

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/23276392>

A General Theory of Environmental Noise in Ecological Food Webs

Article in *The American Naturalist* · April 1998

DOI: 10.1086/286116 · Source: PubMed

CITATIONS

79

READS

108

3 authors, including:



Per Lundberg

Lund University

156 PUBLICATIONS 6,625 CITATIONS

[SEE PROFILE](#)



Veijo Kaitala

University of Helsinki

248 PUBLICATIONS 8,229 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Precautionary risk methodology for fisheries [View project](#)



Eco-evolutionary dynamics [View project](#)

A General Theory of Environmental Noise in Ecological Food Webs

Jörgen Ripa,^{1,*} Per Lundberg,¹ and Veijo Kaitala²

1. Department of Theoretical Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden;

2. University of Helsinki, Division of Population Biology, Box 17, FIN-00014, University of Helsinki, Finland, and Systems Analysis Laboratory, Helsinki University of Technology, FIN-02150 Espoo, Finland

Submitted March 31, 1997; Accepted September 10, 1997

ABSTRACT: We examine the effects of environmental noise on populations that are parts of simple two-species food webs. We assume that the species are strongly interacting and that one or the other population is affected by the noise signal. Further assuming that a stable equilibrium with positive population densities exists, we are able to perform a complete frequency analysis of the system. If only one of the populations is subject to noise, the relative noise response by both populations is fully determined by the sign of a single element of the Jacobian matrix. The analysis is readily extended to cases when both species are affected by noise or when the food web has more than two species. The general conclusion about relative responses to noise is then less unambiguous, but the power spectra describing the frequency composition of the population variabilities are nevertheless completely determined. These results are entirely independent on the exact nature of the interaction (i.e., predation, competition, mutualism) between the populations. The results show that the interpretation of the "color" of ecological time series (i.e., the frequency composition of population variability over time) may be complicated by species interactions. The propagation of noise signals through food webs and the importance of web structure for the expected response of all parts of the web to such signals is a challenging field for future studies.

Keywords: environmental stochasticity, food webs, population dynamics, power spectra.

No natural population has a constant number of individuals (or density) from one time to another. These varia-

tions may be small or large, regular or irregular. Large regular fluctuations have fascinated ecologists for decades because they hint at fundamental inherent dynamic properties of populations. One important property of population fluctuations is the power spectrum of the time series. The variability in abundance or density, in analogy with the wavelength composition of light, is said to be white when no frequency dominates, red when the fluctuations are dominated by low-frequency long-term variations, and blue when high-frequency fluctuations dominate (e.g., Lawton 1988; Cohen 1995). Data from natural populations indicate that most population dynamics are either red or white (Pimm 1991; Sugihara 1995; Halley 1996). There are two principal explanations to this observation. The fluctuations in the abiotic environment of most organisms are dominated by low frequencies, and the ecological time series we observe are a direct result of that characteristic. Alternatively, the intrinsic dynamics of most plant and animal populations are red, and, with or without environmental noise, that color is what we observe.

The way environmental variability interacts with the dynamics of populations may have several biological implications. For example, it has been shown that the exact nature of the assumed properties of environmental noise (in this case its color) may have profound effects on our estimates of population extinction risk (Mode and Jacobson 1987; Ripa and Lundberg 1996). Thus, our knowledge about the external sources of variation matters in regard to an important conservation issue. The net result of the interaction between the endogenous dynamics of the population in focus and the variability of the environment also influences how we interpret ecological time series. If such time series generally are red, then we would have to expect that the variance of the time series increases as the length of the series increases (Pimm 1991). This should make us less prone to premature decisions about long-term trends in population abundances. The putative trend may just be a part of a long-term variation with both ups and downs. Since most data indicate that ecological time series indeed are reddened,

*To whom correspondence should be addressed; E-mail: jorgen.ripa@teorekol.lu.se.

we then necessarily must ask where the color comes from to understand population variability.

The interplay between intrinsic population dynamics and the properties of environmental noise has been studied in a number of single-species models, the intention being to produce patterns in accordance with observations—that is, the dominance of low-frequency fluctuations (Pimm 1991; Powell and Steel 1995). White et al. (1996) suggest that spatial structure may produce reddened spectra, and it has also been shown that models with delayed density dependence (Turchin 1990; Ranta et al. 1995; Kaitala and Ranta 1996) can do the same job. A complicating factor is that the color of the power spectrum of an ecological time series results from the interplay between external noise and internal dynamics. It has been shown (Kaitala et al. 1997) that depending on whether the deterministic dynamics of the population is stable, cyclic, or chaotic and whether the external noise is red, white, or blue, the resulting power spectrum may be of almost any color.

