

Metapopulation Ecology

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Advanced article

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A metapopulation is a spatially structured population that persists over time as a set of local populations in balance between local extinction and colonization. Starting in 1969, and accelerating since the early 1990s, mathematical models of metapopulations have shown the importance of landscape connectivity and dispersal for persistence of a species or of interacting species. Some metapopulation models have been fit to empirical data. Although pure metapopulations may be rare, there are many empirical studies in which metapopulation processes, primarily local colonization and extinction, have been useful in explaining dynamics of natural and experimental systems. Metapopulation ecology is used in conservation biology and in population genetics where it influences genetic structure, the rate and trajectory of evolution and even what traits are under selection. Finally, communities of species that are distributed in a landscape potentially form metacommunity, which is a concept that shares important characteristics with metapopulations.

Introduction

Virtually all species live in populations with some degree of spatial structure ranging from highly discrete populations that are completely independent of one another, to a

single large well-mixed population. Metapopulations are between these two extremes. A metapopulation is made up of a set of weakly interacting local populations, a population of populations. Whereas population studies keep track of the number of individuals as determined by births and deaths, in metapopulation studies we keep track of the number of local populations as governed by local colonizations and extinctions. The concept of a metapopulation should simplify our understanding of the overall survival and extinction of spatially structured populations.

A species with a metapopulation structure lives in a fragmented habitat made up of patches that are suitable for and accessible to the individuals in the species. Only some of the patches are occupied at a given instant, and there is limited migration between local populations. Several ecological processes characterize metapopulations (1) frequent local extinction and (2) long term survival of the metapopulation being dependent on colonization through local dispersal. In a strict metapopulation the local populations must vary in size asynchronously with each other and are, on their own, not stable over long times. Such a metapopulation only persists over long times because of a balance between local extinctions and colonizations (Figure 1), always with the possibility that by chance, all local populations could go extinct simultaneously and then the metapopulation itself would become extinct.

This strict form of metapopulation may be rare in nature (Harrison and Taylor, 1997), but metapopulation processes have significant roles in many species even if they do not dominate the population dynamics at all times. For instance a species may behave as a metapopulation only at the margin of its range (Holt and Keitt, 2000). Or, a species such as the butterfly *Euphydryas editha* may live regionally with source–sink dynamics, which are distinct from metapopulation dynamics because populations in good habitat patches are constant sources for populations in low-quality patches which experience high mortality. This source–sink structure can revert to a metapopulation if the source populations are destroyed or altered (Boughton, 1999), in which case metapopulation processes may allow

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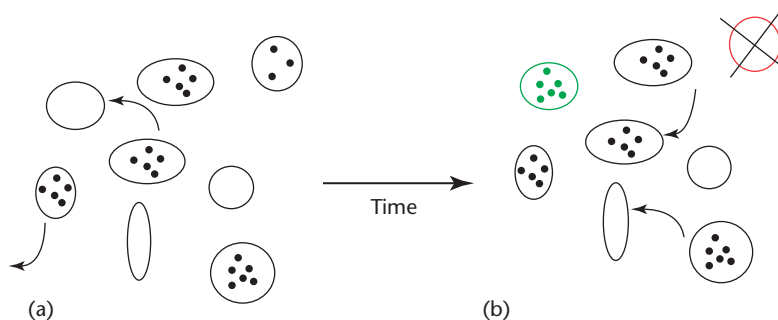


Figure 1 Illustration of metapopulation dynamics. Ellipses with dots are local populations and unfilled ellipses are empty habitat patches. In panel (a) the metapopulation is made up of five local populations. In panel (b), after one time step, there are still five local populations but one of them is newly colonized (green). One empty habitat patch is the result of a local extinction (red).

the species to persist at a lower overall density. While the existence of true metapopulations may be debatable, the importance of metapopulation processes is not.

