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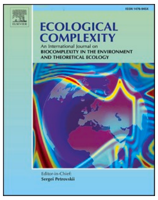

The meta-Allee effect: A generalization from intermittent metapopulations

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ABSTRACT

Intermittent population trajectories are likely to emerge in almost any population that faces a predator yet has a refuge from that predator. Using the well-known model of Pomeau and Manneville for intermittent populations, a collection of a group of inherently unstable subpopulations can survive through the balance of extinction and migration rates, which is a metapopulation. This formulation also generates a meta-Allee point, which is to say a minimal number of subpopulations that must exist to sustain the population over the long term.

There are two key issues of common knowledge about natural populations: 1) all are visited by both predators and diseases, and 2) many are constrained in heterogeneous space, part of which offers refuge from the predator. The pattern can be referred to as the predator/refuge/disease (PRD) pattern, and is arguably a common situation in the natural world, as discussed later. Two generalizations emerge from these seemingly common ecological facts: First, many populations will exhibit intermittent dynamical behavior, as pictured in Fig. 1; Second, a successful metapopulation arises only when a critical number of subpopulations exist, a phenomenon I call a meta-Allee effect. Both generalizations, intermittency and the meta-Allee effect, emerge naturally from these key issues of common knowledge, the PRD pattern.

The inevitability of intermittency can be argued for almost any population that faces a predator in some sites in its habitat yet encounters a refuge from that predator in other sites(i.e., the PRD pattern). When not in the refuge, the prey is consumed sometimes to local extinction, as observed in many classic laboratory studies (Gause et al., 1936; Luckinbill, 1973; Huffaker, 1958). When in the refuge and thus released from control by the predator, it may increase its population dramatically (Vandermeer and Perfecto, 2019). That dramatic increase in population density creates a target for the inevitable disease that visits it (Burdon and Chilvers, 1982) resulting in, ironically, a population crash within that refuge, due to the disease. The combination of two natural enemies (predator and disease) along with this particular form of a spatially heterogenous landscape (i.e., the PRD pattern), results in persistence at a large scale, extinction at a small scale, and a pattern that is best described by the word intermittency (Fig. 1).

While the idea of intermittency is intuitively obvious when assuming the PRD pattern (Fig. 1), the potential emergence of the meta-Allee effect requires some theoretical machinery to understand. With a focus on intermittency a convenient way of dealing with such populations is with the model of Pomeau and Manneville (1980), hereafter PM,

$$X_i(t+1) = \ rX_i(t) + aX_i(t)^b \ Mod\ 1 \tag{1}$$

(presuming $r > 0$, $a > 0$ and $b > 2$), which effectively allocates the result of an overpopulation to a new reflection of the same basic rules. The first term in the model (Eq. (1)) reflects a simple exponential growth behavior and the second term (aXi(t)b) represents an accelerated growth, reflecting the basic ideas illustrated in Fig. 1, and following the same logic as presented elsewhere (Vandermeer and Perfecto, 2019). Illustrations of Eq. (1) are presented in Fig. 2, whence it is clear both why the model is frequently used as a model of intermittent behavior as well as the qualitatively distinct behavior for very similar initiation points, a characteristic normally associated with chaos. As has been noted elsewhere (Klages, 2013; Nee, 2018), the Lyapunov exponent is zero, even though the behavior is chaos-like, leading to the descriptor, “weak chaos.”

While other framings exist, the PM map is an elegant model that captures the essence of intermittency and produces time series that are familiar to most ecologists. The term $rX_i(t)$ is the exponential growth part of the equation, making the parameter “*a*” correspond to an additional growth factor, dependent on a power of X. Although not usually expressed in this way, the idea of niche construction is clearly reflected in this parameter (Vandermeer, 2019). Note that if $r < 1$, regardless the value of *a*, the population is destined to extinction, as is made clear in Fig. 3.

It is thus always true that in an intermittent population (modeled with the PM map), the intrinsic rate of increase, r, must be greater than 1.0 for the population to survive in perpetuity. However, this necessity disappears in a metapopulation (i.e., the overall population is divided

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into a group of subpopulations, each of which is a sink [r < 1.0], but individuals migrate among the subpopulations). The question here is, what is the effect of putting a series of subpopulations with intermittent dynamics and r < 1.0, into a metapopulational framework, with the parameter ("*a*") non-zero?

