

Metapopulation Ecology

Saskya van Nouhuys, *University of Helsinki, Helsinki, Finland*

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Advanced article

Article Contents

- Introduction
- Species Interactions
- History
- Mathematical Models
- Empirical Studies
- Conservation
- Population Genetics
- Evolution of Traits Related to Living in a Metapopulation
- Metacommunity

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A metapopulation is a spatially structured population that persists over time as a set of local populations with limited dispersal between them. At equilibrium, the frequencies of local extinctions and colonisations are in balance. Starting in 1969, and accelerating in the early 1990s, mathematical models of metapopulations have shown the importance of landscape connectivity and dispersal for persistence of a species in fragmented landscapes. Metapopulation ecology is a key concept in conservation ecology. Although pure metapopulations may be rare, there are many empirical studies in which metapopulation processes, primarily local colonisation and extinction, have been useful in explaining dynamics of natural, managed and experimental systems. Metapopulation structure also affects population genetics, the rate of evolution, and the evolution of traits related to habitat use. Finally, just as a population can be structured as a metapopulation, communities inhabiting a heterogeneous landscape can form a metacommunity.

Introduction

Virtually all species live in populations with some degree of spatial structure along a continuum from multiple discrete populations that are completely independent of one another to a single large well-mixed population. A metapopulation lies between these two extremes and is made up of a set of weakly interacting

local populations, a population of populations (Figure 1). While 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 colonisations and extinctions. The concept of a metapopulation should simplify our understanding of the overall persistence of spatially structured populations, as well as their genetic structure and potential for evolutionary change.

A species with a metapopulation structure lives in a 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 characterise metapopulations: (1) frequent local extinction and (2) long-term survival of the metapopulation being dependent on colonisation 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 in the long run. Such a metapopulation only persists over long times because of a balance between local extinctions and colonisations, always with the possibility that by chance, all local populations could go extinct simultaneously and then the metapopulation itself would become extinct (Hanski, 1998).

A classic example of a metapopulation is that of the Glanville fritillary butterfly in the Åland archipelago in Finland. The landscape the butterfly inhabits is made up of about 4000 small patches of suitable habitat in an unsuitable matrix. In any one year, the butterfly occupies about 400 habitat patches with, on average, a balanced number of local extinctions and colonisations annually (Hanski, 2011). The spatial population dynamics have been studied using mark-recapture studies, long-term survey and modelling. It is known that the persistence and size of the metapopulation depends on the dispersal ability of the butterfly, the configurations of suitable habitat patches in the landscape and the degree of synchrony in changes of population size over time. It is also known that the butterfly has evolved on a fine scale in response to the degree of fragmentation of the landscape (summarised in Ojanen *et al.*, 2013). There are other natural (Elmhagen and Angerbjörn, 2001) and experimental systems (Janssen *et al.*, 1997) that fit most aspects of a classical metapopulation. However, in the strict form, metapopulations are rare in nature