The obvious restriction in previous studies has been the focus on single-species models. It is true that much of the multidimensional reality can be reduced by built-in time lags in single-species models (Turchin 1990; Royama 1992), but a consideration of food webs rather than one-dimensional caricatures might add new insights to this problem. For example, we may ask how external disturbances in one part of the food web are transferred to other parts and how those are expected to respond. Also, the question is whether different trophic levels or different types of community components (e.g., omnivores, squeezed-in competitors) respond to and transfer external noise differently.

We report here a first attempt to address these questions by studying a simple two-species community. We let the interaction between the two species be unspecified. It can be of any form: a predator-prey interaction, competition, or even a mutualistic relationship. The only prerequisite is that the system has a stable equilibrium point, which leads to unexpectedly general and simple predictions about how food web components respond to external noise.

A General Model

As a first and simple analysis, we consider a general discrete-time, two-species system, $N_1(t)$ and $N_2(t)$ (the densities of the two populations at time t), with a single noise factor:

$$\begin{cases} N_1(t+1) = f_1(N_1(t), N_2(t), z(t)) \\ N_2(t+1) = f_2(N_1(t), N_2(t), z(t)) \end{cases} \quad (1)$$

where f_i denotes the density-dependent recruitment function for species i . The factor $z(t)$ is any kind of stochastic element in the model; it could be a stochastic model parameter or an additive or multiplicative noise factor, possibly density dependent, to account for different kinds of demographic or environmental stochasticity (see also Ripa and Lundberg 1996 for a discussion of how noise can be included in the model). In a model with several independent sources of stochasticity, additional time-dependent elements would be present, one for each noise source:

$$\begin{cases} N_1(t+1) = f_1(N_1(t), N_2(t), z_1(t), z_2(t), \dots) \\ N_2(t+1) = f_2(N_1(t), N_2(t), z_1(t), z_2(t), \dots) \end{cases} \quad (2)$$

Linearization

Now suppose system (1) has an equilibrium point, (N_1^*, N_2^*) , taken at the average value of the stochastic factor, $E(z(t)) = z^*$:

$$\begin{cases} N_1^* = f_1(N_1^*, N_2^*, z^*) \\ N_2^* = f_2(N_1^*, N_2^*, z^*) \end{cases}$$

The stability of the equilibrium is determined by the Jacobian matrix (e.g., Edelstein-Keshet 1988):

$$\begin{aligned} \mathbf{J} &= \begin{pmatrix} \mathbf{J}_{11} & \mathbf{J}_{12} \\ \mathbf{J}_{21} & \mathbf{J}_{22} \end{pmatrix} \\ &= \begin{pmatrix} \frac{\partial f_1(N_1^*, N_2^*, z^*)}{\partial N_1} & \frac{\partial f_1(N_1^*, N_2^*, z^*)}{\partial N_2} \\ \frac{\partial f_2(N_1^*, N_2^*, z^*)}{\partial N_1} & \frac{\partial f_2(N_1^*, N_2^*, z^*)}{\partial N_2} \end{pmatrix}. \end{aligned}$$

If all eigenvalues of the Jacobian matrix have modulus smaller than 1, the equilibrium is stable, otherwise not. In the deterministic case ($z(t) \equiv z^*$), system (1) will always approach a stable equilibrium if it is started close to the equilibrium point. Consequently, if the equilibrium is stable and the stochastic disturbances are small, the system will stay in the neighborhood of the equilibrium, and it is justified to use its linearized version, with all higher-order terms eliminated:

$$\begin{cases} x_1(t+1) = \mathbf{J}_{11}x_1(t) + \mathbf{J}_{12}x_2(t) + \frac{\partial f_1}{\partial z}(N_1^*, N_2^*, z^*) \cdot \zeta(t) \\ x_2(t+1) = \mathbf{J}_{21}x_1(t) + \mathbf{J}_{22}x_2(t) + \frac{\partial f_2}{\partial z}(N_1^*, N_2^*, z^*) \cdot \zeta(t) \end{cases}, \quad (3)$$

where $x_i(t) = N_i(t) - N_i^*$, and $\zeta(t) = z(t) - z^*$ or, in vector form,

$$\begin{aligned} \mathbf{x}(t+1) &= \mathbf{J}\mathbf{x}(t) + \mathbf{g}^*\zeta(t), \\ \mathbf{g}^* &= \begin{pmatrix} \frac{\partial f_1(N_1^*, N_2^*, z^*)}{\partial z} \\ \frac{\partial f_2(N_1^*, N_2^*, z^*)}{\partial z} \end{pmatrix}. \end{aligned} \quad (4)$$

The linear system (4) will be the subject of our further analysis.