Presuming there are S subpopulations in the system and a density-dependent rate of migration among them of m, and migration is universal, we modify Eq. (1) to read,

$$X_i(t+1) = rX_i(t) + aX_i(t)^b + m\sum_{j\neq i}^{S} X_j(t) - mX_i(t) \quad Mod\ 1. \tag{2}$$

It is clear from inspection that the oscillations of each of the subpopulations will remain intermittent. It is also clear that even if the inevitability of extinction criterion (r <1) is not met, setting an arbitrary lower critical level of extinction can force an inevitable extinction. Yet the timing of that extinction is not fixed, but rather can be viewed as a probability within a fixed time frame. Central to the general argument of this paper, the probability of descending to some critical extinction level

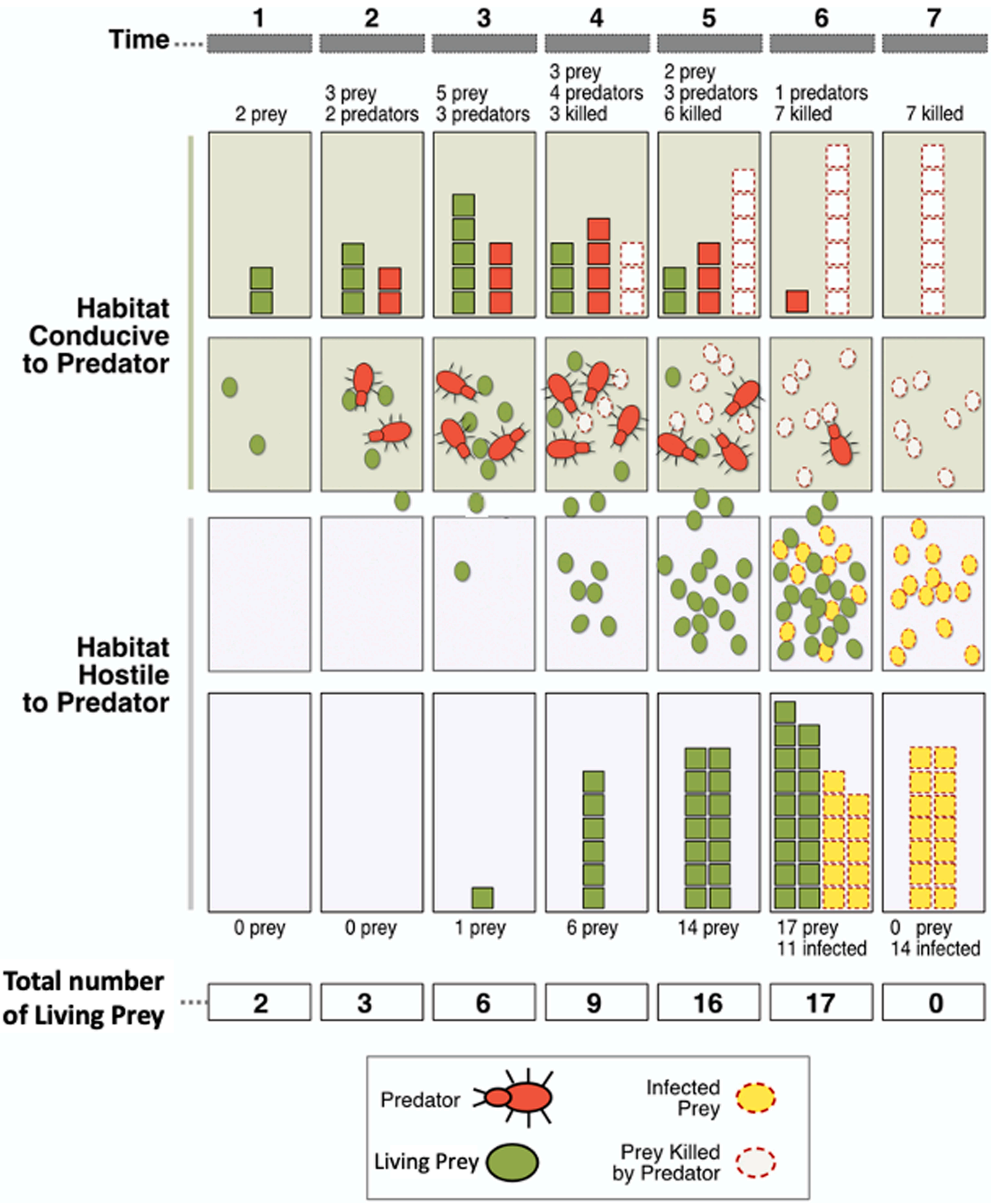

Fig. 1. Cartoon version of the underlying structure of intermittency in a population subject to predation and a disease, distributed in both space and time. Beginning from time 1, the system proceeds through time 7 and then cycles back to time 1, generating the time series 2, 3, 6, 9, 16, 17, 0, 2, 3, 6, 9, . . ., illustrating the boom and bust dynamics of the prey population as expected from the basic natural history of this relationship. At each time frame the total number of individuals in either the "conducive to predator" or "hostile to preditor" is counted separately, with the individuals outside of those categories meant to imply in the process of migration and thus not counted.

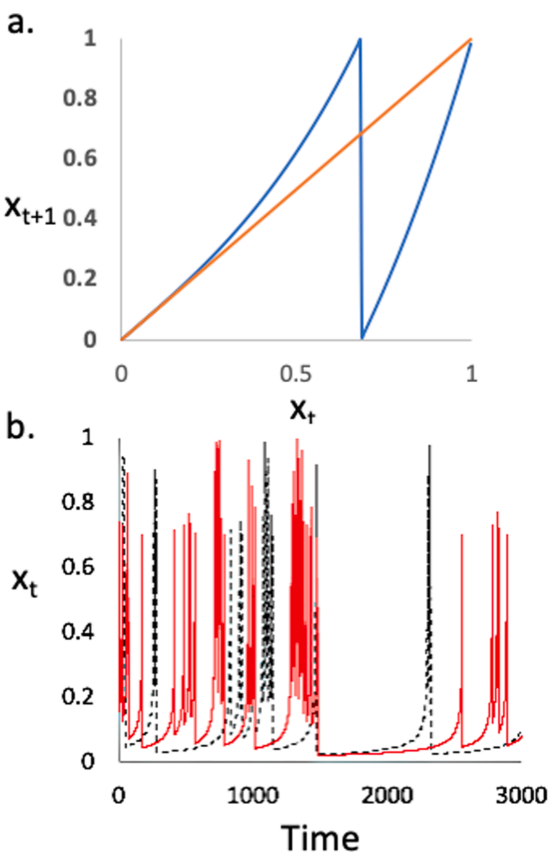

Fig. 2. The Pomeau–Manneville map (equation 1). a. the recursion map (equation 1) with the switch from 1 to 0 connected with a vertical line for clarity and the 45 degree line representing the X(t+1) = X(t) state. b. time series illustrating the dramatically different patterns for trajectories initiated at similar starting points. Parameters are r = a =1.0, b = 3. Black dashed line initiated at x(0) = 0.4001, red solid line initiated at x(0) = 0.4000. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

