

Antagonistic effects of long- and short-term environmental variation on species coexistence

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Abstract

The impact of environmental fluctuation on species coexistence is critical for understanding biodiversity loss and the ecological impacts of climate change. Yet, determining how properties like the intensity, frequency, or duration of environmental variation influence species coexistence remains challenging because we lack a theoretical framework that generates testable predictions in realistic biological systems. Here, we model the impact of environmental change at different temporal scales on species coexistence in nonequilibrium systems by employing the concept of performance curves to incorporate niche differences within a stochastic Lotka-Volterra framework. We discover that short- and long-term environmental variability have contrasting effects on species coexistence, such that short-term variation favors species coexistence, whereas long-term variation promotes competitive exclusion. Consequently, we show the complex set of environmental variability and species coexistence relationships found in previous studies can all be synthesized within a general framework by explicitly considering both long- and short-term environmental variation.

Introduction

Environmental fluctuation not only influences an organism's physiology and reproduction directly, it can also impact an organism's fitness indirectly by driving species interactions (Davis *et al.* 1998; Tylianakis *et al.* 2008; Gilman *et al.* 2010). Although it is often assumed that niche differences need to be greater for competing species to coexist in fluctuating environments because stochastic environmental fluctuation can favor one species and exclude others by chance (May & MacArthur 1972; May 1973, 1974), depending on the intensity of disturbance, environmental fluctuation can either promote or prevent species coexistence (Hutchinson 1953; Hutchinson 1961). For example, one of the key arguments behind the intermediate disturbance hypothesis is that species can reach an equilibrium state and exclude other competing species under reduced environmental fluctuation, whereas increased fluctuation make species more vulnerable to extinction and few species can coexist (Hutchinson 1953; Hutchinson 1961; Grime 1973; Connell 1978; Roxburgh *et al.* 2004). Consequently, intermediate levels of disturbance are predicted to promote coexistence.

Modern coexistence theory proposes that species can only coexist when the fitness differences between them—defined as relative population growth rates in response to environmental condition and intra- or interspecific competition—are smaller than their niche differences in a shared environment (i.e. differences in resource utilization in space and time) (Carroll *et al.* 2011; Ke & Letten 2018). Accordingly, environmental fluctuation potentially promotes species coexistence either by equalizing the effects that minimize average fitness differences between species or by creating different temporal niches. Most theoretical models of species coexistence have focused on systems in equilibrium by assuming stationary environments. In other words, fluctuating environments are represented by the mean environmental condition because the environmental

state at any given time recurs with a predictable long-run frequency (i.e. environmental states are at equilibrium) (Chesson 2017). Consequently, these studies argue that mean environmental conditions, instead of environmental fluctuation, are crucial for determining patterns of coexistence (Chesson & Huntly 1997; Fox 2013). How environmental fluctuation influences species coexistence in nonequilibrium systems remains poorly understood. Since natural systems are largely considered to be in a nonequilibrium state (Rohde 2005; Shimadzu *et al.* 2013; Donohue *et al.* 2016), considering species coexistence in nonequilibrium systems will be crucial for understanding real-world scenarios that might influence species coexistence, particularly in a period of increased global climate change where environmental fluctuation is increasing across the world.

The relationship between environmental variation and species coexistence is also likely to be context dependent. Importantly, the degree of environmental fluctuation can vary in intensity, frequency, and duration (Vasseur *et al.* 2014; Lawson *et al.* 2015), meaning it occurs at multiple temporal scales (Chan *et al.* 2016; Dillon *et al.* 2016). For example, variation in temperature lasting days or months may have different effects on adaptation such that higher long-term environmental variation tends to favor niche generalists, whereas higher short-term environmental variation tends to favor niche specialists (Gilchrist 1995; Chan *et al.* 2016). Likewise, fluctuation in temperature occurring near a species' optimum may have different impacts from fluctuation occurring at unfavorable temperatures (Liu *et al.* 2019). Yet, few theoretical models have explicitly addressed the impacts of these different forms of environmental variation on species coexistence, especially in nonequilibrium systems.

