Epiphyte metacommunity dynamics

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Contents

Part 1: Metapopulation dynamics

1.1 What are metapopulations?

A metapopulation consists of several local populations that are connected by immigration and emigration movements (Hanski and Simberloff 1997). Each local population consists of individuals that interact with each other, and that occupy a habitat patch that is surrounded by a hostile matrix (Hanski and Gilpin 1991; Hanski 1999).

To describe an ecological concept it is important to first define the scale at which the dynamics of the system takes place. Hanski and Gilpin (1991) distinguish between three spatial scales when talking about metapopulations: the local scale with local population dynamics, the metapopulation scale with interaction between populations, and the geographical scale which is the geographical range over which the species exists.

Factors and processes that influence the dynamics of a local population include interactions within and between species, density dependent processes, migration movements, genetic, environmental and regional stochasticity, historical effects, and abiotic conditions (e.g. Begon et al. 1986). In a metapopulation network local population dynamics also affect the dynamics of other populations of the same species (metapopulations in e.g. Hanski 1999) as well as the community as a whole (metacommunities in e.g. Leibold et al. 2004). In addition, there are several factors and processes that are of importance for the spatial dynamics in a metapopulation, as they influence the spatial arrangement and connectivity of local populations in relation to each other. Examples are landscape fragmentation and species dispersal strategies (Hanski 1999).

Habitat patches differ in size, quality, and degree of isolation from each other. According to the metapopulation theory a habitat patch is big enough for a local breeding population (Hanski 1999). This means that the scale of a habitat patch depends on the species, and that metapopulations of different species occur on many different scales in the landscape. Examples of habitat patches include meadows for butterfly populations, forest fragments for bird populations, trees for epiphytic species, islands in lakes for small mammals, and ponds for frog populations (e.g. Sjögren Gulve 1994; Hanski 1999; Snäll et al. 2005a). They can be “true” islands that lie in a hostile matrix, such as oceanic islands or trees in a forest, or they can be the remnants of a previous continuous landscape such as fragmented forest landscapes. Patches can have a limited life-span due to natural succession (Hastings 2003; Snäll et al. 2003), or they can become unsuitable for some time as a result of changed local conditions (Thomas 1994). Habitat patches can be created by conservation actions such as set-asides of semi-natural grasslands, or by increasing a biotope area. New patches can be created by natural succession such as dead wood habitats for saproxylic species, the growth of new trees, or by landscape succession such as small forests clearings (Hanski 1999). However, not all organisms live in such relatively clearly defined habitat patches, and the metapopulation concept can therefore not be applied to all species (see 2.1; Hanski 1998; Murphy and Lovett-Doust 2004).

Metapopulation ecology is closely related to the field of landscape ecology, and it is difficult to clearly separate the two. Both disciplines deal with spatial ecology as they are concerned with the effects of spatial structures (such as landscape features) on population dynamics and ecological interactions. The spatial structure of a landscape is thought to influence local populations in a similar way as demographic rates (births and deaths) and species interactions (e.g. competition and predation) (Hanski 1998). The dynamics of populations are affected by the heterogeneity of space. This is different from other ecological approaches where the landscape is simplified as a homogenous continuous or discrete space (Hanski and Gilpin 1991; Hanski 1998). Both, the metapopulation and the landscape ecology disciplines assume that a species occupies certain habitat patches that are surrounded by a hostile matrix. The matrix may facilitate or hinder movements between patches even though it is a hostile environment for the species to live in. While landscape ecologists focus on consequences that landscape composition and spatial arrangements have on abiotic and biotic ecological processes (Murphy and Lovett-Doust 2004), metapopulation ecologists concentrate on colonizations and extinctions of populations in spatially structured habitats (Hanski 1999).

Different authors use terms in different ways, and in the following I define a number of terms that I use throughout the text. A habitat patch can be either occupied (1) or unoccupied (0). It becomes colonized if the patch occupancy changes from 0 to 1, and it becomes extinct if the occupancy changes from 1 to 0. The latter is also referred to as local extinction, in comparison to species extinction in which the whole metapopulation disappears. Colonizations and extinctions, hence, describe changes in occupancy, i.e. dynamics, while occupancy describes a distribution pattern. A metapopulation consists of several local populations that occupy habitat patches in a landscape in which there may be unoccupied habitat patches. In scientific studies a habitat patch is often identified based on species knowledge. It is assumed that unoccupied habitat patches are suitable for colonization. The term “suitable” habitat patch refers to a habitat patch for which the observer cannot identify any feature that hinders colonization. In comparison, an “unsuitable” habitat patch has a feature that prevents it from becoming colonized.

