony of environmental responses φ_e (nine to 11 values, depending on the number of species). We also varied other parameters, in particular the intrinsic rate of natural increase r_m (six values: 0.5, 1, 1.5, 2, 2.5, and 3), the environmental variance σ_e^2 (four values: 0.0001, 0.01, 0.09, and 0.25), and the number of species S (five values: 2, 4, 8, 16, and 32). In total, there were 13,200 combinations of parameter values.

For each of these combinations, we repeated simulations until we obtained 200 time series in which no species became extinct. When species extinctions were too frequent, however, we stopped after 120,000 unsuccessful simulations and analyzed the available set of simulations without extinctions. Extinctions were infrequent when species richness was low, except under two circumstances: (1) when the interspecific competition coefficient was equal to 1 and the synchrony of environmental responses was low, and (2) when dynamics were chaotic ($r_m = 3$). Extinction frequency increased sharply with the number of species and the environmental variance. For a few combinations of parameter values, no simulations without extinctions were available, and hence the corresponding results are missing. In total, we performed more than 100 million simulations.

Each simulation was run over 300 generations (time steps), but only the final 200 generations were analyzed, to remove effects of initial conditions. Each simulation was initiated with a community in which species abundances were approximately, but not exactly (to allow independent deterministic chaotic dynamics between species), equal to their equilibrium values (total carrying capacity divided by the number of species). These initial conditions allowed a stationary regime to be reached after 100 generations (fig. 1). We present only results for one value of the environmental variance and two values of species richness below because other values led to qualitatively similar results.

Effects of Temporal Niche Differentiation on Synchrony

The synchrony of environmental responses φ_e provides a standardized community-wide measure of temporal niche differentiation between species. Smaller values of this synchrony correspond to greater temporal niche differentiation.

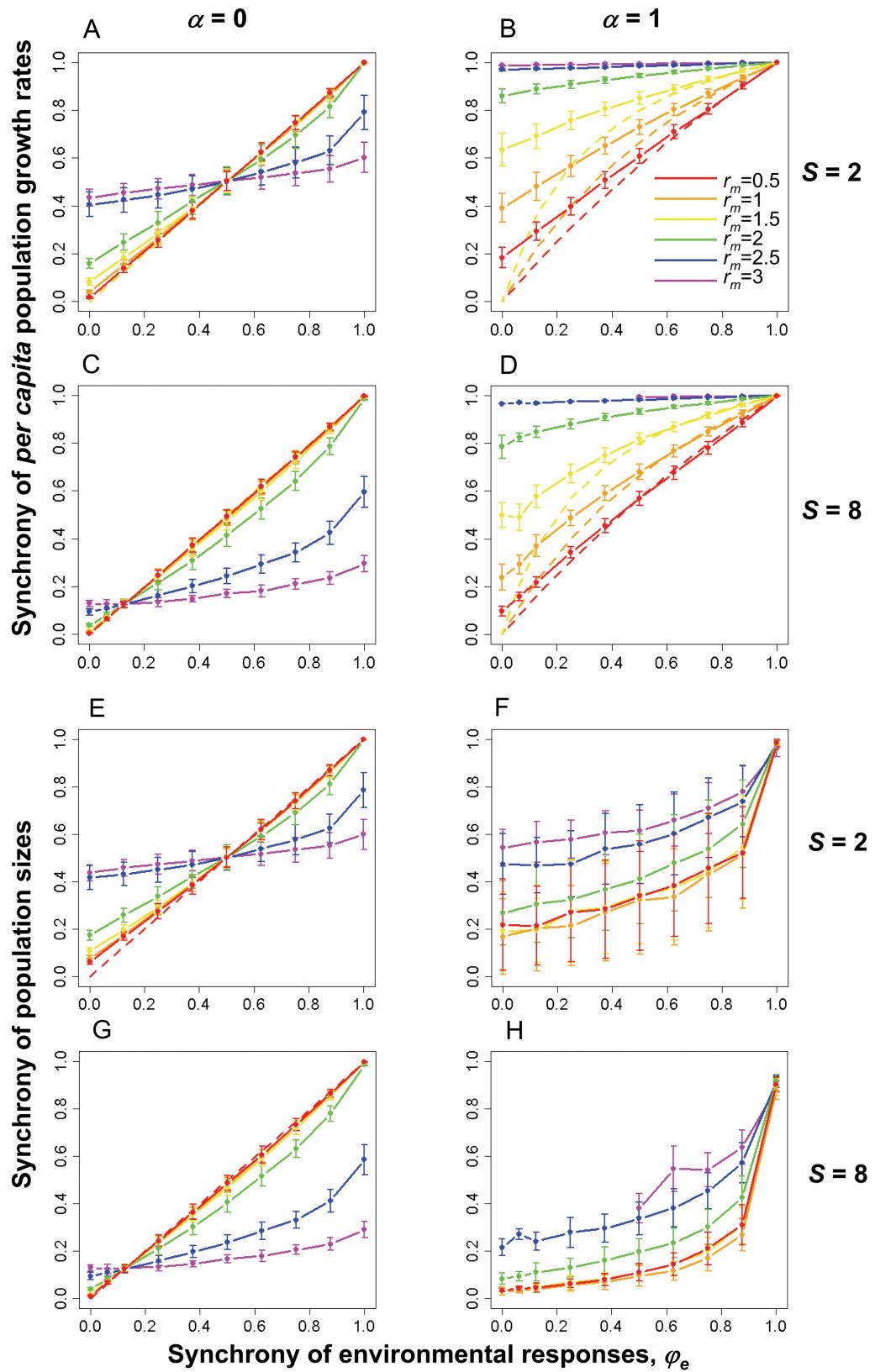
First-order approximations predict that both the syn-

chrony of per capita population growth rates and the synchrony of population sizes should increase linearly with the synchrony of environmental responses when the interspecific competition coefficient is small (eq. [17]). Numerical simulations show that they do so when the validity conditions of the first-order approximation are met, that is, when the intrinsic rate of natural increase is sufficiently small (fig. 2, *left*). Thus, as might be expected intuitively, temporal niche differentiation generally decreases species synchrony.