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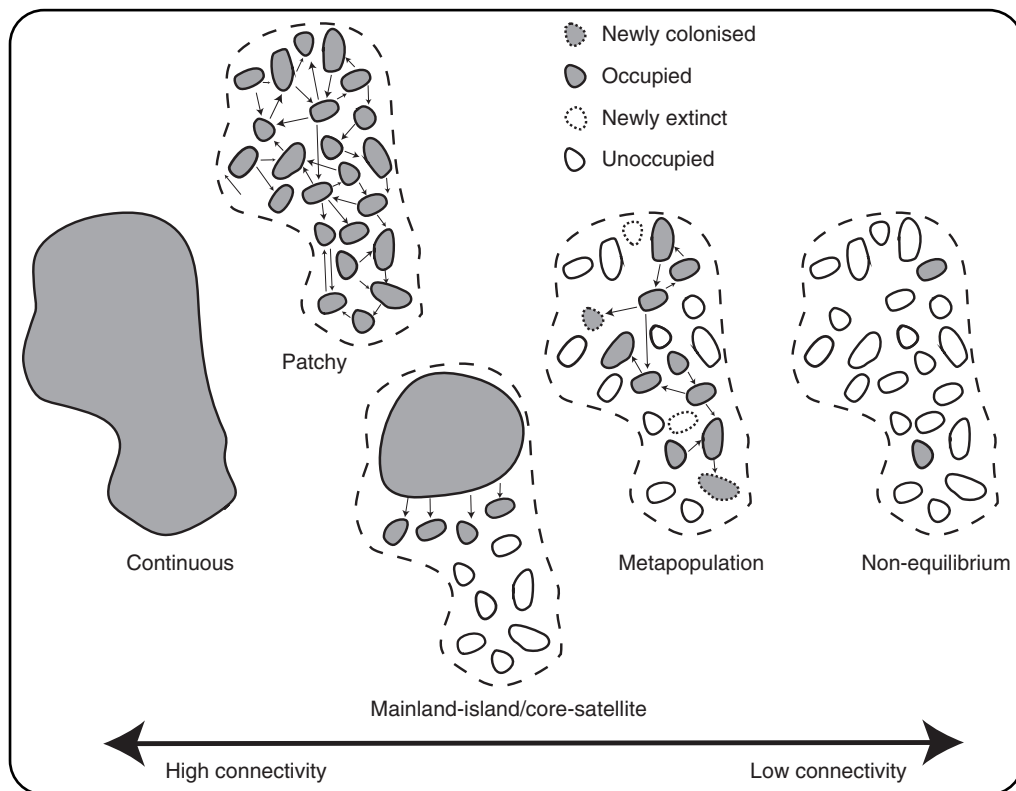


Figure 1 Illustration of the continuum of population structure.

and may represent a transitional state between a larger continuous population and decline to regional extinction (Fronhofer *et al.*, 2012). Nonetheless metapopulation processes have significant roles for 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 in response to habitat fragmentation (Boughton, 1999), or disease (Stapp *et al.*, 2004). Further, the concept is important for understanding the impact of habitat fragmentation on decreasing biodiversity and in designing conservation efforts. **See also: Strategies of Reserve Selection**

Species Interactions

Just as the persistence of a species may be governed by metapopulation processes, so may the outcome of species interactions. Antagonists, such as a predator and its prey or competitors, can persist in a landscape through metapopulation dynamics. This is because newly colonised patches may be refuges for a species that has been excluded, by predation or competition, from other patches. The dispersal ability that allows this refuge effect is often considered to come as a trade-off with local competitive or foraging ability. In competitive interactions, the less competitive species persists in the metapopulation by being mobile and colonising new patches. This trade-off is well established

theoretically (Holt, 1997) and has been observed to occur among competing species (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 metapopulations (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) analysed the dynamics of whooping cough (pertussis) and measles before and after the initiation of vaccination in the United Kingdom. The susceptible people 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 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 population, measles became

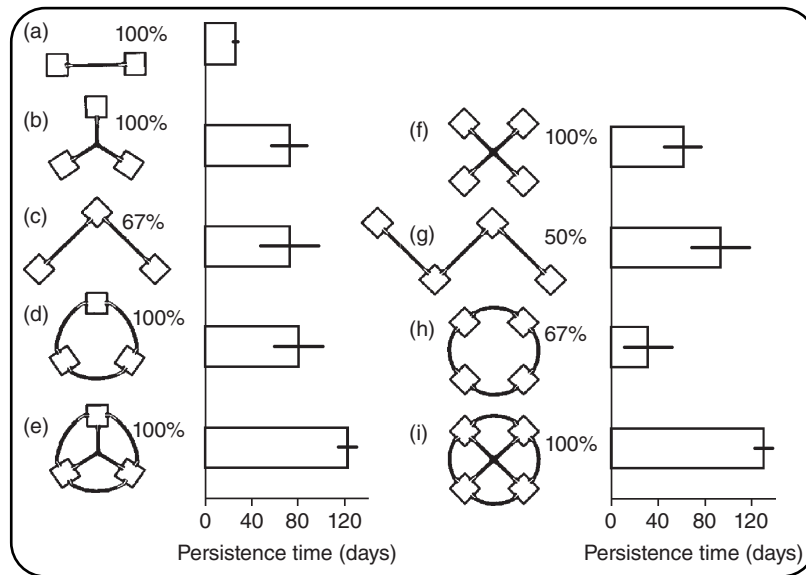


Figure 2 A schematic drawing of the arrangement of microcosms and the mean number of days that a predator population persisted. The percentage values beside each array show the connectedness of the bottles as the mean percentage of other bottles directly connected by tubes averaged across all bottles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

spatially uncorrelated and irregular (as a metapopulation), while whooping cough became spatially and temporally correlated. See also: [Dispersal: Biogeography; Population Biology of Plant Pathogens](#)