Species Interactions

Just as the persistence of a species may be governed by metapopulation processes, so may the outcome of species interactions. Metapopulation structure can stabilize predator–prey (Bonsall *et al.*, 2002) and competitive (Amarasekare, 2003; Chesson, 1985) interactions since, in a metapopulation, newly colonized patches may be refuges for a species that has been excluded by competition or predation from other patches. For competitive interactions the dispersal ability that allows this refuge effect is often considered to come as a trade-off with local competitiveness. The less competitive species persists in the metapopulation by being mobile and colonizing new patches. This trade-off is well established theoretically (Holt, 1997; Amarasekare, 2003) and has been observed to occur among competing plant species (Tilman, 1994), and to some extent among animals (e.g. Hanski and Ranta, 1983; Yu *et al.*, 2004).

Both theoretically and empirically, distances between patches, number of patches, mobility of species, local population sizes, phenology and more subtle factors alter species interactions and subsequent spatial dynamics. Holyoak (2000) tested the hypotheses that (1) predator–prey interaction persists longer in larger (more occupied patches) than in smaller metapopulations and (2) persistence depends on the connectedness (ease of dispersal) between patches. He made arrays of two to four microcosms (bottles) connected by tubes (Figure 2) and measured the length of time that predator and prey protists persisted in the system. Arrays made of two bottles lasted less than 40 days whereas arrays of four bottles lasted more than 100 days. The effect of connectedness was more complex (Figure 2). A somewhat more derived example is the dynamics of diseases in spatially distributed host populations. For instance, Rohani *et al.* (1999) analyzed the dynamics of whooping cough (pertussis) and measles before and after the initiation of vaccination in the UK. The susceptible

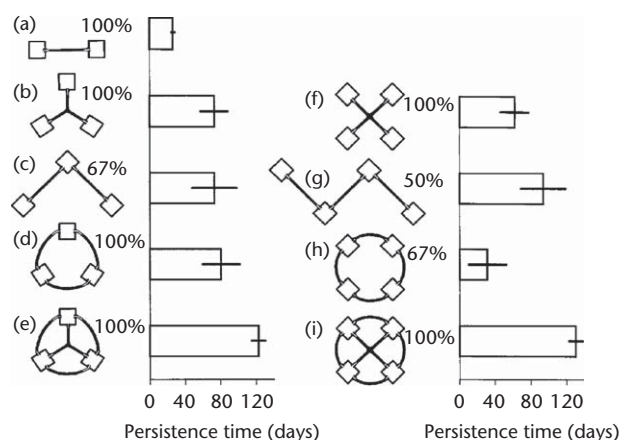


Figure 2 A schematic drawing of the arrangement of microcosms and the mean number of days that a predator population persisted. The % values beside each array show the connectedness of the bottles as the mean percentage of other bottles directly connected by tubes averaged across all bottles in each microcosm. Error bars are + or – SE. Persistence is unknown for predator populations that did not go extinct but was assumed to be 130 d, the duration of the experiment. Reproduced from Holyoak (2000) with permission of University of Chicago press.

humans live in towns (patches), and the disease is dispersed between towns by human movement. Before vaccination there were regular outbreaks of measles (periodic epidemics) occurring over a large area (many patches) simultaneously. Whooping cough on the other hand had irregular spatially uncorrelated outbreaks, as a metapopulation. After vaccination, which decreased the density or size of the susceptible human population, measles became spatially uncorrelated and irregular (as a metapopulation), while whooping cough became spatially and temporally correlated. **See also:** Dispersal: Biogeography

History

The term ‘metapopulation’ was first used by Levins (1969). However the concept of population dynamics taking the form of frequent local extinctions and colonizations was

discussed several decades earlier in the fields of population genetics (Wright, 1931) and population ecology (Nicholson and Bailey, 1935; Andrewartha and Birch, 1954). For the next 20 years after Levins (1969), there was little use of the term, but the closely related theory of island biogeography (MacArthur and Wilson, 1967) became well established in community ecology. According to the theory of island biogeography, the distance of an island from a mainland source community and the size of the island dictate the number of species in an island community. Small isolated islands support meagre communities both because colonization over a long distance is rare, and extinction from a small area is likely. Metapopulation ecology is historically rooted in population biology rather than community ecology and differs significantly from island biogeography because metapopulations lack a stable 'mainland' source population. Since the early 1990s the term metapopulation has continued to increase in use and has progressively been applied more broadly not only in the field of ecology, but also in conservation, evolution and genetics.

