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Environmental autocorrelation: curse or blessing?

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Theory of population dynamics predicts that environmental autocorrelation increases extinction risk. Recent work by Engen and colleagues confirms this and demonstrates how the spatial extent of population synchrony is influenced by dispersal. However, in a new study, Gonzalez and Holt demonstrate that environmental autocorrelation causes substantial increases in the size of populations with negative growth rates, provided that they are sustained by immigrating dispersers. These new findings could change our view of dispersal and sink populations, whilst providing an explanation for previously enigmatic population outbreaks.

Environmental variability influences population dynamics in many ways. Over the past two decades, much attention has been paid to spatial and temporal correlations among environmental features, because correlated environments can cause populations to fluctuate synchronously (the 'Moran effect' [1]), which increases extinction risk [2–5]. Environmental correlation is defined as the covariance of environmental parameters in space or time and I use this neutral term here when the source of the correlation (i.e. spatial or temporal) is not relevant for the effects being discussed. Spatial autocorrelation (e.g. a storm affecting an entire region) could prevent the successful recovery of locally extinct or critically declined populations,

because the distance to the nearest unaffected population might be too great for potential immigrants to overcome. Depending on the degree of isolation, temporal autocorrelation (e.g. a series of bad years) might also decrease population sizes such that the species disappears from a given locality. The spatial scale at which environmental correlation occurs critically influences extinction risk, because large-scale events have a greater impact than do small-scale events. However, a recent study by Gonzalez and Holt [6] sheds new light on the role of environmental correlation in population dynamics. The authors provide both theoretical and empirical evidence that environmental correlation can inflate the sizes of populations with negative growth rates, and even lead to population outbreaks. These findings could revolutionize our view of environmental autocorrelation and declining populations.

Environmental autocorrelation leads to inflated sizes of sink populations

Gonzalez and Holt [6] used a system of spatially separated populations in which some populations, so-called 'sink populations', could persist only because of immigration from 'source populations' [7,8]. Evidence for source–sink dynamics comes from several empirical studies [9,10]. Gonzalez and Holt [6] showed mathematically that, in constant environments, the equilibrial size of populations with negative growth rates equalled the immigration:absolute value of growth rate ratio. Hence, the equilibrial

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abundance of sink populations can be high if the negative growth rate is not too far from zero and immigration is present. The authors also showed how temporal environmental autocorrelation can lead to periods with positive growth; hence to switching from a sink to a source status. This inflationary effect increased with the magnitude of variation in growth rates. Such bursts of growth potentially have a substantial effect on average abundance in the system. The authors corroborated these theoretical predictions by using experiments on the ciliate protozoan *Paramaecium tetraurelia*. They created sink populations and imitated immigration by moving individuals from other cultures to them. Environmental correlation was simulated by autocorrelated temperature fluctuations. The observed effects were in line with the theoretical predictions of inflated sizes of sink populations owing to environmental fluctuation and population outbreaks in sink populations when fluctuations were autocorrelated.

Hence, in source–sink systems, where the growth rate of populations is only weakly negative, environmental autocorrelation can have positive, rather than negative, effects on population size. The authors conclude that, for instance, global climate change might lead to outbreaks in the abundance of endangered species by altering environmental correlation structure. For example, this would occur if density dependence were weak in sink populations, because high mortality or reduced immigration (because of high local density) counteracts population growth [11]. Additionally, the generation time of such species should be on a similar or smaller temporal scale than is the environmental correlation, because otherwise a run of good conditions would not be reflected in enhanced reproductive rates. A promising approach to test these ideas is to analyze long-term data sets of populations (insect or amphibian species are good potential candidates) that fulfill the criteria for potential outbreaks.

The role of sink populations in population dynamics
The potential for inflated sizes of sink populations also sheds new light on the role of sink populations in spatial population dynamics, which is still controversial. Sink populations can have negative effects on the persistence of source populations by drawing away individuals [12–14]. However, sink populations can also have positive effects by serving as temporary residence (stepping stones) whilst individuals wait for an opportunity to disperse back to source populations [10,15–17]. Based on Gonzalez and Holt's study [6], it seems that sink populations can contribute substantially to regional abundance. It would be interesting to explore how population outbreaks in sinks affect a source–sink system, and whether there are systems that can only persist because of such periodical outbreaks. Switching from source to sink status and *vice versa* has been reported from several real populations [16,18,19] and it would be exciting to explore whether these processes are in accordance with the evidence provided by Gonzalez and Holt [6].

Dispersal, population synchrony and extinction risk
Environmental autocorrelation is only one factor leading to synchronized population fluctuations. Another important one is the exchange rate of individuals among populations. Dispersal is a major determinant of the spatial extent of population synchrony [20]. Using a continuous stochastic population model, Engen and colleagues [4] demonstrated that even low dispersal rates over short distances might substantially increase the spatial scale of population synchrony, which could elevate extinction risk. However, the same authors also showed positive effects of dispersal, such as buffering fluctuations of local populations, and dampening the impact of stochastic environmental effects, such as storms or fires [5]. Their study, and numerous other empirical, theoretical and modelling work, demonstrates how dispersal among populations prevents population decline [21–23]. Hence, dispersal is a 'double-edged sword' [24], because declining populations can be rescued by immigration, but populations synchronized by dispersal still face an elevated extinction risk compared with asynchronous populations. Gonzalez and Holt [6] add a new perspective by showing that dispersal in combination with environmental autocorrelation can actually increase the population size when individuals move into sink populations. Such dispersal has been viewed as maladaptive because reproductive success and/or survival in sink habitats are, by definition, lower than in source habitats. Given that sink populations can turn into sources, as demonstrated by Gonzalez and Holt [6], dispersal into sink populations might not be selected against. This potentially provides an additional explanation for the persistence of source–sink dynamics in some natural systems.

Implications for applied ecology
The studies by Engen and colleagues [4,5] and Gonzalez and Holt [6] show that the interplay of environmental autocorrelation, dispersal and extinction risk is far from being fully understood. Knowledge of these processes, however, could have practical implications for a variety of fields in ecology. For instance, it has been shown that vaccination against measles desynchronizes populations and facilitates global persistence of the disease [25]. If we assume a declining disease population (i.e. a sink) experiencing a series of good years, such as a consistently high number of susceptible hosts, we can expect an outbreak of the disease. Such scenarios are purely speculative and many other factors contribute to disease epidemiology, but it might be worth searching for patterns of unexplained outbreaks of diseases of declining incidence.

Furthermore, the potential for outbreaks in sink populations could give us hope for declining populations, when the major factors that initially caused the decline are under control. Sink populations can now be given special attention in the management of endangered species, for example, provided that sufficient immigration is present. Further research is needed, however, to assess how population outbreaks in sinks affect the specific risks of small populations, such as stochastic extinctions or depletion of genetic diversity.

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Letters

Value of the IUCN Red List

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Possingham *et al.* [1] have warned against the improper use of threatened species lists. However, their characterization of misuse masks the essential role of these lists in conservation. Although threatened species lists are indeed typically problematic, the IUCN Red List provides quantitative measures, rather than qualitative estimates, of extinction risk and, as such, is a major exception [2].

We agree with Possingham *et al.*'s [1] main point that '(i)t is naïve and counterproductive from all points of view to use threatened species lists alone to allocate resources

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