The vector \mathbf{g}^* contains the relative strength of the external disturbance to each population. An element equal to 0 means that this specific population is not directly influenced by the noise. We note here also that a system like system (2), with several noise sources, has a linearized form,

$$\mathbf{x}(t+1) = \mathbf{J}\mathbf{x}(t) + \mathbf{g}_1^*\zeta_1(t) + \mathbf{g}_2^*\zeta_2(t), \quad (5)$$

with notation analogous to equation (4). This, however, introduces no further complexity, since the effect of each noise factor, if they are independent, can be treated separately. Using equation (4) twice, once with $z_1(t)$ and once with $z_2(t)$ as the stochastic disturbance, gives two time series $\mathbf{x}(t)$. The sum of these two time series is the solution to equation (5). Thus, it is sufficient to use equation (4) to obtain complete knowledge of the system's response to any set of independent external disturbances; treat them separately, and add the result.

Frequency Analysis

A frequency analysis of the linear system (4), as described in appendix A, gives the power spectra of the populations:

$$\mathbf{P}_x(f) = |(e^{i2\pi f}I - \mathbf{J})^{-1}\mathbf{g}^*|^2 P_z(f), \quad (6)$$

where $|\cdot|^2$ denotes element-wise squared magnitude, $\mathbf{P}_x(f)$ is a vector of power spectra for each population, and $P_z(f)$ is the power spectrum of the external noise $z(t)$, all functions of f , frequency. Equation (6), on its own, yields the whole predicted power spectra of the populations in a food web. It is general and independent of food web size and structure. The only assumption so far is the applicability of the linear approximation.

Moreover, with several independent sources of stochasticity, the separate power spectra emerging from using equation (6) several times, once for each noise factor, can be added to get the total power spectrum of the system. This is valid in the context of expected power spectra. We give no proof of this here, but the result is re-

lated to the well-known fact that the variance of the sum of several independent stochastic variables is equal to the sum of the variances.

Now we return to the two-species case, in which further predictions emerge. Suppose only species 1 is subject to external noise ($g_2 = 0$). Then the ratio of the power spectra of the two populations becomes (app. A)

$$\frac{P_1(f)}{P_2(f)} = \frac{1 + J_{22}^2 - 2J_{22}\cos(2\pi f)}{J_{21}^2}. \quad (7)$$

Note that this ratio is independent of the noise spectrum. This is an increasing function in the appropriate frequency interval ($0 \leq f \leq 0.5$) if and only if J_{22} is positive. If the ratio (7) is increasing, the spectrum of population 1 will be more dominated by high frequencies than population 2's spectrum. Population 1 will therefore have a bluer spectrum than population 2. A negative J_{22} gives a decreasing function and the opposite relationship between the colors of the two power spectra. If $J_{22} = 0$, ratio (7) is still valid, but there will be no color difference between the two spectra, only a difference in overall magnitude, expressed as different variance of the two time series. Of course, the numbering of the species is arbitrary.

To summarize, we state the following principle of relative spectrum color of population dynamics. Consider a stable, discrete-time, two-species system. If population 1 is subject to external noise, the sign of one single element of the Jacobian matrix, J_{22} , determines the relative noise response by the populations. Whenever J_{22} is positive (negative), population 1 will be bluer (redder) than population 2.

This analysis is easily extended to a case when a single noise source is affecting both species. The vector \mathbf{g} in equation (6) now has both of its elements greater than 0. This leads to equations similar to equations (A7) and (A8), albeit less tractable. The quotient of the two power spectra (eq. [A9]) will also be less unambiguous. We note also that all of the Jacobian elements now play a role in determining the relative response of the populations to external noise.

The generalization to n -species cases is also straightforward, and a quotient between two species, just like that in equation (7), can be calculated for any pair of species in the web. Note that equation (6) still is the key to the problem and that the vector of power spectra it represents may have any length (i.e., any number of species).

The calculations leading to equation (7) are easily transformed to the time-continuous case (app. A). The results are, however, somewhat different. The ratio corresponding to equation (7) is an always increasing function

(eq. [A12]), regardless of the values of the elements of the Jacobian matrix. This means that, in the time-continuous case, the disturbed population will always have a bluer spectrum than the other.

Two Examples

To illustrate our results and to test their robustness, we simulated two different two-species systems and carried out frequency analysis of their corresponding linearized versions.