The observed patterns deviate increasingly from the predictions of the first-order approximation as the intrinsic rate of natural increase increases, thus yielding cyclic or chaotic population dynamics, and as the interspecific competition coefficient comes close to 1 (fig. 2). In the latter case, the synchrony of per capita population growth rates (fig. 2B, 2D) changes in a much more linear and predictable (less variable) way with the synchrony of environmental responses than do either the first-order approximation or the synchrony of population sizes (fig. 2F, 2H). The considerable discrepancy between observed and predicted results when interspecific competition is strong and environmental responses are strongly asynchronous (fig. 2B, 2D) appears to be due to ecological drift. Species abundances are then highly uneven for extended periods of time, thus preventing species' compensatory responses from fully operating. As a result, community size fluctuates more widely than predicted, which enhances the synchronizing role of shared density dependence in population dynamics.

Effects of Species Richness on Synchrony

First-order approximations predict that increasing species richness S should decrease species synchrony for a given value of the synchrony of environmental species responses when the interspecific competition coefficient is small (eq. [17]). This occurs because increasing the number of species decreases the population size of each species, thus increasing the role played by demographic stochasticity. This effect, however, depends on the relative strength of demographic stochasticity, as measured by σ_d^2/K , compared with that of environmental forcing, as measured by the environmental variance σ_e^2 , in the community as a whole. Since demographic stochasticity was fairly weak ($\sigma_d^2/K \ll \sigma_e^2$) in our simulations, species richness should have only a weak effect on species synchrony. When the interspecific competition coefficient and the intrinsic rate of natural increase are both small, the effect of species richness on the synchrony of both per capita population growth rates and population sizes is weak, as expected (fig. 2, *left*). But this effect gets stronger as the intrinsic rate of natural increase increases when the interspecific competition coefficient is small (fig. 2, *left*) because species fluctuations



are then more independent, yielding a synchrony that is closer to $1/S$ (see “Effects of the Intrinsic Rate of Natural Increase”). Species richness also reduces species synchrony when interspecific competition is strong and environmental responses are strongly asynchronous, that is, when ecological drift is important (fig. 2, *right*), because species abundances are then less uneven, which reduces the synchronizing effect of shared density dependence discussed in “Effects of Temporal Niche Differentiation on Synchrony.”

Effects of the Strength of Interspecific Competition on Synchrony

Contrary to traditional expectations, increasing the strength of interspecific competition does not desynchronize but instead synchronizes fluctuations in per capita population growth rates (fig. 3A–3D). As the strength of interspecific competition increases, density dependence is increasingly coupled between species and hence contributes to synchronizing their short-term fluctuations, as captured by per capita population growth rates.

The effect of interspecific competition on the synchrony of population sizes is more complex. When the synchrony of environmental responses is 0, the first-order approximation predicts that the synchrony of population sizes should be very low because demographic stochasticity is weak compared with environmental forcing (eq. [17]). The full approximation (eq. [B23]) could be used to show that increasing the interspecific competition coefficient should generally further decrease the synchrony of population sizes (as is apparent in fig. 3H). The simulation results show a relatively flat response, as expected (fig. 3E, 3G), but it is significantly higher than that predicted when species richness is low (fig. 3E). This deviation from the first-order approximation occurs because when there are only two species, their relative abundances often differ substantially through ecological drift, as explained in “Effects of Species Richness on Synchrony.”

When the intrinsic rate of natural increase is large, the synchrony of population sizes shows a hump-shaped relationship with the interspecific competition coefficient (fig. 3E, 3G). This pattern is the result of two counteracting factors. At first, increasing the strength of interspecific

