Comment on “Metapopulation Persistence with Age-Dependent Disturbance or Succession”

In an elegant and useful report, Hastings (1) showed that persistence of a species in a patchy environment is predicted correctly by measuring population extinction rate as the reciprocal of mean patch age, rather than as the patch extinction rate. This work casts important light on the interpretation of commonly measured quantities in patchy systems. However, the report fails to note a key point that greatly simplifies interpretation of its main result: Due to symmetry, the mean patch age is exactly equal to the mean future lifetime of a patch randomly selected from the landscape. Additionally, the relationship between patch extinction rate and population extinction rate can be written in a simple form that further aids in interpretation.

Hastings’ result can be understood in terms of the classical waiting-time paradox (2). In its simplest form, this paradox considers buses that leave the station once every 10 minutes, on average, with a memory-less (exponential) distribution. A rider who arrives at the bus stop at a random time will wait 10 minutes on average. Similarly, looking backwards in time, the rider arrives, on average, 10 minutes after the previous bus. Thus, on average, there are 20 minutes between buses.

The resolution of this paradox is that the average interval observed by a randomly arriving rider is longer than the average of all intervals. The probability of arriving during a given interval is proportional to the length of the interval. The average observed interval for a general distribution is thus given by \( m(1 + C^2) \), where \( m \) is the mean and \( C \) is the coefficient of variation of the distribution of interval lengths (3, 4). In the special case of the exponential distribution, \( C = 1 \), so the observed interval is \( 2m \), as we have seen. Since the rider is equally likely to arrive at any point within a given interval, both the expected time until the next bus and the expected time since the last bus are half of this interval length, or \( a = m(1 + C^2)/2 \).

The age-dependent patch renewal process considered by Hastings is exactly analogous. If the expected lifetime of a patch at birth is \( m \), then the average patch extinction rate must be \( 1/m \). If a patch is arrived at in a random colonization event, however, the mean patch age (and the expected future patch lifetime) is \( a = m(1 + C^2)/2 \). The fact that mean patch age is equal to expected future patch lifetime provides a simple explanation of Hastings’ observation that the reciprocal of the mean patch age is the critical rate of colonization required for a population to persist. The theory of basic reproductive numbers allows us to conclude directly that the product of colonization rate and future patch lifetime must exceed one for a population to persist (5, 6). The formula \( a = m(1 + C^2)/2 \) further clarifies Hastings’ observation that mean patch age can be as small as half the expected patch lifetime, and may be infinitely large, and allows us to add the caveat that an arbitrarily small colonization rate can only allow persistence if the variance (and thus the coefficient of variation) of the expected patch lifetime at birth is infinite.

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References and Notes

4. The result in (3) is derived for spatial clustering; the temporal analog discussed here is often referred to as length-biased sampling.
6. Note that when studying the invasion process, we may ignore the possibility of two colonization events in the lifetime of a single patch. Thus, colonization times are uniformly distributed.
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