Here, we employ the newly developed standardized approach for characterizing temperature variation across temporal scales (Dillon *et al.* 2016) within a stochastic Lotka-Volterra competition model framework to explore patterns of species coexistence in stochastic environments. We use thermal performance curves to explicitly describe temperature-dependent fitness (Huey & Kingsolver 1989; Angilletta Jr & Angilletta 2009). Although we focus on temperature, our approach can be applied to other climatic measures like precipitation. In addition, we limit our study to nonequilibrium (or unstable) species coexistence (Hutchinson 1961; Chesson 2000; Loreau 2010) because (1) many competing species in fluctuating environments are unlikely to exist in a state of stable coexistence (Edmunds *et al.* 2003; Cothran *et al.* 2015; Donohue *et al.* 2016) and (2) numerous empirical studies have shown that environmental fluctuation is critical for influencing patterns of species coexistence (Shimadzu *et al.* 2013; Chisholm *et al.* 2014). Our model can thus explore environmental fluctuations of large magnitude in nonequilibrium systems, which supplements previous models focusing on stable coexistence at equilibrium states (Chesson 1994) or fixed population sizes (Ellner *et al.* 2016). Ultimately, our model provides a basic framework for understanding patterns of species coexistence in fluctuating and unpredictable environments, a topic that will have critical implications for studying and conserving biodiversity in an era of anthropogenic climate change.

Methods

Population dynamics

We investigate the conditions promoting coexistence using a stochastic Lotka-Volterra competition model with two competing species regulated by the population density of its own and the opposing species. Although this design is similar to the classic form of this model (May & MacArthur 1972; May 1974), instead of integrating all fitness responses of environmental conditions, we leave them as continuous responses to the environment (i.e. temperature) and explicitly model environmental conditions through time. That is, the population dynamics follow

$$\frac{dN_i}{dt} = r_i N_i w_i(T) \left(1 - \frac{N_i}{K_i w_i(T)} - \frac{\alpha N_j}{K_i w_i(T)} \right) - d_i N_i (1 - w_i(T)), \quad (1)$$

where i, j identifies the species, T is temperature, and N stands for the size of the population. Similarly, K, r, α , and d denote carrying capacities, intrinsic growth rates, levels of interspecific interaction, and temperature-dependent mortality, respectively.

Although most parameters remain constant, the population growth rate changes with temperature and depends on the thermal performance function ($w_i(T)$), which is adapted from previously published estimates

of thermal performance curves (Deutsch *et al.* 2008; Vasseur *et al.* 2014),

$$w_i(T) = \begin{cases} \exp\left(-\left(\frac{(T-T_{opt,i})}{2\sigma_i}\right)^2\right) + w_{base}, & \text{if } T < T_{opt,i} \\ 1 - \left[\frac{(T-T_{opt,i})}{(T_{opt,i}-T_{max,i})}\right]^2 + w_{base}, & \text{if } T \geq T_{opt,i} \end{cases}. \quad (2)$$

This function has a maximum value of 1 at T_{opt} . When T is below T_{opt} , thermal performance decreases exponentially with decreasing temperature, whereas when T is above T_{opt} , thermal performance decreases quadratically and eventually reaches the minimum value, w_{base} , at T_{max} . We assume that there are high temperature-adapted species (orange) and a low temperature-adapted species (blue) (Fig. 1a).

Temporal scales of environmental variation

We introduce stochasticity into the model by allowing environmental conditions (i.e. temperature) to change over time. We design two types of variation with different temporal scales that differ in resampling frequency to capture this idea. Specifically, temperatures are determined by the mean and variation of the short-term distribution,

$$T \sim \text{Norm}(T_{\text{mean}}, \sigma_{\text{short}}^2), \quad (3a)$$

where the mean of the short-term distribution, T_{mean} , is sampled from a long-term distribution,

$$T_{\text{mean}} \sim \text{Norm}(T_{\text{mean}}, \sigma_{\text{long}}^2). \quad (3b)$$

Under this scenario, environmental fluctuation is controlled by three factors: (1) the mean temperature of the long-term distribution (T_{mean}); (2) long-term variation (σ_{long}^2); and (3) short-term variation (σ_{short}^2). Thus, we model a nonequilibrium system in the sense that environmental conditions vary stochastically and, therefore, the carrying capacities of competing species change dynamically, which prevents populations from reaching equilibrium states.