Theoretical Studies

Metapopulation studies have attempted to describe metapopulations as mathematical equations, or models. Initially these models were deterministic, with probabilities of colonization and extinction of local populations only appearing in a deterministic average sense. Levins (1969) was the first to formulate a representation of the rate of change of the fraction of habitat patches occupied by a species in a landscape (p). Interestingly, he used essentially the same logistic differential equation that is used in classical population models, but with the number of individuals replaced by the fraction of occupied patches p ,

$$dp/dt = cp(1 - p) - ep$$

Here c is the rate constant for colonization of empty patches and e is the rate constant for extinction of local populations. Levins' model includes an intrinsic exponential growth rate cp for colonization as well as a term that inhibits growth once the metapopulation is large ($-cp^2$) and there are few available sites to colonize. Local extinction and colonization result from many factors that are simply amalgamated into this equation. Colonization is the result of immigration from surrounding local populations. The rate of colonization is a function of the size of local populations, the distances among them and the mobility of the migrants as well as the permeability of the surrounding matrix. In the Levins model, the rate of extinction is simply proportional to the fraction of occupied patches. That is, the probability e of extinction of one patch is independent of the others. Extinction might be caused by environmental (extrinsic) disturbances, such as drought or human persecution, or biological (often intrinsic) disturbances such as predation and parasitism. The basic result of this model is, as for the logistic population models, if $c > p$ then an

initially small metapopulation grows towards equilibrium. At equilibrium p^* , $dp/dt = 0$ so the rates of local extinction (ep^*) and colonization ($cp^*(1-p^*)$) are equal. **See also:** [Population Dynamics: Introduction](#)

Some early metapopulation models added various features to the Levins equation to better mimic reality. Hanski (1985) takes into account that extinction rate tends to be low where a high fraction of habitat patches are occupied, primarily because sites that go extinct are immediately recolonized (the 'rescue effect'). Similarly, a large local population is less likely to become extinct than a small population, and a large patch is more likely to be colonized than a small one as modelled in Hastings and Wolin (1989). The persistence of interacting species has also been modelled using a general form of Levins model (Nee and May, 1992).

The deterministic models above, interpreted literally, are models of infinite metapopulations. They assume such a large number of local populations that the rate of growth of the fraction of patches occupied is governed by average probabilities. These deterministic models do not have a key feature of later explicitly probabilistic models, that extinction of the entire metapopulation is possible. In the stochastic patch occupancy models below, a patch is occupied if it has been colonized and has not yet gone extinct, and individual patches are tracked over time. Where the Levin model above uses continuous time, the patch occupancy models typically use discrete time.

The most well known of the stochastic patch occupancy models is Hanski's (1994) incidence function model where the probability of colonization of a given patch is determined by how well the patch is connected to other patches. Patch i has connectivity C_i that is determined by its distance from all the other occupied patches and the areas A_j of those occupied patches (Moilanen and Nieminen, 2002). The area of an occupied patch is used as a proxy for the local population size. A given patch's connectivity C_i also depends on a characteristic species-specific dispersal distance d . For example, the probability of one occupied site causing the colonization of a neighbouring site might depend on distance x as $e^{-x/d}$. The probability of extinction of a local population in a given time interval is only dependent on patch area. Starting with an initial list of occupied patches, the incidence function model generally uses numerical simulation to track the distributions of occupied patches as a function of time. Because the model is probabilistic, the same initial conditions result in different outcomes with each simulation. Multiple simulations can then predict the average of the fraction of patches that are occupied, and average survival time of a metapopulation. As noted earlier, in this probabilistic model the metapopulation always eventually goes extinct, although the time until extinction can be very long. The incidence function model is practical for modelling empirically collected data because it does not explicitly use local population sizes, which are often unknown in practice. Many researchers have modified the incidence function model to incorporate relevant ecological phenomena, such as dynamic rather than static patch networks (e.g. Verheyen

et al., 2004), and Bayesian methods have been used to fine tune parameter estimates (e.g. O'Hara *et al.*, 2002).