A Predator-Prey System

First we studied the well-known predator-prey model suggested by Beddington et al. (1975). We used multiplicative noise at the prey level:

$$\begin{cases} N(t+1) = N(t) e^{r(1-[N(t)/K])} e^{-aP(t)} (1+z(t)) & z(t) \in N(0, \sigma^2) \\ P(t+1) = cN(t)(1 - e^{-aP(t)}) \end{cases} \quad (8)$$

Successive noise terms are independent and equally distributed; that is, the external noise is white, and no frequencies dominate its spectrum. A representative simulation is presented in figure 1. First, note the good correspondence between the predicted power spectra (eq. [6]) and the power spectra calculated from the simulated time series, although the disturbing noise has a quite large amplitude and the populations often move far away from the equilibrium densities. Second, it is readily shown that J_{22} of the Jacobian matrix of model (8) is always positive. Hence, the principle of relative spectrum color predicts that the prey spectrum will be bluer (i.e., more dominated by high frequencies) than the predator spectrum. This is also easily seen in figure 1.

Two-Species Competition

We also studied a simple competitive system from Hassel and Comins (1976), with one of the parameters being stochastic:

$$\begin{cases} N_1(t+1) = N_1[\theta_1 + \gamma_1(t)(N_1 + \alpha N_2)]^{-b_1} \\ N_2(t+1) = N_2[\theta_2 + \gamma_2(N_2 + \beta N_1)]^{-b_2} \end{cases} \quad (9)$$

We choose $\gamma_1(t)$ to have a colored, not white, power spectrum. It is generated according to

$$\gamma_1(t) = 1 + \eta(t),$$

where $\eta(t) = a \cdot \eta(t-1) + \epsilon(t)$, $-1 < a < 1$. The stochastic variables $\epsilon(t)$, $t = 1, 2, \dots$, are independent with normal distribution with zero mean and variance σ^2 . The expected value, variance, and power spectrum of $\gamma_1(t)$ are

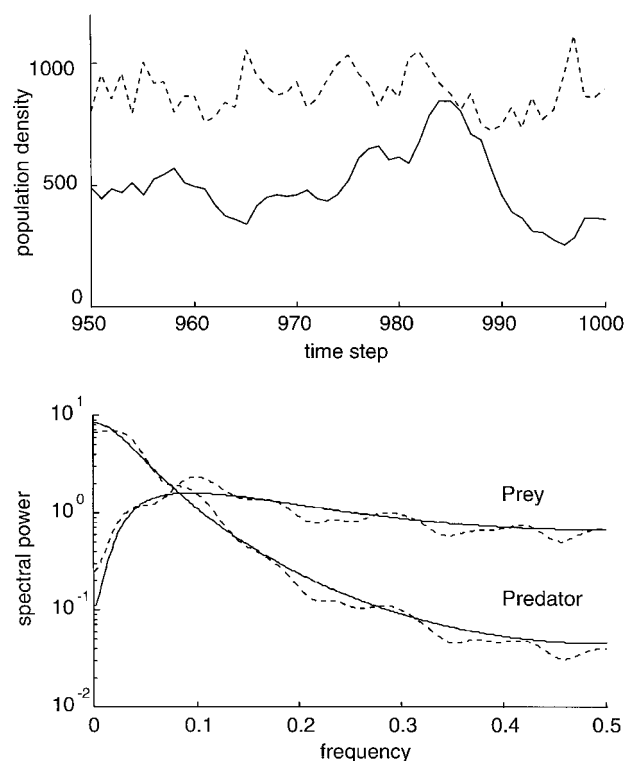


Figure 1: The top panel shows the last 50 yr of the simulated time series of predators (times 50; solid line) and prey (dashed line) according to equation (8) with white external noise with zero mean and variance equal to 0.1^2 affecting the prey population. The lower panel shows the corresponding power spectra (dashed lines) for the two populations along with the predicted spectra (solid lines) according to the linearized version of equation (8). The parameter values in equation (8) were $r = 1.0$, $K = 1,000$, $a = 0.012$, and $c = 0.1$. The equilibrium densities were 883 and 9.7 for prey and predator, respectively, and J_{22} of the Jacobian matrix was 0.94. To facilitate color comparisons, the spectra are normalized to unit variance.

$$E(\gamma_1(t)) = 1;$$

$$\text{var}(\gamma_1(t)) = \sigma^2/(1 - a^2); \quad (10)$$

$$P_\gamma(f) = \sigma^2/[1 + a^2 - 2a \cos(2\pi f)].$$

An $a > 0$ means that $\gamma_1(t)$ is positively autocorrelated; hence, $\gamma_1(t)$ has a red power spectrum. In this example we chose $a = 0.5$. (See Ripa and Lundberg 1996 or any textbook on time series analysis for further details on this kind of process.)