In a typical viable metapopulation habitat patches undergo colonizations, extinctions, and re-colonization events over time (Levins 1969; Hanski 1999). Local extinctions can have deterministic or stochastic causes (Hanski 1998). If the number of local colonization and extinction events is equal in the long term (no change in number of occupied patches over time) the population is said to be in equilibrium. A population is presumed to be viable if local extinctions do not exceed colonizations (Hanski 1999). Species extinctions, in comparison to local extinctions, have been shown to depend on deterministic causes such as human predation, introduction of new species, and habitat alteration, with stochastic extinctions playing only a very small role (Thomas 1994). Thomas (1994) argues that for the long-term persistence of a metapopulation the availability of suitable habitat patches is more important than the effects of local demographic and environmental stochasticity. Local extinctions may indicate a change in the habitat patch that made it unsuitable. After a local extinction event the habitat patch might therefore remain empty. In such a scenario extinctions are likely to exceed colonizations unless empty suitable patches arise so that colonization can take place. Examples of habitat patches that become unsuitable after some time are disturbance and succession habitats. Thomas suggests that species that are able to track suitable habitat patches for colonizations will persist in the long-term (Thomas 1994). Snäll et al. (2003) coined the term patch-tracking metapopulations. Their model describes populations whose extinction rate is set by the rate of patch destruction. These patch-tracking metapopulations are affected by the natural dynamics of the patches they live on as these patch dynamics lead to dynamics in the occupancy structure of the metapopulation. Compared to Thomas (1994) local extinction events are negligible in these systems. Patch-tracking metapopulations are e.g. formed by epiphytic species. Their dynamics are described in more detail in part 3.

The number of species living in fragmented landscapes, and thus in metapopulation structures, has increased over the past years due to human’s vast impact through habitat destruction and division (e.g. Hanski 1999). Metapopulation models can help to explain habitat patch occupancy patterns and processes, and predict which habitat patches are important for the future persistence of a species (Hanski 1998; Snäll et al. 2005a). This includes investigation of effects of different landscape management scenarios and restoration actions on the long-term persistence of species (Snäll et al. 2005a). The field of metapopulation ecology is therefore an important component in conservation biology.

1.2. Extinction threshold, extinction debt, and metapopulation capacity

As described above, metapopulations undergo local colonization and extinction events, which depend on features that affect local population size (e.g. habitat patch size and quality), habitat patch location in the landscape, and species specific properties (Hanski and Ovaskainen 2002). In Levins' classical metapopulation local colonization and extinction events are assumed to occur at the same rates over time. This means that the metapopulation is at equilibrium, and the species persists in the long-term (Levins 1969). A decrease in habitat quality, habitat patch number, or habitat connectivity disturbs the equilibrium state. In such a scenario local extinctions exceed colonizations and the size of the metapopulation decreases. After some time a new equilibrium point will be reached. This equilibrium point is at lower patch occupancy or it is at extinction (a trivial state) of the metapopulation (Hanski 1998). The smallest habitat patch network that a metapopulation requires in order to persist in the long-term is termed the extinction threshold of the metapopulation (Hanski 1998; Hanski and Ovaskainen 2000).

Species react differently to habitat destruction. The time for a metapopulation to reach a new equilibrium stage after habitat loss depends on three factors (Hanski 2001), (1) the strength of perturbation, (2) species and landscape properties, and the (3) distance of a metapopulation to its extinction threshold. After habitat destruction some metapopulations in the landscape may have passed their extinction threshold. However, a species response to this environmental change may be delayed so that the metapopulation still exists in the landscape. This time delay between habitat destruction and decline of the metapopulation is termed extinction debt (e.g. Tilman et al. 1994; Hanski 1998; Hanski and Ovaskainen 2002). Hanski and Ovaskainen (2002) show that the extinction debt increases the closer the metapopulation had been to its extinction threshold when habitat loss and fragmentation occurred. The reason for this is that in a metapopulation that has been close to its extinction threshold only the largest habitat patches are likely to still exist, and in these big areas the risk for stochastic extinctions is lower. When analysing species in landscapes that have experienced habitat destruction, loss, or fragmentation it should be realized that a population that appears to be viable might in reality already be below its extinction threshold (Hanski and Ovaskainen 2002).

In order to describe how species are influenced by the landscape structure Hanski and Ovaskainen (2000) introduced the term metapopulation capacity (λ_M). It summarizes landscape properties as it describes size, quality, and connectivity of all habitat patches in a metapopulation. The threshold condition for metapopulation persistence is summerized as $\lambda_M > e/c$, with e being extinction rate and c colonization rate. If the metapopulation capacity value decreases so that $\lambda_M \leq e/c$ then a species will have reached or fallen below its extinction threshold.