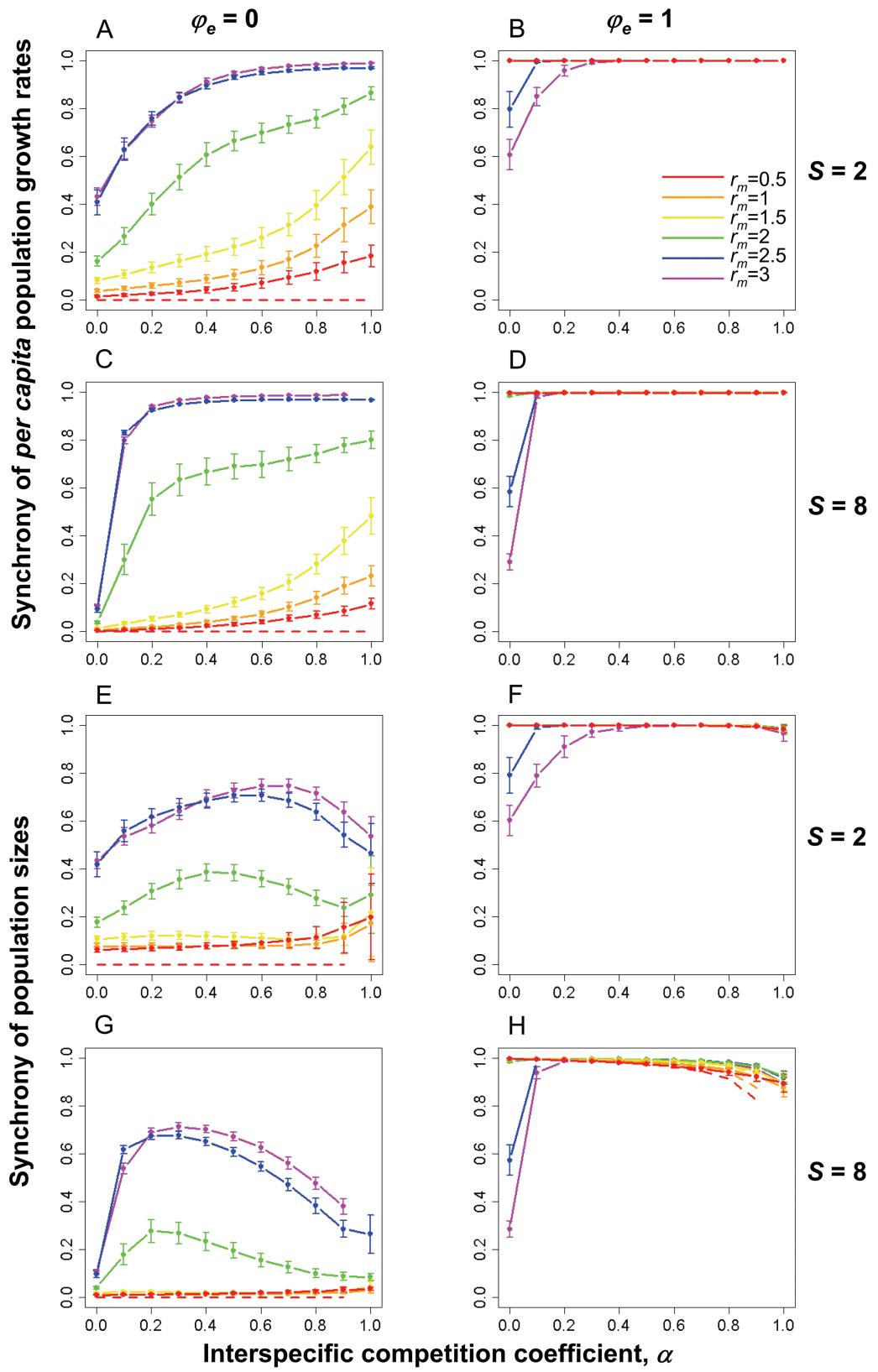
competition synchronizes population sizes, just as it does for per capita population growth rates, because it couples strong density dependence between species. But as the interspecific competition coefficient approaches 1, species become increasingly equivalent. Ecological drift then plays a major role, desynchronizing long-term fluctuations in population sizes despite the increased synchrony of short-term fluctuations in per capita population growth rates. Similar results are obtained when species environmental responses are strongly synchronized (fig. 3F, 3H).

Effects of the Intrinsic Rate of Natural Increase on Synchrony

By controlling the strength of density dependence and hence the dynamical behavior of the community, the intrinsic rate of natural increase has strong, complex effects on community-wide synchrony. As the intrinsic rate of natural increase increases, the synchrony of per capita population growth rates increases when the synchrony of environmental responses is low (fig. 3A, 3C), but it decreases when the synchrony of environmental responses is high (fig. 3B, 3D). Higher values of the intrinsic rate of natural increase lead to larger population fluctuations driven by density dependence, including limit cycles ($r_m = 2.5$) and chaos ($r_m = 3$). The larger these endogenous population fluctuations, the more they dominate population dynamics and overwhelm the effects of exogenous environmental forcing. Thus, counterintuitively, internal instability generated by strong density dependence acts to synchronize populations that have asynchronous responses to extrinsic environmental variations because the latter play a comparatively small role in population dynamics (fig. 3A, 3C). Conversely, internal instability generated by strong density dependence tends to desynchronize populations that have synchronous responses to extrinsic environmental variations for the same reason (fig. 3B, 3D).

As a result, the synchronies of both per capita population growth rates and population sizes are less dependent on the synchrony of environmental responses when the intrinsic rate of natural increase is higher, yielding larger population fluctuations (fig. 2). When interspecific competition is weak (fig. 2, *left*), stronger density dependence makes species fluctuations more independent (the syn-

Figure 2: Community-wide synchrony (mean \pm 1 SD) of species per capita population growth rates (A–D) and population sizes (E–H) as a function of the synchrony of environmental responses, φ_e , for two values of the interspecific competition coefficient, α (*left*: $\alpha = 0$; *right*: $\alpha = 1$), and two values of species richness, S (A, B, E, and F: $S = 2$; C, D, G, and H: $S = 8$), in the nonneutral Poisson model. The six solid curves in each panel correspond to different values of r_m , as indicated in B. Dashed lines (sometimes confounded with solid lines or with each other) show the corresponding first-order approximations for the three values of the intrinsic rate of natural increase that yield a stable equilibrium. First-order approximations of the synchrony of population sizes are not available for $\alpha = 1$ (F, H). A few data points are missing in D and H because no simulation without species extinctions was available for these combinations of parameter values. Other parameter values: $K = 20,000$ and $\sigma_e = 0.3$.



chrony of per capita population growth rates and population sizes is closer to $1/S$) because it tends to act independently in the various species. In the special case where the interspecific competition coefficient and the correlation between species environmental responses are both 0, species fluctuations are perfectly independent since all the forces that drive population dynamics (density dependence, environmental forcing, and demographic stochasticity) affect species independently. The synchrony of environmental responses is then equal to $1/S$ (see "A New Measure of Community-Wide Synchrony"), and hence the synchrony of population sizes is also equal to $1/S$ (eq. [17]), irrespective of the value of the intrinsic rate of natural increase. As a result, all the curves intersect at the point $(1/S, 1/S)$ in the left-hand panels of figure 2. By contrast, when interspecific competition is strong (fig. 2, right), stronger density dependence synchronizes species fluctuations because density dependence tends to act on the community as a whole, thus dragging all species into the same endogenous fluctuations.

Discussion

Three main forces drive population dynamics: intra- and interspecific density dependence, environmental forcing, and demographic stochasticity. Our mechanistic neutral model provides quantitative predictions of their joint effects on species synchrony in neutral communities consisting of equivalent species. It predicts that the covariances and correlations between the per capita population growth rates of equivalent species are always positive and that their magnitude depends on the relative strengths of community regulation and environmental forcing on the one hand, which tend to synchronize population fluctuations, and demographic stochasticity on the other hand, which tends to desynchronize population fluctuations.