History

The term ‘metapopulation’ was first used by Levins (1969). However, the concept of population dynamics taking the form of frequent local extinctions and colonisations in a landscape was discussed several decades earlier in the fields of population genetics (Wright, 1931) and population ecology (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 inhabiting an island. Small isolated islands support small communities both because colonisation 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 from island biogeography because metapopulations lack a stable ‘mainland’ source population. Therefore, the ‘species pool’ available in a fragmented landscape is less than in a hypothetical mainland-island system (Hanski, 2013). Since the early 1990s, the term metapopulation has continued to increase in use and has progressively been applied more broadly.

Mathematical Models

Mathematical models of metapopulations have been developing over the past five decades to explore theoretical features of spatial population dynamics, and as practical tools for making land-use management decisions and studies of disease epidemiology. Initially, these models were deterministic, with probabilities of colonisation and extinction of local populations only appearing in a deterministic average sense. Levins (1969) formulated the rate of change of the fraction of habitat patches occupied by a species in a landscape (p). He used 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 ,

$$\frac{dp}{dt} = cp(1-p)ep$$

Here, c is the rate constant for colonisation of empty patches and e the rate constant for extinction of local populations. Levins’ model includes an intrinsic exponential growth rate cp for colonisation as well as a term that inhibits growth once the metapopulation is large ($-cp^2$) with few available sites left to colonise. Colonisation is the result of immigration from neighbouring populations. In a real population the rate of colonisation, c , 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 with the probability e of extinction of each patch being independent. These extinctions 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 that, 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 colonisation ($cp^*(1 - p^*)$) are equal. **See also: Population Dynamics: Introduction**

Some early metapopulation models added 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, because sites that go extinct are immediately recolonised owing to 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 colonised than a small one as modelled by Hastings and Wolin (1989). The persistence of interacting species has also been modelled using a general form of Levins model, starting with 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 due to stochastic deviations from a stable equilibrium is possible. In the stochastic patch occupancy models below, a patch is occupied if it has been colonised 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 colonisation of a given patch is determined by how well the patch is connected to other patches. Each patch has connectivity that is determined by its distance from all the other occupied patches and the areas of those occupied patches. The area of an occupied patch is used as a proxy for the local population size. A given patch's connectivity also depends on a characteristic species-specific dispersal distance d . For example, the probability of one occupied site causing the colonisation 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. 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 require direct measure of population size, which is often unknown in practice.

Models in a third class are 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 (Adler and Nuernberger, 1994). Such models have the benefit that some features of the metapopulation can be

extracted without a host of simulations. Related Bayesian models have also been developed to increase the accuracy of population viability analysis by, for instance, allowing local extinction and colonisation probabilities to change due to habitat change (Heard *et al.*, 2013), or within-patch dynamics (Smith *et al.*, 2014).

Another class of metapopulation models is individual- or agent-based models in which behaviour of each individual animal, plant or seed is modelled (Uchmański, 2016). All manner of plausible behaviours can be included in these models, with the disadvantage of large numbers of possibly unknown parameters and computationally intense simulations. Diffusion models, in which population density is considered as a continuous function of position and time that evolves according to deterministic rules, lie between the models that track individuals and those that track only patch occupancy. For more information about these see **Individual-based Models in Population Ecology**

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 quantify. For similar reasons, microbial species have been used for experimental studies. Long-lived species, such as trees, are challenging because their population dynamics are so slow; local extinctions and colonisations are not easily recorded if the generation time is many decades. 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 colonisation or extinction. Finally, species that are very mobile, migratory or live in superficially continuous habitat, such as oceans, may be subject to the basic metapopulation processes but in ways that are hard to recognise or quantify.