may be curtailed by the migration parameter. In simple simulations (and by simple examination of Eq. (2)) it is evident that falling below any stipulated threshold for any individual population is a virtual certainty and that any level of migration reduces that certainty (Fig. 4). In classical metapopulation language, the probability of extinction for each individual population is a measure of the inherent probability of falling below the extinction threshold and is a measure of the inherent dynamics within individual subpopulations, independent of their inter-population migrations. Migration, a function of the quality of the matrix within which the subpopulations are located, reduces that inherent probability (Fig. 4). Not surprisingly, changing the migration rate (m) has the effect of raising the number of subpopulations surviving. Furthermore, the change in surviving populations over time stabilizes after about 100 iterations for a variety of parameter settings and initial values.

With this metapopulation framing, there is an important relationship between the number of subpopulations at an initial time period and the survival of the overall metapopulation. Fig. 5 illustrates this effect, wherein initiating the metapopulation with 60 subpopulations results in a long term average of 3.25 subpopulations surviving, initiating with 55 sub populations (same parameter values) results in a long term average of 1.25 surviving populations. Generalizing, we see a critical transition phenomenon, wherein there is a critical number of subpopulations that must exist for the metapopulation to survive in the long term, what might be referred to as a “meta-Allee “ point, as shown in Fig. 6.