1.3 The development of metapopulation models

1.3.1 Introduction

The classical metapopulation theory was developed by Richard Levins (Levins 1969), who also coined the term “metapopulation”. A predecessor of this was the theory of island biogeography by MacArthur and Wilson (MacArthur and Wilson 1967). Both theories are useful in understanding basic principles of population dynamics on islands and in fragmented habitats. However, they do not take into account that real landscapes and habitats are diverse, spatially structured, and influenced to various extents by connectivity to each other. Models in which all populations are equally connected are termed ‘spatially implicit’, while in ‘spatially explicit’ models distance dependent migration is taken into account (Hanski 1999). Further development of the metapopulation theory by Hanski and others (e.g. Hanski and Gilpin 1991; Hanski 1998; Hanski and Ovaskainen 2000) has lead to spatially realistic metapopulation models such as the incidence function model (IFM, Hanski 2001). As the name suggests these models assume diverse and structured landscapes, which make them more spatially realistic.

1.3.2 The dynamic theory of island biogeography

The dynamic theory of island biogeography (MacArthur and Wilson 1967) describes the distribution patterns of species communities on oceanic islands, and thus has species number in focus. The model presumes regular migration movements from a permanent mainland population to island habitats of different sizes and distances from the mainland. The number of species on each island depends on the degree of isolation as well as the size of the island. Colonization and extinction are constant parameters, and, due to the constant flow of individuals from the mainland, no island population can become permanently extinct.

1.3.3 Levins' classical metapopulation theory (Levins 1969)

The classical metapopulation theory by Levins has many simplifying assumptions. However, the theory can be used as a basis for more realistic metapopulation theories. The metapopulation in Levins' model occupies an unlimited large network of habitat patches that have the same size. Local populations behave identically and independently from other habitat patches. The risk of extinction is therefore equal for all patches. Colonization events depend on the fraction of unoccupied habitat patches, and migration occurs evenly from all local populations to all unoccupied patches. In comparison to the island biogeography model the focus of this theory is on the proportion of occupied patches by a single species, and not on the number of species at each patch (e.g. Levins 1969; Hanski 1999).

The model can be used to examine the rate of change in metapopulation size. This is measured by looking at the proportion of occupied patches P at time t. The more patches that are occupied the more patches can go extinct, as shown by the linear function for the extinction rate in Fig.1 (after Hanski 1999). Colonization depends on the amount of available patches [1-P], in which 1 equals the total number of patches and P the proportion of occupied patches. During equilibrium the number of occupied patches over time is constant, so that the rate of colonization minus the rate of extinction is zero [$dP/dt = cP(1-P) – eP = 0$]. The equilibrium point can change. E.g., if patches are removed the rate of colonization decreases (Fig.1b), and if the patch area is reduced colonization rates decrease and extinction rates increase (Fig.1c). In turn, if more patches are added (increased density of patches) the rate of colonization will increase, and if the patch area is increased the extinction rate will decrease as larger areas support larger populations. A change in the rates of c or e leads to a new equilibrium point (Fig.1; Hanski 1999).

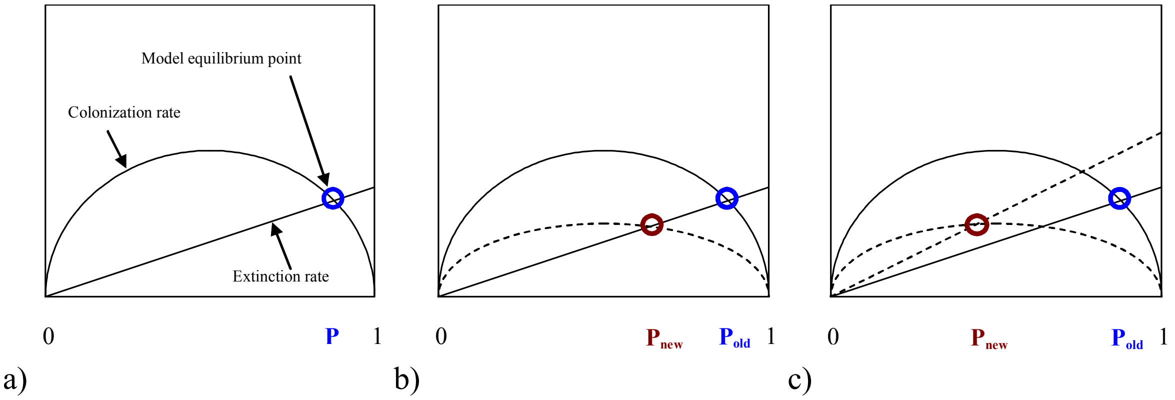

Figure 1. Changes in the equilibrium point as assumed in Levins' model (after Hanski 1999). The illustration shows (a) colonization and extinction rates plotted against the proportion of occupied patches (P), (b) colonization and extinction rates after removal of patches, and (c) colonization and extinction rates after reduction of patch area. Straight line = extinction rate; dashed straight line = increase of extinction rate; parabola = colonization rate; dashed parabola = decreased colonization rate; circle = model equilibrium point.