The characteristics of short- and long-term variation can be visualized using fast Fourier transformation (FFT) to decompose the time series of temperature into frequency and amplitude domains (Fig. 1a-c) (Dillon *et al.* 2016). Since frequencies with the greatest amplitudes contribute more to the pattern of variation, if we change one type of variation at a time, we can see that increasing short-term variation increases the amplitude of higher frequencies more than of lower frequencies (Fig. 1d-e). Similarly, increasing long-term variation expands the amplitude of lower frequencies more than of higher frequencies (Fig. 1e-f). These settings capture the characteristics of stochastic fluctuation at different temporal scales. For instance, body temperature may vary over the course of few minutes due to a difference in wind speed, whereas variation in weather (e.g. a tropical storms or heat waves) may last for weeks. Further, global events like El Nino may occur at considerably irregular intervals at the temporal scale of years. These examples illustrate how stochastic events can occur at both short- and long-term temporal scales. Importantly, long- and short-term variation should be viewed as two points along a continuum of temporal environmental variation. Although we do not directly focus on the number of variation types or the relative temporal scale of updating the environmental conditions (i.e. δ), it is possible to extend our model to incorporate more complex and realistic patterns of environmental variation (see Table 1 for summary of all parameters).

Results

Short- versus long-term environmental variation

We first explore how the temporal scale of variation and mean temperature influence species coexistence under scenarios of (1) continuous short-term variation with discrete long-term variation and (2) discrete short-term variation with continuous long-term variation. When short-term variation is continuous and long-term variation discrete, there is a uniform trend such that the proportion of species coexisting increases with an increase in short-term variation, regardless of the magnitude of the long-term variation (Fig. 2a-d).

Similarly, when that the range of continuous long-term variation is constant, the area of high coexistence also increases with increasing short-term variation (Fig. 2e-h). In contrast, we observe the opposite effect of long-term variation, which mainly promote exclusion (Fig. 2a-d and 2e-h). Together, these results suggest that greater short-term environmental variation promotes coexistence, whereas greater long-term environmental variation leads to a reduction in species coexistence.

Environmental variation can both promote and inhibit species coexistence

Given that long-term environmental variation tends to hinder species coexistence and short-term variation tends to facilitate coexistence, what happens when environmental fluctuation occurs over both short- and long-term scales (e.g. environmental temperature can vary at daily, monthly, and yearly temporal scales)? Here, we alter the pattern of both long- and short-term temperature variation simultaneously (Fig. 3d-i), generating a “coexistence-exclusion-coexistence” pattern where variability first inhibits coexistence but then promotes it when variability becomes even greater (Fig. 3a-c).

Changes in mean temperature can generate alternative patterns of species coexistence

With the knowledge that combinations of different temporal scales of environmental variation do not have a uniform or consistent effect on species coexistence, the final question we ask is whether mean temperature itself affects patterns of species coexistence (Fig. 4). The previous coexistence-exclusion-coexistence result occurs at a mean temperature (20 degrees) that lies in between the optimal temperatures of the two competing species and allows coexistence in a stable environment (Fig. 3a and 4g). However, if the mean temperature increases (and becomes closer to the optimum of species 1), species coexistence only occurs when variation is large (Fig. 4f). Furthermore, if the mean temperature increases further, even greater environmental variation will not generate species coexistence. In other words, when mean temperature deviates from the intermediate temperature that is non-optimal for both of the competing species and approaches the optimum of either species, the relationship between environmental variation and species coexistence may shift from coexistence-exclusion-coexistence (Fig. 4g-i) to one that promotes coexistence (Fig. 4d-f) to one that favor coexistence but has relatively weaker influence (Fig. 4a-c).