A third class of models is like the incidence function model, in that they track individual patches, but are deterministic like the Levins model in that they keep track of the probability of occupancy of each patch over time rather than whether or not a patch is occupied. Such models have the benefit that some features of the metapopulation can be extracted without a host of simulations (e.g. Adler and Nuernberger, 1994; Ovaskainen and Hanski, 2001).

Another class of metapopulation models is individual- or agent-based models in which behaviour of each individual animal, plant or seed is modelled. All manner of plausible behaviours can be included in these models, with the disadvantages of a large numbers of possibly unknown parameters and computationally intense simulations. Between the models which track individuals and those which just track patch occupancy are diffusion models in which population density is considered as a continuous function of position and time that evolves according to deterministic rules.

Many models have variants such as the inclusion of size of local population instead of just 'incidence', various realistic landscape features, change of patch quality with time, multiple species, various density effects on migration, colonization and extinction and continuous or discrete time. Some of these models are intended primarily as conceptual to reveal qualitative features of spatial population dynamics and others are designed for the purpose of being fit to empirical data, even for use as a practical tool for making land-use management decisions.

Empirical Studies

Empirical studies of metapopulation ecology cover many types of organisms. Arthropods, primarily insects, are the most studied, undoubtedly because they live on a spatial

and temporal scale that we can easily observe. For similar reasons microbial species have been used for experimental studies (e.g. Holyoak and Lawler, 1996). Long-lived species, such as trees are challenging because their population dynamics are so slow; local extinctions and colonizations are not easily recorded if the generation time is many decades. One lesson learned from considering these long-lived species is of the idea of extinction debt. Extinction debt is when a species is present, even in high numbers, but has fallen below the threshold metapopulation occupancy rate necessary for persistence over a long time (Hanski and Ovaskainen, 2002; Vellend *et al.*, 2006). Many plants and some zooplankton have the additional complication of dormant stages (e.g. seed banks). This creates an alternate phase for occupied habitat patches and makes it difficult to measure occupancy, population size and rate of colonization or extinction (Ouborg *et al.*, 2004). Finally, species that are very mobile, migratory or live in a seemingly continuous habitat such as the sea may be subject to the basic metapopulation processes but in ways that are hard to recognize or study.

Metapopulation studies are generally motivated by a desire to understand how existing or potential habitat fragmentation might affect population dynamics of a species. However, a second question is simply whether a species is living as a metapopulation. There are observational studies, such as the butterfly and parasitoid shown in **Figure 3** (van Nouhuys and Hanski, 2002) and manipulative experiments both in the field and in the laboratory. These studies generally seek to learn about the effects of one, or more often several, of the following factors: patch size, number or quality; population size; distance between patches; matrix quality and species mobility. Many studies combine some of the parameters into a measure of the overall metapopulation connectivity (Moilanen and Nieminen, 2002). Depending on the scope of the study, the importance of these factors are evaluated with respect to

