How does environmental variation translate into biological processes?

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Birth and death rates, as so many other biological processes, are usually not linearly related to environmental variation. Common examples of non-linear response forms include unimodal “optimum-type” responses and various saturating responses. These responses filter the signal coming from the environment to a corresponding biological process. We explored how different types of environmental signal may be transformed to a biological process. We were interested in the effect of the filter on modulation of (1) the variance of the signal, on (2) the variance-covariance structure between the signal and the filtered signal, and on (3) the match between the power spectra of the signal and the filtered signal. We found that the filters will change the frequency distribution (mean, variance, modality) of the signal. Especially symmetric filters that have a single peak of optimum will change signal structure so that there either exists or does not exist a correlation between the signal and the filtered signal. When the correlation exists it may be either positive or negative depending on the signal’s mode relative to the filter structure. Also, the power spectrum properties of the signal may be dramatically transformed after passing the filter, e.g., blue noise can turn into red noise. Our results strongly suggest that studies on the influence of external signals on biological processes, such as population dynamics, should explicitly consider how the signal is transferred to biological processes.

It is tempting to assume a simple linear relationship between environmental noise and biological processes influenced by them (e.g., Belgrano et al. 1999). However, it is more likely that biological responses are non-linearly related to the signal range. A very common reaction is a response that has a unimodal optimum with respect to, e.g., temperature, salinity or some other dimension of the ecological niche (e.g., Begon et al. 1990). For simplicity of our argument the relationship how variability of a relevant environmental variable is transformed to variability of a biological process will be here referred to as a “filter”. The list of filters to be explored includes (A) asymptotic, (B) symmetric and peaked (“optimum-type”) and (C) sigmoidal filters (Fig. 1).
Using a theoretical frame we shall report here how properties of the external signal may change when transformed after having passed the filter. In short, a filter acts as a transformation for a time-series (e.g., Box and Jenkins 1970). Negligence of these modifications may result into erroneous conclusions about the relationship between environmental fluctuations and biological processes, and may thus potentially lead to faulty management acts.

External signal and biological filters

Let \( x_t \) represent an external signal (e.g., temperature) at time \( t \) affecting some biological process, and consequently, let \( y_t \) represent the corresponding biological outcome. For example in

\[
y_t = f(x_t)
\]

the function \( f \) represents the filter transforming the environmental signal \( x \) to the biological outcome \( y \). For function \( f \) consider the following three non-linear forms

\[
y_t = \frac{x_t + a}{x_t + b}, \quad (2a)
\]

\[
y_t = a - x_t^b, \quad (2b)
\]

and

\[
y_t = \frac{\exp(bx_t)}{1 + \exp(bx_t)}, \quad (2c)
\]

Here \( a \) and \( b \) are parameters. We used the following choices to achieve an asymptotic filter, eq. (2a): \( a = 1, b = 1.1 \), a symmetric “peaking” filter, eq. (2b): \( a = 1, b = 2 \), and for the sigmoidal filter, eq. (2c): \( b = 10 \).

To generate the signal \( x_t \), we used the autoregressive process generator (e.g., Ripa and Lundberg 1996)

\[
x_{t+1} = \alpha x_t + \beta e_t
\]

where \( e_t \) is normally distributed random noise and \( \alpha \) and \( \beta \) are constant parameters. Parameter \( \alpha \) ranges between \(-1\) and \(1\), and defines the autocorrelation structure of the time series. For positive values of \( \alpha \) there is a dominance of low-frequency components (referred to as red spectra) and for negative values of \( \alpha \) we get a dominance of high-frequency fluctuations (blue spectra), the colour of the time series indicating the difference from white-time series (\( \alpha = 0 \)). This method produces normally distributed time series over the entire range of \( \alpha \). For our purposes, we generated \( x_t \) of length 4096 for all values of \( \alpha \) (from \(-0.95\) to \(0.95\), with step 0.025). The series were standardised to fit the generated values between \(-1\) and \(1\) with zero as the expected value (Heino 1998). This ensures the three filter forms (Fig. 1A–C) with the above selection of parameter values.