Discussion

We have shown that the mean and variability of environmental fluctuation can have complex yet predictable effects on patterns of species coexistence. Notably, environmental variation can either promote or hinder species coexistence depending on the temporal scale of variation. This is because short-term environmental variation generally favors species coexistence, whereas long-term environmental variation promotes exclusion of competing species. Thus, if environments fluctuate simultaneously on different temporal scales (e.g. daily, seasonal, and annual patterns of temperature fluctuation), which commonly occur in nature, diverse relationships between environmental variability and species coexistence are expected. The mean environmental condition also plays a critical role in shaping the effects of environmental variation on species coexistence, depending on whether the mean condition approaches the optimal condition of one of the species or whether it occurs between the optimal conditions of the competing species.

Many seemingly contradictory results of species coexistence and environmental fluctuation from previous studies can be viewed as special cases of a more general result described here (Fig. 5). For example, Hutchinson (1953; 1961) discussed the impact of temporal scales of environmental variation on species coexistence in a nonequilibrium setting (i.e. species could go extinct by chance due to environmental fluctuation). He argued that both overly fast and overly slow fluctuations promote competitive exclusion between competing species because whichever species competes best on average will exclude the other. Thus, only environmental fluctuation occurring at an intermediate temporal scale will favor species coexistence. Our model partially agrees with Hutchinson’s hypothesis such that intermediate- and long-term environmental fluctuation favor species coexistence and exclusion, respectively. Nevertheless, our model demonstrates that short-term fluctuation is also predicted to facilitate species coexistence rather than exclusion. The key difference between long- and short-term environmental fluctuation is that fast-changing environments allow each competing species to experience their optimal and adverse environmental conditions prior to extinction, which prevents

competitive exclusion, whereas slow-changing environments last longer and, thus, can favor one of the competing species to exclude the other. However, May and colleagues (May & MacArthur 1972; May 1973, 1974) proposed that niche differences need to be larger in fluctuating environments than in stable environments for species to coexist. Consequently, competitive exclusion is predicted to occur more easily in fluctuating environments than in stable environments. However, our model shows that May and colleagues' prediction is a special case such that it is only valid for long-term environmental variation in a nonequilibrium, stochastic model setting.

Our model may also help resolve the longstanding debate over the intermediate disturbance hypothesis (Grime 1973; Connell 1978; Fox 2013; Huston 2014), which states that species richness of competing species will be "maximized at intermediate frequencies and/or intensities of disturbance or environmental change" (Fox 2013). Our model shows that there can be diverse patterns of species coexistence in relation to environmental variability. Therefore, with the right combination of long- and short-term environmental variation, intermediate disturbance *can* generate higher species richness relative to higher or lower disturbance scenarios (e.g., Fig. 5b, left arrow). However, it is also true that intermediate disturbance does not *always* lead to the highest species richness because species coexistence depends at least partially on the temporal scale of environmental variation. The main differences between our model and previous models are that (1) environments in our model fluctuate stochastically and, therefore, species can go extinct by chance if they happen to experience unfavorable environments for an extended period of time (Adler & Drake 2008; Adler *et al.* 2010; Gravel *et al.* 2011), and (2) we explicitly consider the temporal scale of environmental variation, while simultaneously considering the effect of the mean environmental condition (i.e. environmental mean, variance, and their interaction are included in our model). Accordingly, we urge future studies testing the intermediate disturbance hypothesis to carefully distinguish between different properties of environmental disturbance (e.g. intensity and frequency) on the richness of competing species (Dillon *et al.* 2016; Vázquez *et al.* 2017).

In conclusion, we show that contrasting results from previously published studies linking environmental variation to species interactions (Hutchinson 1961; May & MacArthur 1972; Chesson 2000) can be viewed as special cases of a more general framework that we develop here (Fig. 5). By explicitly taking into account different temporal scales of environmental variation, simultaneously considering the mean environmental condition, and modeling different types of stochastic environments, we develop a framework that can be used to explore rich patterns of species coexistence. This framework will be useful for developing testable predictions at a time when environmental fluctuation is increasing globally.