Figure 2 shows an example simulation and the corresponding power spectra. To calculate the predicted power spectra, we used equation (10) as the noise spectrum in equation (6). Again, there is very good correspondence between the simulated and predicted power spectra. In this case, however, the sign of J_{22} depends on

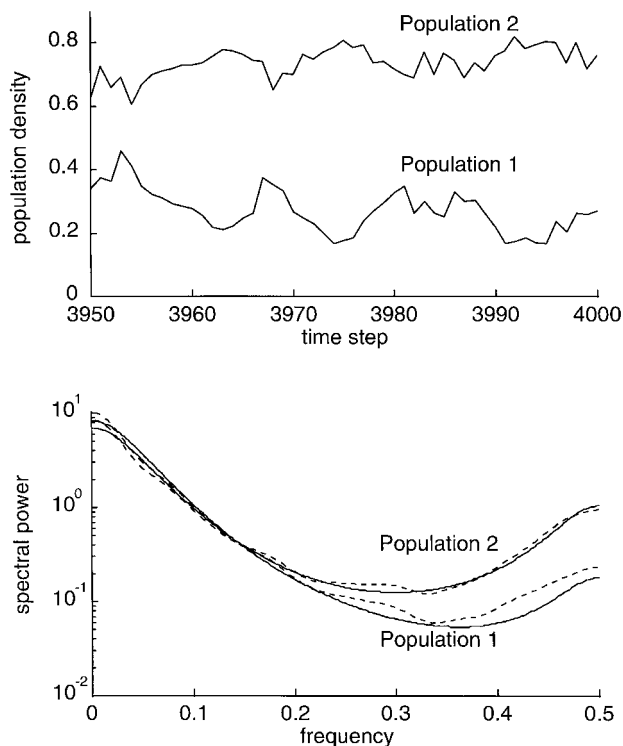


Figure 2: The last 50 yr of a simulation of two competing species according to equation (9). The parameter $\gamma_1(t)$ is a stochastic process with a red power spectrum; see the text for details. The lower panel shows the corresponding power spectra (dashed lines) for the two populations along with the predicted spectra (solid lines) according to the linearized version of equation (9). The parameter values in equation (9) were $\theta_1 = 0.2$, $\theta_2 = 0.1$, $\gamma_2 = 1.0$, $\alpha = 0.7$, $\beta = 0.6$, $b_1 = 2.0$, and $b_2 = 2.0$. With these parameter values, the equilibrium densities are 0.29 and 0.72 for populations 1 and 2, respectively; J_{22} of the Jacobian matrix is -0.45 . To facilitate color comparisons, the spectra are normalized to unit variance.

the chosen parameter values. In our example, J_{22} is well below 0, which predicts that population 1 will have a redder spectrum than population 2. This prediction is also well confirmed in figure 2.

Discussion

Our most notable result is that the conclusions about how a simple food web responds to external noise are general and robust. They are general because the only determinant of the relative response is the sign of one of the elements (J_{22}) of the Jacobian matrix. This element represents the impact the second species has on itself at

equilibrium (i.e., how the rate of change of the second species is influenced by its own density). Therefore, the relative response to external disturbances has nothing to do with the type of interaction between the species. Our results are in principle equally true for a predator-prey system and for two competing species. The results are also robust in that they are independent on the exact nature of the noise signal. The difference in response by the food web species is not affected by the amplitude, distribution, or frequency composition (color) of the external noise.

Apart from the very simple rule determining the relative frequency response by interacting species, our results also have some important ramifications for how we interpret the color of real ecological time series. It has been suggested that the red-shifted population time series we often observe in natural systems is a direct result of the color of the environmental fluctuations (Pimm 1991; Powell and Steele 1995) or other properties of the environment—for example, spatial structure (White et al. 1996). Alternatively, most populations are inherently “red,” and the power spectrum we are able to detect is by and large unaffected by environmental stochasticity. This would be true if, for example, the population is governed by sufficiently strong time-delayed density dependence (which tends to redden the spectrum) that overrides the external noise signal (Ranta et al. 1995; Kaitala and Ranta 1996; Kaitala et al. 1996). We know, however, that the interplay between internal dynamics and external noise may produce a wide variety of frequency responses in the time series such that the observed spectrum may say very little about the relative contribution of the internal and external determination of its properties (Cohen 1995; Blarer and Doebeli 1996; Kaitala et al. 1997). Our results further emphasize this problem. If a population is embedded in a food web, which all populations are, the interactions themselves may significantly modify the expected frequency response, and differently so for different components of the web. This relates also to fundamental questions about food web structure and functioning. The frequency response of a population (i.e., the nature of its variability over time) in a food web may depend not only on the direct influence of environmental noise but also on where a population is positioned and how it is connected to other populations in the web. We still have much to learn about how a noise signal is propagated through a food web and what determines how far it reaches and how quickly. The possible amplifications and dampings of noise signals, in addition to changes in the frequency domain depending on web structure, are all of great ecological interest. We therefore propose that all interpretations of ecological time series in the fre-