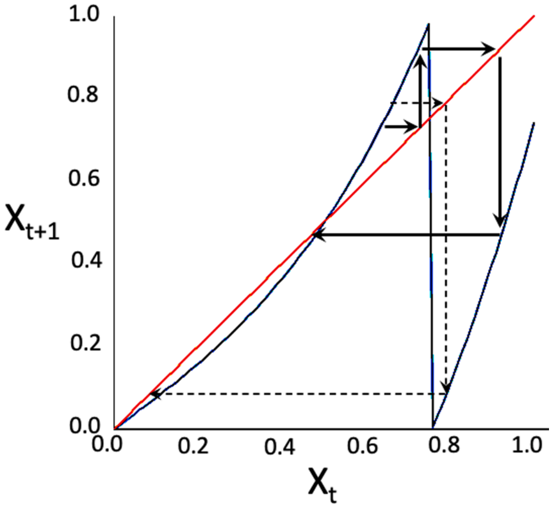

Fig. 3. The apparent inevitability of extinction in an intermittent population with $r < 1$ (parameter settings are $r = 0.75$, $a=0.99$, $b=3$). With $r<1$ the initial rise of the function, (i.e., near zero), is less than needed for population increase. Any population below a critical point (where the function crosses the 45 degree line, in this case at $X = 0.5025$) will descend to zero, and any point above that critical point ultimately projects to the basin of the zero equilibrium, from extensive simulations. The only possible viable population would appear to require $r > 1$.

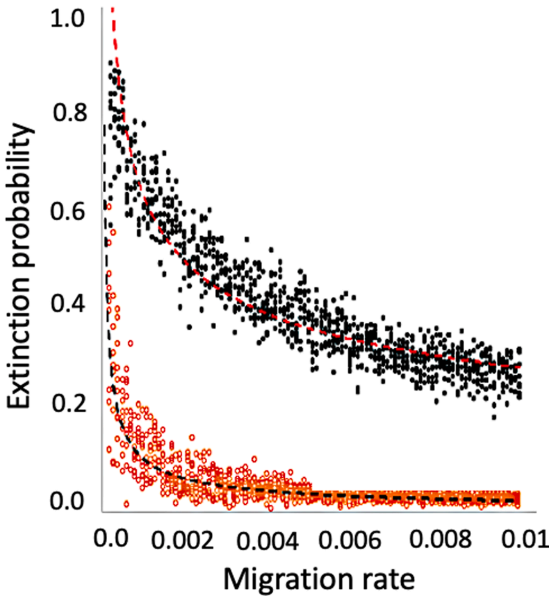

Fig. 4. Probability of falling below critical extinction threshold of 0.05 (lower open circles) and 0.2 (upper closed circles) as a function of the migration rate (m in equation 2). Simulated probabilities (proportion of 100 populations that go extinct) after a time frame of 10,000. Dashed lines connect means (parameters as in Fig. 2). All populations initiated with a random number, $0 < \varepsilon < 1$.

The pattern, arguably common in nature, of a population visited by both predator and prey in a heterogenous environment can easily lead to the circumstances of intermittent population behavior, as illustrated qualitatively in Fig. 1 and quantitatively in Eq. (1). With less than replacement intrinsic growth rate ($r<1$, in Eq. (1)) such an intermittent pattern cannot be maintained (Fig. 3) and the population becomes locally extinct. However, populations of this sort are the equivalent of sink populations and a collection of sink populations may be connected through migration into a classic metapopulation. Such a structure takes on special meaning when populations are intermittent, here modelled with the Pomeau/Manneville map.