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Figure legends and Tables

Figure 1 A demonstration of the species and environmental variation properties in our model. (a) Following the concept of biological performance curves, the difference between the two species can be depicted by the per capita growth rates across all environments (i.e. temperatures). We assume that there is a high temperature-adapted species (orange line) and a low temperature-adapted species (blue line) competing against one another (see methods for more details about the thermal performance curves). The solid black line describes the time series of temperature variation, whereas the dashed black line indicates the average temperature. (b) To more easily visualize environmental fluctuation at different temporal scales, the temperature time series can be decomposed into waves of different frequencies through fast Fourier transformation. (c) For each wave, the amplitude and frequency are plotted as points on a continuous spectrum that characterizes the temperature time series. (d) If the short-term temperature variation increases, the spectrum, (e) would have a larger amplitude in the high frequency regions than in the original spectrum (c, and the grey line in e). (f) Conversely, increasing long-term variation causes the spectrum, g, to have a larger amplitude in the low frequency regions than in the original spectrum.

Figure 2 Short- and long-term temperature variation have contrasting impacts on species coexistence. (a-d) Proportion of simulations producing species coexistence dynamics, where brighter colors indicate greater proportions of coexisting species. Each panel has constant long-term variation (σ_{long} , labeled above each panel) but variable mean temperature (T_{mean} , x-axis) and short-term variation (σ_{short} , y-axis). Species coexistence occurs if both species sustain through 20,000 short-term variations and 286 long-term variations (4-million calculations of population change). Each combination of mean and variability is repeated for 100 times. (e-h) Proportion of coexistence with the same definition, but each panel has constant short-term variation (σ_{short} , labeled above each panel) and variable long-term variation (σ_{long} , y-axis).

Figure 3 Examples of the complex patterns of variability and mean temperature on species coexistence. (a-c) In the first case, we set the mean and short-term variation as constant and only change the magnitude of long-term variation. We find that coexistence occurs most commonly under intermediate magnitudes of long-term variation (b). (d-f) In the second case, we fix the size of the mean and long-term variation. By changing short-term variation alone, we see that coexistence is greatest when short-term variation is high (f). (g-i) In the third case, we set the mean at another value (compared to the first case) and only alter the magnitude of the long-term variation. We find that species coexistence is more likely to occur when long-term variation is low (g).

Figure 4 Patterns of species coexistence changes with different mean temperatures. (a-c) At a high mean temperature ($T_{\text{mean}}=31$), increasing both short- and long-term variation results in greater species coexistence. (d-f) When the mean temperature is lower ($T_{\text{mean}}=27$), higher short- and long-term temperature variation may still promote coexistence. (g-i) However, if the mean temperature decreases further ($T_{\text{mean}}=23$), coexistence occurs at both low levels (g) or high levels (i) of short- and long-term variation.

Figure 5 Different combinations of short-term temperature variation, long-term temperature variation, and mean temperature can generate diverse patterns of species coexistence. (a) Coexistence can be promoted by greater temperature variability. (b) Coexistence may also be supported when temperature variability is intermediate (Hutchinson 1961; Connell 1978) (solid line arrow), or (3) hindered by temperature variability (May & MacArthur 1972) (dashed line arrow). (c) Finally, it is also possible that coexistence is promoted when temperature variability is either high or low. The size of short- and long-term temperature variation are labeled above each panel.

Table 1. List of model parameters.

| Name | Values | Description |
|--------------------------------------|--------|--|
| r_1, r_2 | 0.5 | Scaling factor of intrinsic growth rate. |
| K_1, K_2 | 10000 | Scaling factor of carrying capacity. |
| d_1, d_2 | 0.01 | Scaling factor of environmental-dependent mortality. |
| α | 0.4 | Level of interspecific competition. |
| δ | 70 | Relative duration of long-term variation to short-term variation. |
| $T_{\text{opt},1}, T_{\text{opt},2}$ | 30, 17 | Optimum temperature of the two species. |
| $T_{\text{max},1}, T_{\text{max},2}$ | 35, 23 | Upper boundary of fitness function of the two species. |
| σ_1, σ_2 | 5, 2 | Width parameter of the fitness function for temperature below optimum. |
| w_{base} | 0.001 | Minimum value of fitness function, designed to avoid population deadlock at extreme temperature. |

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