quency domain must be accompanied by at least rudimentary knowledge about the nature of the external noise, the basic properties of the internal dynamics, and the basic food web structure in which the focal population is embedded.

Although this approach requires a lot of detailed ecological knowledge, we nevertheless feel that our results hint at an interesting way of gaining some insight to this problem. Determining food web structure is not a trivial issue, from both a philosophical and practical point of view. We note, however, that in our simple system, only the sign of one of the elements in the community matrix (the Jacobian) is of importance. It is not an impossible task to determine those elements in real systems, provided that we safely can reduce the dimensionality of the web. We therefore call for a cautious interpretation of frequency analyses of ecological time series unless food web structure is taken into account. The basic problem of the lack of long time series remains, of course, but unless we properly account for food web structure, the enigmas of fluctuating population dynamics will continue to be obscured.

Acknowledgments

This study was financially supported by grants from the Swedish Natural Science Research Council, the Swedish Research Council for Forestry and Agriculture, the Academy of Finland, and the Nordic Academy for Graduate Training (NorFA).

APPENDIX A

Frequency Analysis

Discrete-Time Systems

Consider the linear system:

$$\mathbf{x}(t+1) = \mathbf{J}\mathbf{x}(t) + \mathbf{g}\zeta(t), \quad t = 0, 1, 2, \dots, L-1, \quad (\text{A1})$$

where $\mathbf{x}(t) = (x_1(t) \ x_2(t) \ \dots \ x_n(t))^T$ is a vector time series of length L , \mathbf{J} is an n -by- n matrix, \mathbf{g} is a constant vector, and $\zeta(t)$ is a scalar external noise signal. The system (A1) has the discrete Fourier transform

$$e^{i2\pi f} \mathbf{X}(f) = \mathbf{J}\mathbf{X}(f) + \mathbf{g}Z(f), \quad f = k/L, \quad k = 0, 1, 2, \dots, L-1. \quad (\text{A2})$$

(See app. B for exact formulations of the transforms used.) Note that \mathbf{X} and \mathbf{g} are vectors, \mathbf{J} is a matrix, and Z is a scalar function. System (A2) is easily solved with matrix algebra:

$$\mathbf{X}(f) = (e^{i2\pi f} \mathbf{I} - \mathbf{J})^{-1} \mathbf{g}Z(f) = B(f)^{-1} \mathbf{g}Z(f), \quad (\text{A3})$$

where \mathbf{I} is a unit matrix and $B(f) = (e^{i2\pi f} \mathbf{I} - \mathbf{J})$.

The vector $B(f)^{-1} \mathbf{g}$ describes each population's frequency-dependent response to the external noise. The corresponding power spectrum formulation of equation (A3) is (again, see app. B for details)

$$P_x(f) = \frac{1}{L} |X(f)|^2 = \frac{1}{L} |B(f)^{-1} \mathbf{g}|^2 |Z(f)|^2 = |B(f)^{-1} \mathbf{g}|^2 P_\zeta(f), \quad (\text{A4})$$

where $|\cdot|^2$ denotes element-wise squared modulus. Equation (A4) relates the spectrum of the external noise $P_\zeta(f)$ to the spectra of the populations $P_x(f)$. The vector $B(f)^{-1} \mathbf{g}$ tells us all about how this mapping is done.