It is often assumed, implicitly or explicitly, that species should fluctuate independently in the absence of niche differentiation and competition between species (Doak et al. 1998; Tilman 1999; Ernest and Brown 2001; Houlahan et al. 2007). In the real world, however, all communities are subject to fluctuations in their environment. The growth and fitness of any organism are highly dependent on abiotic factors such as climate, and environmental fluctuations drive the dynamics of many populations (Steele

1985; Lawton 1988). Moreover, organisms that coexist on the same resources in the same habitat tend to be affected by their environment in similar ways. Therefore, in the absence of niche differentiation, coexisting species should fluctuate synchronously, not independently. The same is true when population fluctuations are created by endogenous factors. These fluctuations should be synchronized if they are driven by a common factor of density dependence, such as competition for a shared resource. Our model shows that even chaotic dynamics, which might be expected intuitively to be a desynchronizing factor because of its dependence on initial conditions and its long-term unpredictability, is in fact a powerful synchronizing factor because the force that drives this dynamics, that is, density dependence, acts on all competing species.

Demographic stochasticity is the only factor that intrinsically leads to independent fluctuations. But it mainly affects small populations and seldom occurs without the simultaneous presence of density dependence and environmental forcing. Our neutral model shows that demographic stochasticity alone cannot oppose the synchronizing effects of density dependence and environmental forcing; it can only reduce their strength. Therefore, in the presence of interspecific competition and environmental forcing, which are ubiquitous in natural communities, demographic stochasticity alone is unable to generate independent species fluctuations.

Although its formalism is very different, our neutral model may be viewed as a generalization of Hubbell's (2001) for communities in which total community size fluctuates because of both endogenous and exogenous factors. Hubbell's neutral model makes the stringent assumption that community size is constant, an assumption that is violated in many natural communities. Ours relaxes this assumption, which makes it potentially more relevant to the analysis of population fluctuations and ecosystem stability in many natural communities. In our model, species relative abundances obey the same zero-sum-game constraint as do absolute abundances in Hubbell's model. But community size is allowed to vary under the influence of endogenous density dependence and exogenous environmental forcing. Because of these variations in community size, negative correlations between changes in species relative abundances are often accompanied by positive correlations between species absolute abundances. This ex-

Figure 3: Community-wide synchrony (mean \pm 1 SD) of species per capita population growth rates (A–D) and population sizes (E–H) as a function of the interspecific competition coefficient, α , for two values of the synchrony of environmental responses, φ_e (*left*: $\varphi_e = 0$; *right*: $\varphi_e = 1$), and two values of species richness, S (A, B, E, and F: $S = 2$; C, D, G, and H: $S = 8$), in the nonneutral Poisson model. The six solid curves in each panel correspond to different values of r_m as indicated in B. Dashed lines (sometimes confounded with solid lines or with each other) show the corresponding first-order approximations for the three values of the intrinsic rate of natural increase that yield a stable equilibrium. Other parameter values: $K = 20,000$ and $\sigma_e = 0.3$.

plains the empirical observation that many communities have positive covariances between species abundances on average (Houlahan et al. 2007). Such positive covariances, however, do not indicate that competitive interactions are absent.

The nonneutral version of our model shows that niche differentiation has relatively consistent effects on the synchrony of species per capita population growth rates, whether it occurs through a reduction in the strength of interspecific competition or through different species responses to environmental fluctuations. In both cases, increased niche differentiation yields increased asynchrony of species per capita population growth rates. This result contradicts the traditional belief that interspecific competition should desynchronize population dynamics (e.g., Tilman 1999; Ernest and Brown 2001; Houlahan et al. 2007). This traditional view implicitly considers saturated communities and ignores fluctuations in community size driven by endogenous density dependence and exogenous environmental forcing, very much like the neutral theory. Our results are different, and more complex, when long-term fluctuations in species abundances are considered. Interspecific competition synchronizes fluctuations in species abundances when it is relatively weak, but it tends to desynchronize fluctuations in species abundances when it is relatively strong, especially when the intrinsic rate of natural increase is high, generating wide, endogenously driven population fluctuations.

The discrepancy between per capita population growth rates and population sizes arises because these variables are affected by processes that occur on different timescales. Fluctuations in per capita population growth rates capture the short-term effects of the forces that govern population dynamics from one generation to the next, including the predictable effects of community regulation and environmental forcing. By contrast, fluctuations in population sizes are affected to a larger extent by long-term processes such as ecological drift. Counterintuitively, ecological drift is the factor that explains the desynchronization of long-term population fluctuations when interspecific competition is strong, for species then tend to become increasingly equivalent. We suggest that per capita population growth rates have the twofold advantage over population sizes of (1) lending themselves to analytical treatment in the neutral scenario and (2) yielding more consistent, predictable results in nonneutral scenarios because they are less affected by long-term trends in population fluctuations. Thus, our results bearing on species synchrony within a community agree with those of previous studies on spatial population synchrony across communities (Bjørnstad et al. 1999).