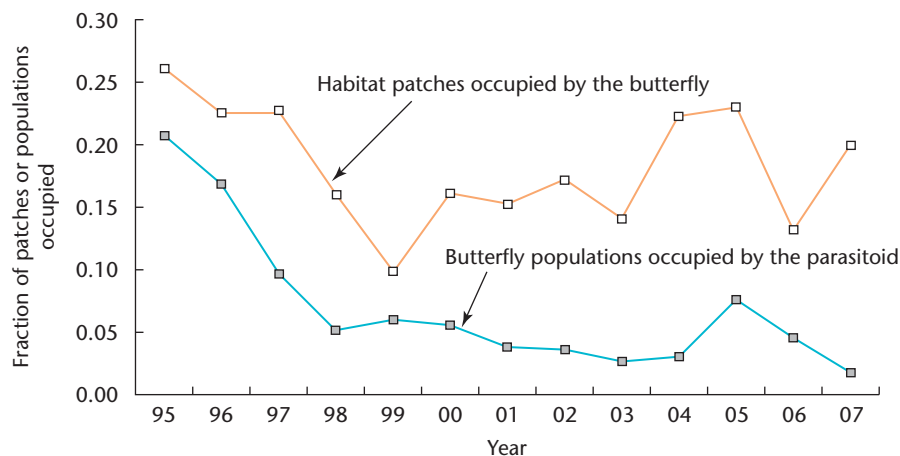


Figure 3 The metapopulation dynamics of the butterfly *Melitaea cinxia* and the parasitoid *Cotesia melitaeorum* from 1995 to 2007. The fraction of habitat patches occupied by the butterfly *Melitaea cinxia* (orange line) is always greater than the fraction of local host populations occupied by the parasitoid (blue line). A subset of these data is presented in van Nouhuys and Hanski (2002).

local population size, metapopulation persistence or patch occupancy, colonization and extinction in a landscape.

Rapid anthropogenic landscape change is a source of mismatch between present landscape structure and observed population dynamics. Depending on the rate of local colonizations and extinctions, the present distribution of a species in a landscape may better be explained by past than current landscape structure. For example, a population may currently inhabit a patch that was once part of a continuous habitat, but is now isolated. Once it declines it will be unlikely ever to be recolonized. Lindborg and Eriksson (2004) illustrate the effects of anthropogenic landscape change by showing that the distribution of some grassland plant species can be better explained by historic, more widespread grassland distribution than by the fragmented current grassland distribution. The temporal mismatch of species with their habitat structure and the overall prevalence of species living in 'extinction debt' need much more empirical study.

The majority of empirical studies of metapopulation processes are concerned with a single species, but there are also studies of species interactions whose persistence seems to depend on metapopulation processes. Species interactions in metapopulations have mostly been approached experimentally in the laboratory. For instance, protists in microcosm (bottle) arrays (Holyoak and Lawler, 1996), herbivorous and predatory mites on bean plants (McCauley *et al.*, 2000), and a beetle and a parasitoid in a series of cages (Bonsall *et al.*, 2002) have all been used to illustrate that dispersal among patches facilitates persistence of predator–prey systems. A handful of observational studies of natural systems have also shed light on the role of metapopulations processes for species interactions (e.g. Hanski and Ranta, 1983; Cronin, 2004). Recently researchers have observed interactions other than direct competition and predation in metapopulations. For instances, van Nouhuys and Laine (2008) studied an indirect interaction that was positive rather than adversary. They suggest, on the basis of a long-term survey data on the occurrence of a plant, phytopathogen, herbivore and parasitoid, that the metapopulation dynamics of a parasitoid are influenced by metapopulation dynamics of a phytopathogen. Herbivore populations that share a habitat patch with the plant pathogen are more likely to be colonized by the wasps than those without the plant pathogen. This facilitation probably occurs because the phytopathogen indirectly causes the parasitoid population to have a female-biased sex ratio, which increases the parasitoids ability to found a new population. Metapopulation studies of direct positive relationships, such as between a plant and a pollinator, or between an ant and aphids that it tends, should also prove interesting.

Conservation

Metapopulation ecology is central to conservation biology for two reasons. First, a main mechanism behind the loss of

biodiversity is through habitat fragmentation. Second, metapopulation concepts underpin some methods of species conservation and restoration, such as reserve design. **See also:** [Convention on Biological Diversity](#)

Habitat fragmentation and global change

While few species may live as metapopulations in the strict sense, many species depend on metapopulation processes. That is, a species regional persistence depends on asynchronous local dynamics and dispersal. As a landscape becomes fragmented due to anthropogenic changes, such as agricultural intensification and deforestation, habitat that had been continuous becomes fragmented, causing some species to become locally extinct and others to persist in part through metapopulation processes. Species decline, some even to regional extinction, as their habitat becomes sparse and rate of local extinction exceeds the rate of local colonization. A minimum or threshold patch network size is necessary for persistence of many types of organisms, which leads to the generalizations that habitat fragmentation results in low biodiversity (Fahrig, 2003). **See also:** [Biological Impacts of Climate Change](#); [Landscape Ecology](#)

With global change, landscapes change at the scale of entire species ranges (Parmesan *et al.*, 1999). Range expansion, which depends on rates of local colonizations and extinctions of new habitat patches (Holt and Keitt, 2000) as well as range contraction, can be metapopulation processes. Additionally, environmental change may alter the rate of local colonization or extinction by reducing the quality or phenology of individuals (Parmesan, 2006).