For a two-by-two matrix, the inverse is

$$B = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} \Rightarrow B^{-1} = \frac{1}{\det(B)} \begin{pmatrix} b_{22} & -b_{12} \\ -b_{21} & b_{11} \end{pmatrix}. \quad (\text{A5})$$

In our case, we get

$$B(f)^{-1} = (e^{i2\pi f} \mathbf{I} - \mathbf{J})^{-1} = \frac{1}{\det(B(f))} \begin{pmatrix} e^{i2\pi f} - J_{22} & J_{12} \\ J_{21} & e^{i2\pi f} - J_{11} \end{pmatrix}. \quad (\text{A6})$$

Now consider a two-species system:

$$\mathbf{x}(t) = \begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix},$$

with external noise on level 1 only:

$$\mathbf{g} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}.$$

Equation (A6) inserted into equation (A4) now gives

$$P_x(f) = |B(f)^{-1} \mathbf{g}|^2 P_\zeta(f) = \frac{P_\zeta(f)}{\det(B(f))^2} \left| \begin{pmatrix} e^{i2\pi f} - J_{22} & J_{12} \\ J_{21} & e^{i2\pi f} - J_{11} \end{pmatrix} \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right|^2 = \frac{P_\zeta(f)}{\det(B(f))^2} \left| \begin{pmatrix} e^{i2\pi f} - J_{22} \\ J_{21} \end{pmatrix} \right|^2 = \begin{pmatrix} P_1(f) \\ P_2(f) \end{pmatrix}, \quad (\text{A7})$$

where

$$P_1(f) = \frac{P_\zeta(f)}{\det(B(f))^2} |e^{i2\pi f} - J_{22}|^2 = \frac{P_\zeta(f)}{\det(B(f))^2} (1 + J_{22}^2 - 2J_{22} \cos(2\pi f))$$

and

$$P_2(f) = \frac{P_\zeta(f)}{\det(B(f))^2} J_{21}^2. \quad (\text{A8})$$

Equations (A7) and (A8) describe the power spectra of the two populations. The quotient between the two power spectra is

$$\frac{P_1(f)}{P_2(f)} = \frac{1 + J_{22}^2 - 2J_{22} \cos(2\pi f)}{J_{21}^2}, \quad (\text{A9})$$

which is an increasing (decreasing) function in the interval $0 \leq f \leq 0.5$ if and only if $J_{22} > 0$ ($J_{22} < 0$). This means that the power spectrum of population 1 will be more dominated by high frequencies than the power spectrum of population 2 if $J_{22} > 0$. In other words, population 1 will have a bluer power spectrum than population 2.

Continuous-Time Systems

The continuous-time system corresponding to system (A1) is

$$\frac{d\mathbf{x}(t)}{dt} = \mathbf{J}\mathbf{x}(t) + \mathbf{g}\zeta(t), \quad (\text{A10})$$

with notation analogous to that of equation (A1).

A Fourier transform of equation (A10) gives (see, e.g., Nisbet and Gurney 1982)

$$i2\pi f \mathbf{X}(f) = \mathbf{J}\mathbf{X}(f) + \mathbf{g}Z(f). \quad (\text{A11})$$

Assuming external disturbance of population 1 only, calculations very similar to those of equations (A3)–(A9) give

$$\frac{P_1(f)}{P_2(f)} = \frac{J_{22}^2 + (2\pi f)^2}{J_{21}^2}, \quad (\text{A12})$$

which is an always increasing function of f . In other words, population 1 will always have a power spectrum more dominated by high frequencies than population 2, irrespective of the power spectrum of the external noise and the elements of the Jacobian matrix.

APPENDIX B

The Discrete Fourier Transform and the Power Spectrum

Any time series, $x(t)$, $t = 0, 1, 2, \dots, L - 1$, has a well-defined discrete Fourier transform:

$$X(f_k) = \mathbf{F}(x(t)) = \sum_{t=0}^{L-1} e^{-i2\pi f_k t} x(t), \quad (\text{B1})$$

where $f_k = k/L$, $k = 0, 1, \dots, L - 1 \Rightarrow 0 \leq f_k < 1$. Here $X(f)$ is a function with complex values, f has a direct interpretation as frequency (periods per time step), and the amplitude of $X(f)$ reflects the relative importance of different frequencies in $x(t)$. Equation (B1) has the inversion formula

$$x(t) = \mathbf{F}^{-1}(X(f_k)) = \frac{1}{L} \sum_{k=0}^{L-1} e^{i2\pi f_k t} X(f_k). \quad (\text{B2})$$

When dealing with time delays, one uses

$$\mathbf{F}[x(t + k)] = e^{i2\pi f k} \mathbf{F}(x(t)) = e^{i2\pi f k} X(f). \quad (\text{B3})$$

To apply equation (B3), one has to consider the periodic expansion of $x(t)$, meaning $x(t \pm kL) = x(t)$. For long time series, this has no importance. The frequency contents of the time series is most often studied through the power spectrum, $P(f)$:

$$P_x(f) = \frac{1}{L} |X(f)|^2. \quad (\text{B4})$$

The power spectrum describes different frequencies' relative contribution to the variance of $x(t)$:

$$P_x(0) = L\bar{x}^2, \quad (\text{B5})$$

and

$$\frac{1}{L} \sum_{k=1}^{L-1} P_x(f_k) = \text{var}(x(t)) = \sum_{t=0}^{L-1} \frac{(x(t) - \bar{x})^2}{L}. \quad (\text{B6})$$