Like any model, ours have limitations. In particular, we assumed that environmental stochasticity affects per capita

population growth rates additively. We chose this simple form because it is a first-order approximation of any form of environmental stochasticity that acts on a per capita basis, and it is consistent with a large body of theoretical and empirical studies in stochastic population dynamics (Lande et al. 2003). Environmental forcing, however, could affect population dynamics in different ways, for instance, though changes in the carrying capacity. We show in appendix E that this form of environmental stochasticity has effects identical to that included in our models after appropriate rescaling, as long as population fluctuations are small. But their effects are likely to be different when population fluctuations are large, especially when endogenous dynamics are cyclic or chaotic. We standardized the carrying capacity of each species, such that the expected value of community size is independent of the strength of interspecific competition, to remove the confounding effect of community size on variability (Ives et al. 1999). A side effect of this assumption, however, is that the population size of each species is reduced by the presence of other species, thus implying interspecific competition operating in a different way. Thus, the interspecific competition coefficient in our model controls the degree of coupling of density dependence among species, but it leaves out any effect of interspecific competition on population size. We believe that this is a strength of our model because it allows a clear interpretation of the results by removing confounding factors, but the corresponding weakness is that our analysis does not consider some of the effects of competition. Future studies based on different assumptions and scenarios will be necessary to make predictions on species synchrony under more realistic conditions applicable to real communities.

We suggest that the covariances or synchrony of species per capita population growth rates predicted by the neutral model should serve as the proper null hypothesis to test for nonneutral, deterministic asynchrony driven by niche differences between species. Since niche differentiation, in the form of either decreased interspecific competition coefficients or decreased correlations between species environmental responses, steadily decreases the expected synchrony of species per capita population growth rates, comparing the observed synchrony of species per capita population growth rates with the corresponding values predicted by the neutral model potentially provides a simple test of deterministic asynchrony in a community. Quantitative predictions under the null hypothesis, however, require estimates of demographic and environmental variances based on individual data on survival and reproduction, and these are currently scarce for organisms other than vertebrates and for entire communities (Lande et al. 2003). We hope that the theory we outline here will stimulate the collection of new empirical data on vital statistics

as well as the development of new methods to collect and analyze these data.

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APPENDIX A

Temporal Variances and Covariances in the Neutral Model

The temporal variances and covariances of per capita population growth rates in the neutral model (eq. [2]) are obtained as follows. For species that do not become extinct, the fluctuations in $\ln N_i(t)$ are bounded. Therefore, the expected value of their per capita population growth rate, $E(r_i)$, is 0 (Levins 1979). Since the expected values of the random variables associated with environmental and demographic stochasticity, $E(U_e)$ and $E(U_{di})$, are also 0, $E(N_T) = K$.

Also, since $U_e(t)$ and $U_{di}(t)$ are independent random variables, they are uncorrelated with each other and with community size $N_T(t)$. Therefore, the temporal variance of the per capita population growth rate of species i reduces to

$$\sigma_{r_i}^2 = \frac{r_m^2 \sigma_{N_T}^2}{K^2} + \sigma_e^2 + \frac{\sigma_d^2}{\tilde{N}_i}, \quad (\text{A1})$$

where $\tilde{N}_i = 1/E(1/N_i)$ is the harmonic temporal mean of population size.

Similarly, the temporal covariance between the per capita population growth rates of two species i and j has three components. The first two components, those due to regulation of community size and environmental forcing, are identical in all species and hence equal to the corresponding variance components. The third component, that due to demographic stochasticity, is 0 because the population fluctuations driven by demographic stochasticity are independent and uncorrelated. Therefore,

$$\text{Cov}(r_i, r_j) = \frac{r_m^2 \sigma_{N_T}^2}{K^2} + \sigma_e^2. \quad (\text{A2})$$

The dynamics of relative log abundances are obtained from equation (2) following the same procedure as in Lande et al. (2003). Define the relative log abundance of species i at time t as $\nu_i(t) = \ln N_i(t) - \overline{\ln N(t)}$, where $\overline{\ln N(t)} = (1/S) \sum_{i=1}^S \ln N_i(t)$ is the average log abundance at time t , and the change in the relative log abundance of species i between times t and $t+1$ as

$$\gamma_i(t) = \nu_i(t+1) - \nu_i(t) = \ln N_i(t+1) - \overline{\ln N(t+1)} - \ln N_i(t) + \overline{\ln N(t)} = r_i(t) - \bar{r}(t). \quad (\text{A3})$$

The long-term temporal variances and covariances of changes in relative log abundances are, then, respectively,

$$\sigma_{\gamma_i}^2 = \text{Var}(\gamma_i) = \sigma_{r_i}^2 - \frac{2}{S} \sum_{j=1}^S \text{Cov}(r_i, r_j) + \frac{1}{S^2} \sum_{j=1}^S \sum_{k=1}^S \text{Cov}(r_j, r_k) = \sigma_d^2 \left[\left(1 - \frac{2}{S} \right) \frac{1}{\tilde{N}_i} + \frac{1}{S \tilde{N}} \right] \quad (\text{A4})$$

and

$$\text{Cov}(\gamma_i, \gamma_j) = \text{Cov}(r_i - \bar{r}, r_j - \bar{r}) = \sigma_d^2 \left(-\frac{1}{S \tilde{N}_i} - \frac{1}{S \tilde{N}_j} + \frac{1}{S \tilde{N}} \right), \quad (\text{A5})$$

where $\tilde{N} = 1/\overline{E(I/N)}$ is the general harmonic temporal mean of population size across all species.

Changes in relative log abundances on average co-vary negatively. This is easily seen when all species have the same harmonic temporal mean abundance ($\tilde{N}_i = \tilde{N}$ for all i); in this case, the temporal correlation of changes in relative log abundances reduces to $\rho_{\gamma_i \gamma_j} = -1/(S-1)$, that is, the minimum possible correlation compatible with the number of species S (app. C). It is also apparent from equations (A4) and (A5) that the variances and covariances of changes in relative log abundances are entirely driven by demographic stochasticity.