Results

An inspection of the filters on the out-coming signals [Fig. 1, here \( \alpha = 0 \) in eq. (3)] shows that the three simple filter types very effectively alter central features of the

![Fig. 1](image-url)
Fig. 2. (A–C) Correlation between the original signal and the signal after passing the three different filters. (a–c) Difference between the slope of the spectrum of the original signal and the slope of the spectrum of the filtered signal. The three signal types (i–iii) differ in the mode (relative to the range of the filter) where the signal enters the filter (see Fig. 1). The signal colour (see text for definition) changes from blue (parameter $a = 0.95$) via white ($a = 0$) to red ($a = 0.95$) along the $x$-axis in the graphs. Note that in panels (A), (a), (C) and (c) the scale of the $y$-axis is truncated.

signal frequency distribution (Fig. 1A–Ciii). The variance of the filtered signal can decrease or increase relative to the original signal depending on the location of the range of the input noise with respect to the filter. Steep parts of the filter function increase the variance whereas flat parts of the filter decrease the variance (Fig. 1). The frequency distribution of the filtered noise signal generally becomes asymmetric and more peaked. However, in the case of the sigmoid filter and centred signal, the frequency distribution of the filtered signal can become flat or even two-peaked provided that the filter is steep enough. The correlation between input signal and the filtered signal also depends on the filter types and the location of the signal range on the filter (Fig. 1). We may readily argue here that a strong linear correlation may be observed if the signal hits the sloping part of the filter (Fig. 2A–C). The symmetric filter can yield either positive or negative correlations depending on which part of the filter the signal is located in. However, the correlation may also disappear, as on the flat parts of asymptotic and sigmoid filters, or it may be a combination of all these three options, as around the peak of the symmetric filter (Fig. 2B).

To reveal how the filters may affect the temporal patterns of the input signal, we calculated power spectra of the signal before and after the filtering. A match in the temporal structure of the two series can be assessed, e.g., by comparing slopes of the two spectra. Thus, if the filtering changes the power spectra (colour) of the signal, the slopes are different. When the noise is white (i.e., uncorrelated) the filtering has no effect on the spectra (Fig. 2a–c). Coloured noise, however, can have a dramatic effect on the signal colour. A striking red shift in spectra occurs when blue noise (a time series dominated by high-frequency changes) passes through the centre of the symmetric filter (Fig. 2b); also other filters produce a similar, although milder effect and the only situation in which filtering had no effect on the spectra is when noise hits exactly the centre of a sigmoid filter (Fig. 2c, type ii). In the red region filtering can make the signal colour turn blue. However, the strength of this effect depends on where the input signal hits the filters (Fig. 2a–c).

Discussion

We have studied the problem of how environmental fluctuations or noise may be seen in the biological processes. This problem can be posed, for example, by questioning whether one is able to identify any meaningful correlation between weather and population numbers (e.g., Leirs et al. 1997, Grenfell et al. 1998, Henderson and Corps 1999, Lima et al. 1999), or what determines the spectral properties of biological dynamics (e.g., Cohen 1995, Kaitala and Ranta 1996, Kaitala et al. 1997).

In the present study, we show that the correlation between the original unfiltered time series and the resulting filtered time series may fluctuate from highly positive to highly negative, depending on the filter type and where the signal mode lies relative to the range of the filter. Thus, identifying covariation between the environmental noise signal and the biologically filtered signal may not always be possible, and any failure in doing this may be due to the non-linear biological response to environmental disturbances. Moreover, the unreliability of the correlation estimate, especially with red noise modulated by the symmetric filter (Fig. 2b), suggests that biological processes may be strongly controlled by the environment, but it is not always possible to separate this effect, e.g., from population dynamics data using linear correlation analysis. This may be especially important when analysing real population data because the environmental fluctuations are commonly red-shifted (e.g., Lawton 1988, Cuddington and Yodzis 1999).

We have shown that filtering the noise using biologically plausible, non-linear response curves always changes the frequency distribution of the filtered signal relative to that of the original one, and in some cases also the variance and spectral properties of the noise
may change. This is likely to have consequences on, e.g., population dynamic processes, as some values of environmental variables become more important for the organism’s performance than others, and the outcome of temporal fluctuations can fluctuate more rapidly or slowly than the environmental conditions. These results suggest that the nonlinear responses of organisms to environment should be explicitly considered in investigations of the noise-population dynamics relationship when adequate information is available.

The strong filter-induced red shift in the spectral properties of the noise suggests that the filter phenomena can be one mechanism in addition to, e.g., abiotic environment (Lawton 1988, Cuddington and Yodzis 1999), delays and species interactions (Kaitala et al. 1997), which increases the probability of observing red-shifted time series in biological data even when the environmental variation is blue and strongly forcing the biological processes.

In summary, knowledge on the specific form of the nonlinear response of the biological system to the environmental noise may help to distinguish the role of the environment in the dynamics of biological data more efficiently.

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References