Rapid anthropogenic landscape change is a source of mismatch between present landscape structure and observed population distribution and size. Depending on the rate of local colonisations 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 recolonised. 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. Similarly, while some animals may appear not to be suffering greatly from habitat fragmentation, they undoubtedly are, but the effect may only be apparent in the short term under extreme conditions (Pardini *et al.*, 2010). The temporal mismatch of the prevalence of species living in a landscape and the level of fragmentation of that landscape is called 'extinction debt'. It occurs when species are still present in a degraded landscape, even in high numbers, but the habitat has declined so that it is unsuitable for persistence over a long time (Hanski, 2013).

The majority of empirical studies of metapopulation processes are concerned with a single species, but there are also studies of persistent antagonistic species interactions that depend on metapopulation processes. These have mostly been approached experimentally. For instance, protist microcosms (Fukumori *et al.*, 2015), herbivorous and predatory mites on bean plants (McCauley *et al.*, 2000) and a beetle and a parasitoid in a series of cages (Bull *et al.*, 2007) 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, including disease dynamics (Borer *et al.*, 2016). Metapopulation dynamics can also play a role in species interactions that are not antagonistic. van Nouhuys and Laine (2008) describe an indirect interaction that is positive rather than adversary. They suggest, on the basis of long-term survey data on the occurrence of a plant, phytopathogen, herbivore and parasitoid, that metapopulation dynamics of a parasitoid are facilitated by metapopulation dynamics of a phytopathogen. Local herbivore populations that share a habitat patch with the plant pathogen are more likely to be colonised by the parasitoid wasps than those without the plant pathogen. This facilitation probably occurs because the phytopathogen causes the parasitoid population to have a female-biased sex ratio, which increases the parasitoids ability to found new local populations.

Conservation

A main mechanism behind the global loss of biodiversity is through habitat fragmentation. Metapopulation processes are central to the persistence of species in fragmented landscapes. Metapopulation concepts also underpin methods of species conservation and restoration, such as reserve design. **See also:** [Convention on Biological Diversity](#)

Habitat fragmentation and global change

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 the rate of local extinction exceeds the rate of local colonisation. A minimum or threshold patch network size is necessary for persistence of many types of organisms, which leads to the generalisations 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. Range expansion, which depends on rates of local colonisations and extinctions of new habitat patches (Holt and Keitt, 2000) as well as range contraction, can be metapopulation processes. In addition, environmental change may alter the rate of local colonisation or extinction by reducing the quality or

changing the phenology of individuals (Parmesan, 2006) which then changes the size or stability of the metapopulation.

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), as has the role of corridors in facilitating dispersal among conserved areas. Reserve design that is based in metapopulation ecology emphasises 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. 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 population subdivision. 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. In contrast, in metapopulations, there is extinction and colonisation of local populations in the landscape. Slatkin (1977) first combined metapopulation and population genetics models to address effects of colonisation–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 species. 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 colonisation 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). **See also:** [Effective Population Size](#). 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 can lower 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 (Whitlock, 2004).

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 generally show the negative effects of inbreeding (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 within populations declines with population structuring, variability among local populations will be higher and limitations to gene flow can cause genetic differentiation among local populations promoting local adaptation (Wade and McCauley, 1988). See also: **Ecological Genetics; Evolution: Shifting Balance Theory**

With increasing access to molecular tools and the development of genomics, the study of evolution in metapopulations has become more sophisticated, leading to studies of evolution of particular genes or gene groups, quantitative traits or whole-genome patterns of 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. 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, at least on a short time scale. 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 the 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 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. For example, 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 should evolve low dispersal, as 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 in an unstable environment. 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 3**. Theoretical models for the evolution of dispersal in metapopulations have addressed rate, cost, type (directed or random) and motivation for dispersal (Berdahl *et al.*, 2015). Understandably there are few empirical studies of evolution of traits related to living 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. In contrast, a recent experimental study using the herbivorous mite, *Tetranychus urticae*, found that life history traits, including lifespan, size and fecundity evolved in response to habitat patch size and connectivity, but dispersal did not (De Roissart *et al.*, 2016).