APPENDIX B

First-Order Approximations in the Nonneutral Model

First-order approximations of the temporal variance of community size, the temporal variances and synchrony of population sizes, and the temporal variances and synchrony of per capita population growth rates in the nonneutral version of our model are obtained as follows (Ives 1995; Hughes and Roughgarden 1998; Ives and Hughes 2002). Equation (12) can be rewritten as

$$N_i(t+1) = N_i(t) \exp \left\{ r_m \left[1 - \frac{(1-\alpha)N_i(t) + \alpha N_T(t)}{K'} \right] + \varepsilon_i(t) + \frac{\sigma_d U_{di}(t)}{\sqrt{N_i(t)}} \right\}. \quad (\text{B1})$$

Let $n_i(t) = N_i(t) - K/S$ denote the deviation of species i 's abundance from its equilibrium value K/S in the absence of environmental and demographic stochasticity. Equation (B1) can be Taylor expanded around $n_i(t) = \varepsilon_i(t) = U_{di}(t) = 0$ to yield, after dropping terms of order two and higher,

$$\mathbf{n}(t+1) = \mathbf{An}(t) + \mathbf{z}(t), \quad (\text{B2})$$

where $\mathbf{n}(t)$ is the vector of deviations of species abundances from their equilibrium value, \mathbf{A} is the community matrix, and $\mathbf{z}(t)$ is a vector that encapsulates the effects of environmental and demographic stochasticity, whose elements are

$$z_i(t) = \frac{K}{S} \varepsilon_i(t) + \sqrt{\frac{K}{S}} \sigma_d U_{di}(t). \quad (\text{B3})$$

The community matrix \mathbf{A} has elements a_{ij} such that

$$a_{ij} = \begin{cases} 1-x & i=j \\ -\alpha x & i \neq j \end{cases} \quad (\text{B4})$$

where $x = r_m/[1 + (S-1)\alpha]$.

Equation (B2) describes a set of S linear equations for the S species. Summing these S equations yields a linear equation for the dynamics of $n_T(t) = \sum_{i=1}^S n_i(t)$, the deviation of community size from its equilibrium value:

$$n_T(t+1) = (1 - r_m)n_T(t) + \frac{K}{S} \sum_{i=1}^S \varepsilon_i(t) + \sqrt{\frac{K}{S}} \sigma_d \sum_{i=1}^S U_{di}(t). \quad (\text{B5})$$

Taking the variance of both sides of this equation, noting that $\text{Var}(n_T(t+1)) = \text{Var}(n_T(t)) = \sigma_{n_T}^2$, and solving for $\sigma_{n_T}^2$ yields

$$\sigma_{n_T}^2 = \frac{(K/S)^2 \text{Var}(\sum_{i=1}^S \varepsilon_i) + (K/S) \sigma_d^2 \text{Var}(\sum_{i=1}^S U_{di})}{1 - (1 - r_m)^2}. \quad (\text{B6})$$

The variance of the sum of species environmental responses ε_i is equal to the sum of their variances and covariances; that is,

$$\text{Var}\left(\sum_{i=1}^S \varepsilon_i\right) = S\sigma_e^2 + S(S-1)\bar{\rho}_e\sigma_e^2 = S^2\varphi_e\sigma_e^2, \quad (\text{B7})$$

where $\bar{\rho}_e$ is the average correlation between species environmental responses and φ_e is their synchrony as defined by equation (9).

Since the random variables U_{di} are independent, the variance of their sum is simply the sum of their variances, that is, S . Therefore,

$$\sigma_{n_T}^2 = \frac{K^2(\varphi_e\sigma_e^2 + \sigma_d^2/K)}{r_m(2 - r_m)}. \quad (\text{B8})$$

This variance is positive and finite when $0 < r_m < 2$, which is a necessary condition for the stability of the equilibrium.

To obtain first-order approximations of the temporal variances of individual population sizes, equation (B2) has to be studied in a new set of coordinates. Let $\lambda_1, \dots, \lambda_S$ be the S eigenvalues of the community matrix \mathbf{A} , \mathbf{D} a diagonal matrix that has these S eigenvalues along the main diagonal and 0s elsewhere, and \mathbf{T} an $S \times S$ matrix whose columns are the eigenvectors of \mathbf{A} . We then have

$$\mathbf{T}^{-1}\mathbf{AT} = \mathbf{D}. \quad (\text{B9})$$

Left-multiplying the two sides of equation (B2) by \mathbf{T}^{-1} and using equation (B9) yields

$$\mathbf{n}^*(t+1) = \mathbf{D}\mathbf{n}^*(t) + \mathbf{z}^*(t), \quad (\text{B10})$$

where

$$\mathbf{n}^*(t) = \mathbf{T}^{-1}\mathbf{n}(t) \quad (\text{B11})$$

and

$$\mathbf{z}^*(t) = \mathbf{T}^{-1}\mathbf{z}(t). \quad (\text{B12})$$

Equation (B10) describes a set of S linear equations for the S species:

$$n_i^*(t+1) = \lambda_i n_i^*(t) + z_i^*(t). \quad (\text{B13})$$

Taking the covariances of both sides of this equation, noting that $\text{Cov}[n_i^*(t+1), n_j^*(t+1)] = \text{Cov}[n_i^*(t), n_j^*(t)] = \text{Cov}(n_i^*, n_j^*)$, and solving for $\text{Cov}(n_i^*, n_j^*)$ yields

$$\text{Cov}(n_i^*, n_j^*) = \frac{\text{Cov}(z_i^*, z_j^*)}{1 - \lambda_i \lambda_j}. \quad (\text{B14})$$

Variances are obtained using the same equation by regarding them as a special case of covariances; that is, $\sigma_{n_i^*}^2 = \text{Cov}(n_i^*, n_i^*)$.