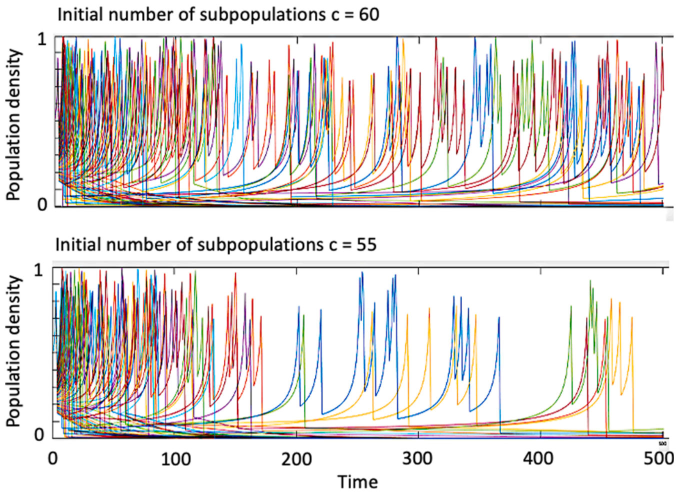

Fig. 5. Examples of time series for two initial subpopulation numbers in a locally unstable scenario (parameters same as in Fig. 3, with migration coefficient = 0.001). For an initial number of 60 the average number of subpopulations over the last 100 iterations (from 400 to 500) is 3.25 (for a p* of 0.054). For an initial number of 55, the average number of subpopulations over the last 100 iterations is 1.25 (for a p* of 0.023).

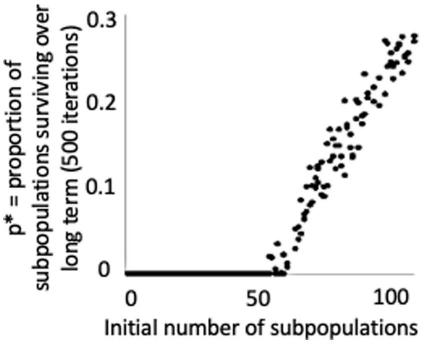

Fig. 6. Long term equilibrium proportion of subpopulations surviving as a function of the initial number, illustrating the existence of a meta-Allee point (parameters as in Fig. 5). The initial number of subpopulations is the number of subpopulations that are initiated at the beginning of a run, for example, 60 and 55 as displayed in Fig. 5.

While the idea of metapopulation stability is similar to classic notions, the framework herein leads to a distinct idea, that of a "meta-Allee" point. As implied in Fig. 5 and made more explicit in Fig. 6, there is a critical minimal number of subpopulations that must exist to begin with, if the overall intermittent metapopulation is to be sustained over the long term. Thus, it is not simply that a metapopulation emerges from connecting unstable subpopulations through migration, as is the case in a classic metapopulation, but it takes a minimal number of subpopulations for the metapopulation to form. The parallel with the classic notion of an Allee point is evident.

A variety of qualifiers need to be added to the assumption that all subpopulations are the same. Indeed, there is substantial literature on the heterogeneity of ecological background states, whether exogenous (e.g., Alemu, et al., 2021; Xue et al., 2021) or self-organized through genetic our behavioral structure (Huang et al. 2021; Garnier and Lafontaine, 2021). For example, the Allee effect for an individual population in a spatially explicit context can lead to either an expanding or contracting range, but also to a range that is "pinned" between expansion and contraction (Keitt et al., 2001), a phenomenon that warrants further study in the context of meta-Allee points. Surendran and colleagues (2020), using an individual based model show that a population may survive even though its mean field approximation predicts extinction, similar to the meta-Allee effect reported here. Metapopulation biology coupled with the Allee effect has also been clearly implicated, theoretically, in the spatial structure of intraspecific population density (Osorio-Olvera et al, 2019). Adding such spatially explicit components to the present analysis will be of considerable interest for future studies.

The implications of these results may apply to diverse subfields of ecology, such as conservation and pest control. For example, the conservation of a species when examined through the lens of the traditional metapopulation model suggests that even very small numbers of habitat patches might be sufficient for conservation as long as the migration rate exceeds the local extinction rate. In the intermittent metapopulation context the idea of a meta/Allee point emerges, suggesting that there is a critical lower number of patches that must contain subpopulations if the population is to survive in perpetuity. That critical number represents an "extinction threshold," (Bascompte and Solé,1996) in the sense that if the subpopulation count goes below it, the overall population will disappear. In pest control applications if the population of concern is a pest and the potential subpopulations are agricultural fields, the model suggests that there is a critical number of agricultural fields housing the pest that could lead to its emergence as a problem (Sylvén, 1968), below which it would remain at very low levels, or become extinct. Concomitantly, of course, is the possibility of pest control over a large region by management on fewer than all of the farms.

Author statement

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Declaration of Competing Interest

The author has no conflicting interests to declare.

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