Restoration

A main concern of conservation biology is choosing, negotiating and engineering area to set aside to promote biodiversity or to preserve particular species. The relative importance of patch area and number of patches has been debated since the 1970s (SLOSS: single large versus several small patches in a reserve) (Diamond, 1975; Ovaskainen, 2002), as has the role of corridors in facilitating dispersal among conserved areas (Soulé, 1987). Currently, reserve design emphasizes networks of sites rather than isolated sites, with the implicit or explicit understanding that regional persistence of species will be greater in a network of patches within dispersal range than in isolated sites (unless very large). One approach to conservation planning takes into account that persistence in the long run depends not only on the abundance of the species at the onset, but also on the natural dynamics of the species, and even on changes in the habitat and surrounding landscape over time. Few models include both population dynamics of species and dynamics of the habitat (Cabeza *et al.*, 2004). However, models based on static, rather than dynamic, populations predict greater species loss from networks (Rodrigues *et al.*, 2000; Verheyen *et al.*, 2004). With increasing awareness of the vulnerability of biodiversity, metapopulation ecology plays an increasingly important

role in conservation biology. **See also:** [Strategies of Reserve Selection](#)

Population Genetics

The connection between metapopulation ecology and population genetics is strong because both are concerned with spatial population structure and rate of migration. The population geneticist Wright (1931) used a model of a subdivided population made up of demes (local populations) with gene flow (migration) among them to model changes in gene frequency due to natural selection and genetic drift. He assumed as did Levins (1969) that all of the demes were the same size and equally connected. His model, and subsequent population genetics models generally, differ from metapopulation models because the local populations persist over time, and what changes is gene frequencies within and among them. Slatkin (1977) first combined metapopulation and population genetics models to address effects of colonization-extinction dynamics on genetic differentiation among populations. This has been followed by others (reviewed by Whitlock, 2004) who explore the effects of spatial structure on genetic drift, genetic variability, accumulation of deleterious alleles and other forms of inbreeding depression, and different types of selection. **See also:** [Population Structure](#)

Metapopulation structure imposes a mating structure on a population. Individuals are most likely to mate and reproduce locally. Local dynamics of small populations can lead to random elimination of genetic lineages through extinction, and colonization events can limit genetic diversity ('founder effect'). An important outcome of metapopulation structure is that genetic drift plays a larger role than it would in a well-mixed population because the effective population size (N_e) is reduced (Wang and Caballero, 1999). This reduction of effective population size is because individuals mating in local populations are more closely related to each other than random. Furthermore, spatial structure lowers N_e by increasing the overall variation in reproductive success because individuals in a local population are both closely related and also likely to experience similar conditions.

Because response to natural selection and genetic drift are opposing forces, metapopulation structure has a negative effect on the response to natural selection by promoting genetic drift. In most models adaptive evolution across the whole metapopulation is low. However, the response to selection depends on genetics of the traits under selection, and the degree of spatial structure (as in F_{st} value: the average genetic difference among local populations). For instance if selection is uniform over the entire metapopulation, then under hard selection spatial structure is not important because phenotypic differences among individuals do not matter. Under soft selection, as mentioned above, spatial structure decreases the rate of fixation of new advantageous alleles. In contrast, metapopulation-wide selection against recessive deleterious alleles is

efficient because heterozygosity is low in structured populations (Whitlock, 2004). Consequently, in theory, the effects of inbreeding due to accumulation of deleterious alleles should be low in a metapopulation. However, the efficient loss of recessive deleterious alleles only holds for species living naturally as a metapopulation at equilibrium. Unfortunately, species in fragmented habitats, even if they have characteristics of metapopulations, do show the negative effects of inbreeding (e.g. Saccheri *et al.*, 1998).