Often $P_x(0)$ is set to 0, which is equivalent to removing the mean from the time series. To interpret a power spectrum, one only studies the frequencies $0 \leq f < 0.5$. If a power spectrum is dominated by high frequencies, $0.25 < f < 0.5$, it is said to blue. Blue light is also dominated by high frequencies, hence the term. A power spectrum dominated by low frequencies, on the other hand, is considered red. White noise is a time series of independent, identically distributed, stochastic variables. It has equal parts of all frequencies; hence, its expected power spectrum is a constant function:

$$P_w(f) = \sigma^2, \quad (\text{B7})$$

where σ^2 is the variance of the stochastic variables.

For a single realization of white noise, however, there are considerable random deviations from equation (B7), similar to the noisiness of an autocorrelation plot. Therefore, some smoothing technique is commonly used in power spectrum plots of real time series.

The preceding formulas and rules also apply to vector

functions $\mathbf{x}(t)$. The Fourier transform and the power spectrum of a vector function is also a vector function:

$$\begin{aligned} \mathbf{F}(\mathbf{x}(t)) &= \mathbf{F} \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix} = \begin{pmatrix} \mathbf{F}(x_1(t)) \\ \mathbf{F}(x_2(t)) \\ \vdots \\ \mathbf{F}(x_n(t)) \end{pmatrix} \\ &= \begin{pmatrix} X_1(f) \\ X_2(f) \\ \vdots \\ X_n(f) \end{pmatrix} = \mathbf{X}(f), \end{aligned} \quad (\text{B8})$$

and

$$\mathbf{P}_x(f) = \begin{pmatrix} P_{x_1}(f) \\ P_{x_2}(f) \\ \vdots \\ P_{x_n}(f) \end{pmatrix}. \quad (\text{B9})$$

Literature Cited

- Beddington, J. R., C. A. Free, and J. H. Lawton. 1975. Dynamic complexity in predator-prey models framed in difference equations. *Nature (London)* 255:58–60.
- Blarer, A., and M. Doebeli. 1996. In the red zone. *Nature (London)* 380:589–590.
- Cohen, J. E. 1995. Unexpected dominance of high frequencies in chaotic nonlinear population models. *Nature (London)* 378:610–612.
- Edelstein-Keshet, L. 1988. *Mathematical models in biology*. Random House, New York.
- Halley, J. M. 1996. Ecology, evolution, and $1/f$ noise. *Trends in Ecology & Evolution* 11:33–37.
- Hassel, M. P., and H. N. Comins. 1976. Discrete time models for two-species competition. *Theoretical Population Biology* 9:202–221.
- Kaitala, V., and E. Ranta. 1996. Red/blue chaotic power spectra. *Nature (London)* 381:198–199.
- Kaitala, V., E. Ranta, and J. Lindström. 1996. Cyclic population dynamics and random perturbations. *Journal of Animal Ecology* 65:249–251.
- Kaitala, V., J. Ylikarjula, E. Ranta, and P. Lundberg. 1997. Population dynamics and the colour of environmental noise. *Proceedings of the Royal Society of London B, Biological Sciences* 264:943–948.
- Lawton, J. H. 1988. More time means more variation. *Nature (London)* 334:563.
- Mode, C. J., and M. E. Jacobson. 1987. A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. *Mathematical Biosciences* 3:105–125.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. Wiley, Chichester.
- Pimm, S. L. 1991. *The balance of nature? ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago.
- Powell, T. M., and J. H. Steele. 1995. *Ecological time series*. Chapman & Hall, New York.
- Ranta, E., V. Kaitala, J. Lindström, and H. Lindén. 1995. Synchrony in population dynamics. *Proceedings of the Royal Society of London B, Biological Sciences* 262:113–118.
- Ripa, J., and P. Lundberg. 1996. Noise colour and the risk of population extinctions. *Proceedings of the Royal Society of London B, Biological Sciences* 263:1751–1753.
- Royama, T. 1992. *Analytical population dynamics*. Chapman & Hall, New York.
- Sugihara, G. 1995. From out of the blue. *Nature (London)* 378:559–560.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? *Nature (London)* 344:660–663.
- White, A., R. G. Bowers, and M. Begon. 1996. Red/blue chaotic power spectra. *Nature (London)* 381:198.

Associate Editor: Robert W. Sterner