The variances of population sizes can then be obtained by returning to the initial set of coordinates using the inverse of transformation (B11); that is,

$$n_i(t) = \sum_j t_{ij} n_j^*(t), \quad (\text{B15})$$

where t_{ij} are the elements of matrix \mathbf{T} . Taking the variance of both sides of this equation yields

$$\sigma_{n_i}^2 = \sum_j \sum_k t_{ij} t_{ik} \text{Cov}(n_j^*, n_k^*). \quad (\text{B16})$$

In our linearized system (eq. [B2]), the eigenvalues of the community matrix \mathbf{A} are

$$\lambda_i = \begin{cases} 1 - r_m & i = 1 \\ \lambda_2 = 1 - (1 - \alpha)x & 2 \leq i \leq S \end{cases}. \quad (\text{B17})$$

Computing the corresponding eigenvectors and applying equation (B12) gives

$$z_i^*(t) = \begin{cases} \frac{1}{S} \sum_j z_j(t) = \bar{z}(t) & i = 1 \\ z_i(t) - \bar{z}(t) = z_i(t) - z_1^*(t) & 2 \leq i \leq S \end{cases}. \quad (\text{B18})$$

Taking the variances and covariances of these transformed variables yields, after some algebraic manipulation,

$$\sigma_{z_i^*}^2 = \begin{cases} \left(\frac{K}{S}\right)^2 \left(\varphi_e \sigma_e^2 + \frac{\sigma_d^2}{K}\right) & i = 1 \\ \left(\frac{K}{S}\right)^2 \left[(1 - \varphi_e) \sigma_e^2 + (S - 1) \frac{\sigma_d^2}{K}\right] & 2 \leq i \leq S \end{cases}, \quad (\text{B19})$$

$$\text{Cov}(z_i^*, z_j^*) = \begin{cases} 0 & i = 1, 2 \leq j \leq S \\ \left(\frac{K}{S}\right)^2 \left[\left(\frac{\varphi_e - 1}{S - 1}\right) \sigma_e^2 - \frac{\sigma_d^2}{K}\right] & 2 \leq i, j \leq S \end{cases}. \quad (\text{B20})$$

Finally, applying equations (B14) and (B16), we obtain

$$\sigma_{n_i}^2 = \frac{K^2 \{ [\varphi_e \mu_2 + (1 - \varphi_e) \mu_1] \sigma_e^2 + [\mu_2 + (S - 1) \mu_1] \sigma_d^2 / K \}}{S^2 \mu_1 \mu_2}, \quad (\text{B21})$$

where

$$\mu_i = 1 - \lambda_i^2. \quad (\text{B22})$$

This variance is positive and finite when $0 < r_m < 2$ and $\alpha < 1$. In the limit when $\alpha = 1$, $\lambda_2 = 1$, hence $\mu_2 = 0$, and the long-term temporal variance of population sizes becomes infinite because populations are no longer regulated around an equilibrium size.

A first-order approximation of the community-wide synchrony of population sizes is then easily obtained by substituting equations (B8) and (B21) into equation (9):

$$\varphi_n = \frac{\mu_2 (\varphi_e \sigma_e^2 + \sigma_d^2 K)}{[\varphi_e \mu_2 + (1 - \varphi_e) \mu_1] \sigma_e^2 + [\mu_2 + (S - 1) \mu_1] \sigma_d^2 / K}. \quad (\text{B23})$$

When $\alpha = 0$, $\mu_1 = \mu_2 = r_m(2 - r_m)$ and equation (B23) reduces to equation (17).

First-order approximations of the temporal variances and community-wide synchrony of per capita population growth rates can be obtained following a similar procedure. Per capita population growth rates (eq. [12]) are approximately

$$r_i(t) = -\frac{xS}{K} \left[n_i(t) + \alpha \sum_{j \neq i} n_j(t) \right] + \varepsilon_i(t) + \sqrt{\frac{S}{K}} \sigma_d U_{di}(t). \quad (\text{B24})$$

The temporal variance of this approximation is

$$\sigma_{r_i}^2 = \frac{x^2 S^2}{K^2} \{ [1 + (S - 1)\alpha^2] \sigma_{n_i}^2 + [2 + (S - 2)\alpha](S - 1)\alpha \text{Cov}(n_i, n_j) \} + \sigma_e^2 + \frac{S\sigma_d^2}{K}. \quad (\text{B25})$$

Using equations (B14) and (B15), we obtain, after some algebraic manipulation,

$$\text{Cov}(n_i, n_j) = \sum_k \sum_l \frac{t_{ik} t_{jl} \text{Cov}(z_k^*, z_l^*)}{1 - \lambda_k \lambda_l} = \frac{K^2}{S^2 \mu_1 \mu_2} \left\{ \left[\varphi_e \mu_2 - \frac{(1 - \varphi_e) \mu_1}{S - 1} \right] \sigma_e^2 + \frac{(\mu_2 - \mu_1) \sigma_d^2}{K} \right\}. \quad (\text{B26})$$

Substituting equations (B21) and (B26) into equation (B25) then yields

$$\sigma_{r_i}^2 = \frac{2[(2 - r_m + \alpha x S \varphi_e) \sigma_e^2 + (2 - r_m + \alpha x) S \sigma_d^2 / K]}{(2 - r_m)[2 - (1 - \alpha)x]}. \quad (\text{B27})$$

Note that, in contrast to the variance of population sizes, this variance is positive and finite when $\alpha = 1$.

The variance of the sum of per capita population growth rates is approximately

$$\sigma_{r_T}^2 = \text{Var} \left(\sum_i r_i(t) \right) = \frac{S^2 r_m^2 \sigma_{N_T}^2}{K^2} + S^2 \varphi_e \sigma_e^2 + \frac{S^2 \sigma_d^2}{K} = \frac{2S^2 (\varphi_e \sigma_e^2 + \sigma_d^2 / K)}{2 - r_m}. \quad (\text{B28})$$

A first-order approximation of the community-wide synchrony of population sizes is then easily obtained by substituting equations (B27) and (B28) into equation (9):

$$\varphi_r = \frac{[2 - (1 - \alpha)x](\varphi_e \sigma_e^2 + \sigma_d^2 / K)}{(2 - r_m + \alpha x S \varphi_e) \sigma_e^2 + (2 - r_m + \alpha x) S \sigma_d^2 / K}. \quad (\text{B29})$$

When $\alpha = 0$, $x = r_m$, and this equation reduces to equation (17).