In a natural setting, local populations probably do not all experience the same selection. Where selection is heterogeneous, metapopulation structure can either hinder or facilitate evolution. Although genetic variability declines with population structuring, variability among local populations will be higher, and limitations to gene flow can cause genetic differentiation among local populations (Wade and McCauley, 1988) and allow local adaptation. Unsurprisingly, there is quite a lot of empirical evidence that spatial subdivision causes genetic subdivision, and in some cases, local adaptation (Reznick and Ghalambor, 2001). Under some conditions this process could lead to the evolution of new forms via Wright's (1931) 'shifting balance theory of evolution', in which advantageous genetic forms arise, become fixed locally and spread to surrounding local populations (Wade and Goodnight, 1998). **See also:** [Ecological Genetics](#); [Evolution: Shifting Balance Theory](#)

With increasing access to molecular tools, the effect of metapopulation structure on genetics has become more sophisticated, leading to studies of evolution of quantitative traits and whole genome patterns of molecular variation. One relatively new line of research turns the issue around and asks how differences in gene frequencies directly translate to population dynamics. We do not generally think of changes in gene frequencies as directly affecting population sizes (Lande, 1988). Detecting the role of genetic changes in population dynamics is illusive because environmental conditions and demography have large direct effects on population dynamics while effects of genetic differences among individuals are small. However, Hanski and Saccheri (2006) showed that local population growth rate in a butterfly metapopulation was associated with genetic variation of a glycolytic enzyme involved in metabolism (*pgi*). Within the metapopulation, local populations had different growth rates that depended on the locally predominant *pgi* genotype. Thus, genetic differences among local populations affect differences in local population size, and subsequent metapopulation dynamics.

Evolution of Traits Related to Living in a Metapopulation

As discussed above, metapopulation processes affect genetics and the rate of evolution. They also cause evolution of traits associated with living in a metapopulation, particularly those related to dispersal, as well as life history

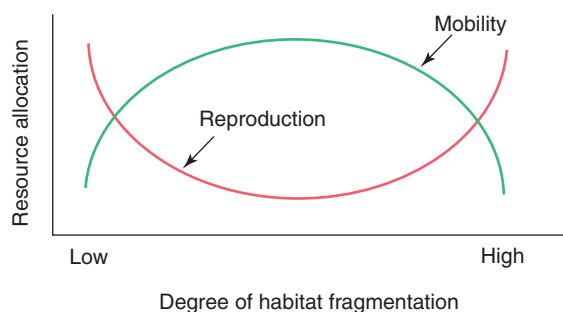


Figure 4 The hypothetical relationship between habitat fragmentation in a metapopulation and the allocation to dispersal (green line) and reproduction (red line). This assumes that mobility comes at a cost to reproduction.

traits such as size, longevity and fecundity. On the one hand, metapopulation structure should lead to the evolution of dispersiveness because mobile colonists found new populations. This might lead to increased allocation of resources to muscles rather than reproduction or storage and to late reproduction, both of which could reduce fecundity. On the other hand, if mortality due to dispersal is high, then species living in a sparse landscape may evolve low dispersal, since mostly sedentary individuals would survive. This could lead to high allocation to reproduction and longevity. However, with that low rate of dispersal the species would also be at risk of extinction. The hypothetical balance between allocation to dispersal and reproduction-related traits in a metapopulation, presuming that one comes at a cost to the other, is illustrated in **Figure 4**. Theoretical models for the evolution of dispersal in metapopulations have addressed rate, cost (directed or random), and motivation for dispersal (e.g. Enfjall and Leimar, 2009; Olivieri *et al.*, 1995; Travis *et al.*, 1999). Understandably there are few empirical studies of evolution associated with migration in metapopulations. One example is work on in the Glanville fritillary butterfly in a fragmented landscape in Finland (Hanski *et al.*, 2006), which strongly suggests the dual evolution of dispersive behaviour in sparsely populated areas and sedentary behaviour where isolated populations are old.

