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IDEA

A roadmap for metapopulation research

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Abstract

The theory of metapopulation dynamics now embraces a diversity of spatially structured populations. New and increasingly realistic models address important details of population and community dynamics. But general results are difficult to glean from such realistic models. Discovering the general behaviour of these models will require meaningful comparison of metapopulations with very diverse structures. A simple parameter space can be constructed to facilitate such comparisons. The axes defining this space determine both the structure of metapopulations and the potential for action of various persistence mechanisms. This exercise clarifies the relationship between metapopulation structure and dynamics, and illustrates future research opportunities.

Keywords

Connectivity, habitat-specific demography, mainland-island, metapopulation, persistence, population, rescue-effects, sink, source

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Progress toward a general theory requires the discovery of general relationships between cause and effect. Metapopulation theory began with a general model linking patch occupancy to local extinction and colonization rates (Levins 1970). Over time, new models have incorporated many additional aspects of population and community dynamics (Gilpin & Hanski 1991; McCullough 1996; Gyllenberg *et al.* 1997; Hanski & Gilpin 1997; Hanski 1998). While these more realistic models may be parameterized to answer questions about specific metapopulations, their general behaviour is difficult to explore (Hanski 1998).

In order to facilitate the discovery of general behaviour in realistic metapopulations, we propose a simple framework to guide research – a sort of *n*-dimensional hypervolume for metapopulations (cf. Hutchinson 1957). The axes of this space describe aspects of metapopulation structure: e.g. population connectivity, patch size diversity, variation in patch quality, and environmental correlation. The position of a metapopulation within the space defined by these structural axes determines its potential to exhibit certain dynamics.

Our purpose here is to emphasize the importance of searching this space for general relationships between metapopulation structure and dynamical mechanisms. Without guidance on the dynamics of intermediate structures, ecologists are encouraged to classify real systems according to their similarity to a specific (and ultimately unrealistic) "type" of metapopulation (Harrison & Taylor 1997). This imposition of "types" may discourage investigation of the several mechanisms that may affect dynamics in each system.

MECHANISMS DRIVING SPATIAL DYNAMICS

Regardless of metapopulation structure, the mechanics of spatial dynamics are familiar. Under the threat of local extinction, regional persistence is achieved only if local extinctions are (a) prevented by population influx or (b) followed by timely colonization. These two favourable outcomes may result from at least six interrelated population dynamic mechanisms:

1 Spatial independence: Low correlation between segments of the population at different locations, resulting from low environmental correlation and/or low connectivity between populations. Spatial independence is a necessary component of most persistence mechanisms, with the exception of some forms of habitat-specific demography.

2 Extinction-recolonization dynamics: A balance between extinction and recolonization of local populations, creating a positive mean level of patch occupancy. This is the only persistence mechanism present in the "classical metapopulations" presaged by Levins' (1970) model. The Levins model assumes an infinite number of local populations and a static extinction rate, resulting in a constant equilibrium occupancy. In real systems, finite

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patch number and temporally varying extinction and colonization rates can accelerate metapopulation extinction. Understanding this mechanism necessitates the study of both extinction and colonization.

3 Rescue effect: A reduction in local extinction rates caused by immigration into occupied sites (Brown & Kodric-Brown 1977). Migration into small populations may augment population size, forestalling extinction. The size of the rescue effect may depend on the size and proximity of the source population(s), and may vary depending on fluctuations in source size(s) or dispersal rates.

4 Population size effect: Recolonization or rescue of smaller populations by individuals emigrating from larger populations. The defining assumption for this effect is that larger populations have lower extinction rates, because extinction mechanisms (e.g. demographic stochasticity) impact mainly small populations (for a review see Foley 1997). Note that this is an effect of population size, not patch size, although patch and population size may covary.

5 Habitat-specific demography: Recolonization or rescue of populations in inferior habitats by individuals emigrating from superior habitats. Patch quality describes any factor that modifies the finite population growth rate (λ), including other species (Pulliam 1988, 1996). This is a complex mechanism in which patch quality can change with population density (Watkinson & Sutherland 1995; Rodenhouse *et al.* 1997).

6 Demography induced by habitat turnover: Creation of habitat patches (e.g. by disturbance) may produce new opportunities for colonization, and patch destruction (e.g. by succession) can eliminate populations within patches, thereby limiting rescue effects. Succession within patches may also alter patch quality, which shares elements with habitat-specific demography. Adding habitat dynamics requires that the spatio-temporal pattern of disturbance is congruent with a favourable extinction-recolonization balance of populations. If habitat turnover is not caused by population dynamics, then it may be useful to include habitat turnover as an axis of metapopulation structure.

What is the relationship between metapopulation structure and these dynamical mechanisms? Population connectivity and environmental correlation determine the potential for independence between local populations, extinction-recolonization dynamics and rescue effects. The potential for rescue also depends on diversity in population sizes or patch qualities and the production of a population size effect or habitat-specific demography. Therefore, the position of a metapopulation in the *n*-dimensional hypervolume describing its structure should suggest its position in the *n*-dimensional phase space describing its dynamics. Changes along structural axes should produce predictable changes in population dynamic mechanisms. We do not intend our list of mechanisms to be exhaustive. Rather, we use it to identify the kinds of dynamical mechanisms and links with metapopulation structures that need to be investigated to understand regional persistence.

PROBLEMS WITH A SIMPLIFIED CLASSIFICATION OF METAPOPULATIONS

Simpler models do not always clarify the relative importance of the various dynamics that may occur within any given metapopulation structure. For example, source-sink models were intended to explore effects of habitat-specific demography (mechanism 5) (Pulliam 1988). However, recolonization (2) or rescue (3) are a necessary part of sink population survival (Pulliam 1988, 1996). Unless emigration perfectly compensates habitat-specific demography, local populations will approach different sizes, causing the population size effects (4) envisaged in "mainland-island" systems (Boorman & Levitt 1973). If all of these dynamics were apparent within a single system, we would need some way of determining their relative importance, in order to guide further research or management.

It is worth emphasizing the continuity between different metapopulation structures, because this continuity of structure implies a continuity of dynamics. However, in a complex parameter space, dynamics can change dramatically between nearby points. When we classify metapopulations according to approximate "types", we lose sight of subtle structural differences that could have dramatic dynamical consequences.

RECOMMENDATIONS

Assessing the potential for certain dynamics and the relative importance of all persistence mechanisms is only possible after the gaps in our knowledge have been explored. Structured metapopulation models (Gyllenberg *et al.* 1997; Moilanen & Hanski 1998) that test the relative impact of pairs or triads of different mechanisms are powerful tools for tackling such questions. Empirical studies should be used to gather information about the position of each physical system along the many axes of metapopulation structure. These qualitative descriptions can (i) define the most relevant portions of parameter space for theoretical exploration, and (ii) predict the most profitable avenues of field research, by suggesting testable hypotheses regarding the relative strength of each persistence mechanism. Knowledge of dynamical mechanisms and quantification of metapopulation structures from the field could also be coupled by using well-designed models to test the relative contributions of different

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measured metapopulation structures to regional persistence. With a sufficient number of tests that separate mechanisms, generalities should begin to emerge.

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