APPENDIX C Negative Correlations in Multispecies Communities

Let $x_i(t)$ be a population-level variable for species i , $x_T(t) = \sum_{i=1}^S x_i(t)$ the equivalent community-level variable, and $\sigma_{x_i}^2$ and $\sigma_{x_T}^2$ their respective temporal variances. Then

$$\sigma_{x_T}^2 = \Sigma \text{Var} + \Sigma \text{Cov}, \quad (\text{C1})$$

where $\Sigma \text{Var} = \sum_i \sigma_{x_i}^2$ is the summed variances of all species and $\Sigma \text{Cov} = \sum_i \sum_{j \neq i} \text{Cov}(x_i, x_j)$ is the summed covariances of all species pairs.

Negative relationships among multiple variables are severely constrained (Brown et al. 2004). Because the variance of the community-level variable $\sigma_{x_T}^2$ is necessarily nonnegative, the minimum value that summed covariances can take is that for which this variance vanishes, that is, from equation (C1),

$$\Sigma \text{Cov}_{\min} = -\Sigma \text{Var}. \quad (\text{C2})$$

Since the number of covariance terms is $S(S - 1)$ while the number of variance terms is only S in a community of S species, this constraint on summed covariances becomes more and more severe as the number of species increases. And since the correlation coefficient is a standardized measure of covariance, it also imposes a lower bounds on the average correlation coefficient.

In particular, when all species have identical variances,

$$\Sigma \text{Cov} = \sum_i \sum_{j \neq i} \rho_{x_i x_j} \sigma_{x_i} \sigma_{x_j} = (S - 1) \bar{\rho}_x \Sigma \text{Var}, \quad (\text{C3})$$

where $\rho_{x_i x_j}$ is the correlation coefficient between x_i and x_j , and $\bar{\rho}_x$ is the average correlation coefficient. The minimum value of the average correlation is then, from equation (C2),

$$\bar{\rho}_{x_{\min}} = \frac{-1}{S-1}. \quad (\text{C4})$$

APPENDIX D Model with Poisson Demographic Stochasticity

When demographic stochasticity is described by a Poisson process, our model becomes

$$N_i(t+1) = \sum_{k=1}^{N_i(t)} \pi_{ik}(t), \quad (\text{D1a})$$

$$\lambda_i(t) = \exp \left\{ r_m \left[1 - \frac{(1-\alpha)N_i(t) + \alpha N_T(t)}{K'} \right] + \varepsilon_i(t) \right\}, \quad (\text{D1b})$$

where $\pi_{ik}(t)$ is a Poisson variable with mean $\lambda_i(t)$, $\lambda_i(t) = e^{r_i(t)}$ is the mean finite per capita growth rate of species i at time t , and $r'_i(t)$ is the corresponding instantaneous per capita growth rate (excluding demographic stochasticity). When population size is large enough ($N_i(t) \gg 1$), the sum of Poisson variables in equation (D1a) can be approximated by a normal variable with a standard deviation equal to the standard error of the mean; that is,

$$N_i(t+1) \approx N_i(t) \left[\lambda_i(t) + \sqrt{\frac{\lambda_i(t)}{N_i(t)} U_{di}(t)} \right] = N_i(t) \lambda_i(t) \left[1 + \frac{U_{di}(t)}{\sqrt{\lambda_i(t) N_i(t)}} \right]. \quad (\text{D2})$$

Taking the log of both sides of equation (D2) yields

$$\ln N_i(t+1) \approx \ln N_i(t) + r'_i(t) + \ln \left[1 + \frac{U_{di}(t)}{\sqrt{\lambda_i(t) N_i(t)}} \right], \quad (\text{D3})$$

and hence, by linear approximation of the last term,

$$r_i(t) \approx r'_i(t) + \frac{U_{di}(t)}{\sqrt{\lambda_i(t) N_i(t)}}. \quad (\text{D4})$$

Comparing equations (12) and (D4) shows that the demographic variance is approximately equal to $1/\lambda_i(t)$ in the Poisson model. Since $E(r'_i) = 0$ (app. A), $E(\lambda_i) \approx 1$, and hence $\sigma_d^2 = 1$, on average.

APPENDIX E Environmental Stochasticity Acting on Carrying Capacity

Assume that environmental stochasticity affects the carrying capacity of each species instead of its per capita population growth rate directly in the nonneutral model. Since the carrying capacity of each species K' was adjusted such that the carrying capacity of the whole community K is constant, let the magnitude of environmental stochasticity be proportional to K' such that its average per capita effect is constant and independent of population size. Model (12) then becomes

$$N_i(t+1) = N_i(t) \exp \left(r_m \left\{ 1 - \frac{(1-\alpha)N_i(t) + \alpha N_T(t)}{K'[1 + \varepsilon_i(t)]} \right\} + \frac{\sigma_d U_{di}(t)}{\sqrt{N_i(t)}} \right). \quad (\text{E1})$$

Taylor expansion of this equation around $n_i(t) = \varepsilon_i(t) = U_{di}(t) = 0$ yields the same first-order approximation as in equation (B2), except for vector $\mathbf{z}(t)$, the elements of which are now

$$z_i(t) = \frac{K r_m}{S} \varepsilon_i(t) + \sqrt{\frac{K}{S}} \sigma_d U_{di}(t). \quad (\text{E2})$$

The only difference with equation (B3) is that environmental stochasticity is multiplied by r_m . Thus, all the results obtained in appendix B for model (12) also apply to model (E1) after rescaling of environmental stochasticity. More generally, any form of environmental stochasticity that has a constant per capita effect leads to the same first-order approximation after appropriate rescaling. This makes sense since environmental and demographic stochasticity were built into our models (2) and (12) in the form of first-order approximations (eq. [1]) in the first place.

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