Metacommunity

A metacommunity is a set of local communities that are linked by dispersal, or more broadly, a spatially structured community. In the early 1990s, as ecologists were becoming familiar with the term metapopulation, Hanski and Gilpin (1991) defined a metacommunity as a 'community of metapopulations'. Wilson (1992) used the term to explain the importance of species interactions for community structure. He pointed out that due to chance differences in initial species assemblages, a metacommunity would be built up of local communities that differ in species composition. With a few exceptions (see Holt, 1997), there was little theoretical development metacommunity models

until the 2000s. Leibold *et al.* (2004) formalized four conceptual models to explain metacommunity structure and dynamics: patch dynamics, species sorting, mass effects and neutral. 'Patch dynamics', directly relates to the metapopulation concept, emphasizing local colonization and extinction dynamics and species interactions in a set of similar habitat patches. An ecological concept that is best approached using the patch dynamics scheme is the relationship between landscape structure and food chain length or food web complexity (Holt, 2002). As a landscape becomes increasingly fragmented, higher trophic level species such as top predators decline to extinction before other species do because they experience greater resource depletion, both in terms of total amount of resources, and distances among resource patches. This concept is illustrated using the Glanville fritillary butterfly, *Melitaea cinxia* in **Figure 3**. The butterfly lives as a metapopulation in a fragmented landscape in Finland. Over time the butterfly inhabits between 10% and 26% of the available habitat patches. The wasp *Cotesia melitaearum*, which is a parasitoid of the butterfly, also lives in a metapopulation. For the parasitoid local butterfly populations are the 'habitat patches'. It inhabits 4–21% of them. Note that on average the parasitoid, the higher trophic level species, inhabits a smaller fraction of patches than does the host. More importantly, when the host metapopulation size is small, the parasitoid metapopulation size is even smaller. This is mostly due to the fact that the parasitoid is dispersal-limited and cannot persist in the sparse and rapidly changing host metapopulation (van Nouhuys and Hanski, 2002). Thus, in this community module, the local community varies from a food chain length of one (only the plant) to three (plant, butterfly and parasitoid), depending on landscape structure.

The second conceptual metacommunity model 'species sorting' is based on the concept of ecological niche in a heterogeneous landscape. Assemblages of species occupy habitat patches for which they are most suited (e.g. Cottenie *et al.*, 2003). 'Mass effects' identifies a third model in which mobile species respond to resource quality and amount, and exhibit source-sink dynamics. Migration greatly influences local population size. Finally according to the 'neutral' model all species are equally competitive and suited to each habitat patch, so the assemblage of species in local communities is random. The relative importance of these four schemes in explaining assembly, composition, persistence and invasibility of particular communities is a topic of current research.

Evolution in metacommunities is a new research field. We expect the process of evolution to vary depending on the type of metacommunity structure that predominates in the system. First, the relative roles of natural selection versus genetic drift will differ depending on which structuring process dominates (patch dynamics, species sorting, mass effect/source sink or neutral). For example, according to the mass effects model migration is frequent and both genetic drift and local adaptation are consequently low. Secondly, different traits should be under selection in each

model. If species are sorting among patches of different quality and there is little migration, we expect local adaptation and evolution of local competitive ability. If patch dynamics is the prevailing structuring force, then we are simply contrasting the trajectory of evolution of a species in a metacommunity with its evolution in a metapopulation. On the one hand we expect a low response to selection in a metacommunity because the effects of drift are equivalent to a metapopulation. Furthermore, due to interactions with other species, there are multiple potentially conflicting forces of selection that might constrain evolution. On the other hand, with more species present coevolution may occur, which is considered an efficient route to evolutionary change. The neutral model would have the same pattern of genetic drift as the patch dynamics model, but selection would act equally on each species, making the generation and maintenance species diversity difficult to conceive.

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