Metacommunity

Strong paired interactions between species, such as predator–prey dynamics and the coexistence of competitors, have generally

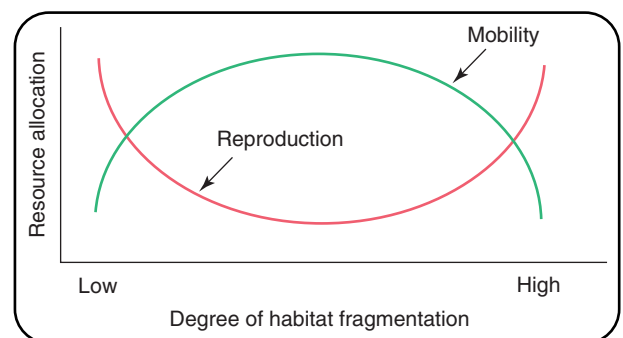


Figure 3 The hypothetical relationship between habitat fragmentation in a metapopulation and the allocation to dispersal (green line) and reproduction (red line). This assumes that mobility comes at a cost to reproduction.

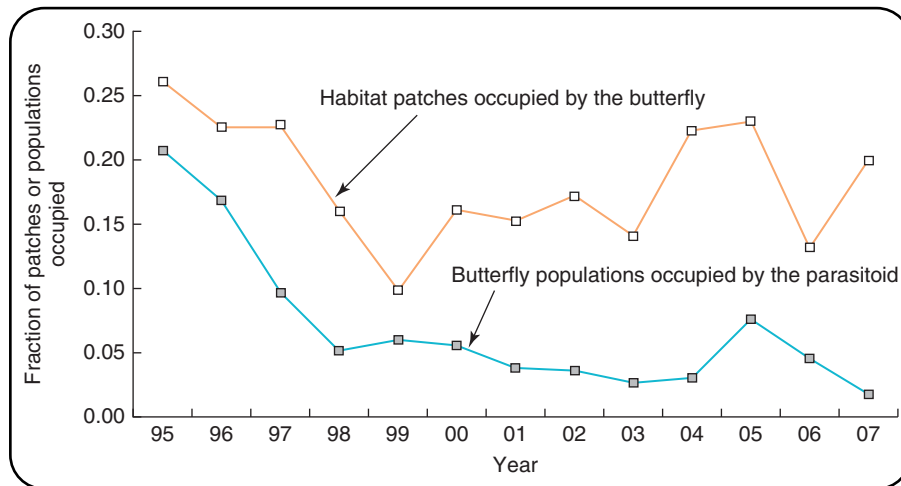


Figure 4 The metapopulation dynamics of the butterfly *Melitaea cinxia* and the parasitoid *Cotesia melitaeorum* in the Åland islands from 1995 to 2007. The fraction of habitat patches occupied by the butterfly *M. cinxia* (orange line) is always greater than the fraction of local host populations occupied by the parasitoid (blue line). A subset of these data is presented in van Nouhuys and Hanski (2002).

been approached from a metapopulation perspective (Holt, 1997). Larger sets of cooccurring species that may or may not directly interact in a heterogeneous landscape are considered a metacommunity. A metacommunity is thus a set of local communities that are linked by dispersal, or more broadly, a spatially structured community. **See also: Metacommunities: Spatial Community Ecology.** 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 owing 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 (Holt, 1997), there was little theoretical development of metacommunity models until the 2000s. Leibold *et al.* (2004) formalised 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, emphasising local colonisation 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, even 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 (Fahrig, 2003). This concept is illustrated again using the Glanville fritillary butterfly, *Melitaea cinxia*, **Figure 4**. The butterfly lives as a metapopulation in a fragmented landscape in Finland. Over time, the butterfly inhabits between 10% and 26% of the ~4000 available habitat patches (Hanski, 2011). The wasp *Cotesia melitaeorum*, which is a specialist 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. Thus, 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 (Holt, 1997; van Nouhuys and Hanski, 2002).

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 (Cottenie *et al.*, 2003). ‘Mass effects’ identifies a third model in which 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 much current research. Evolution in metacommunities is a relatively new research field. We expect the process of evolution to vary depending on the type of metacommunity structure that predominates in the system (Urban *et al.*, 2008).

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