1.3.4 Spatially realistic metapopulation theory

Spatially realistic metapopulation models account for habitat patch size, habitat quality, and isolation from other patches on metapopulation dynamics. The spatial realistic metapopulation theory is a combination of the dynamic theory of island biogeography and Levins' classical metapopulation theory. Instead of looking at number of species (theory of island biogeography) or at the proportion of occupied patches over time (Levins' model) spatially realistic models predict the state of occupancy for each habitat patch P_i. One model therefore consists of as many equations as there are habitat patches in a given metapopulation. The probability of P_i to be occupied depends on the patch specific colonization rate, c, and extinction rate, e. Variables in the model affect these patch specific colonization and extinction rates. As each patch is looked at separately it is possible to include landscape features such as location, isolation and habitat patch area into the model, and this makes it 'spatially realistic' (Hanski 2001).

1.3.4.2 Incidence function models (IFMs)

Incidence function models assume a finite set of habitat patches as well as differences in habitat patch area and isolation (Hanski 2001). They describe the average long-term probability of a patch to be occupied, which is called 'incidence' (Hanski 1994; Hanski 1998). Each habitat patch P_i can have two possible states – it can be occupied or empty. The probabilities colonization c and extinction e determine changes in these two states of P_i.

1.4 Metacommunities

Similar to metapopulations that consist of a network of local populations, local communities that are connected to each other by dispersal can be defined as metacommunities (Leibold et al. 2004; Holyoak et al. 2005). One specific community can be described as a group of species that share the same habitat location, but that is closed and isolated from other local communities. A habitat location is thought to support a local population or community. Community ecology aims to understand abundance, distribution and interaction of species (Leibold et al. 2004; Holyoak et al. 2005). However, this occurs only on one spatial scale. The concept of metacommunities assumes that direct interactions effecting birth and death rates also happen between communities on a larger scale (Leibold et al. 2004). It is important to distinguish clearly between community dynamics, metapopulation dynamics, and metacommunity dynamics (Figure 2; Holyoak et al. 2005). Metacommunities differ from metapopulations in that they comprise at least two interacting species; and they differ from traditional approaches in community ecology as migration movements as well as interactions between species affect the dynamics of each species group in the metacommunity (Holyoak et al. 2005).

The degree of interaction between species in communities and metacommunities is believed to vary, as well as the effects of these interactions on metapopulation dynamics. If there are no interactions between metapopulations of different species with consequences on the dynamics of these metapopulations there is no sense to analyse a metacommunity. Strong interactions between metapopulations of different species might reveal the dominance of one species over the others. However, even weak interactions between metapopulations of different species could affect their dynamics, which can make it important to analyse these metapopulations as a metacommunity (Holyoak et al. 2005).

Leibold et al. (2004) describe four different metacommunity paradigms that they call ‘patch dynamic’, ‘species sorting’, ‘mass effect’, and ‘neutral’. The authors presume that while all paradigms elaborate on important aspects of metacommunity ecology, in reality species in a metacommunity are not likely to follow the same paradigm. The models differ in their assumptions about the variation among local habitat patches. The patch dynamic and neutral model assume that habitat patches differ in species composition only and not in other variables. In comparison, the mass-effect and species sorting model assume that habitat patches differ in several ways from each other so that they are more or less suitable for different species. Another assumption of the models deals with the variation of species in their traits and in the covariance of several traits, e.g. competitive or dispersal ability. Evolution and biogeography shaped the distribution of various traits and trait combinations, which in turn are thought to effect metacommunity processes (Leibold et al. 2004).

The patch dynamic paradigm assumes a metacommunity with several identical patches. Interspecific interactions and dispersal are thought to influence stochastic and deterministic extinctions. In this model trade-offs between competition and colonization are often found. The species-sorting model focuses on abiotic factors that affect patch occupancy of species at different localities, for example in pond plankton communities. In the mass effect approach dispersal has the main effect on local population dynamics. Patches need to differ in their conditions, and adequate connectivity is required. Habitat corridor experiments that show altered communities due to better connectivity are examples for this paradigm. The neutral paradigm assumes that species do not differ from each other in their niche requirements or dispersal abilities. In order to describe differences locally and regionally this model needs to take other ecological processes such as speciation rates into account (Leibold et al. 2004).

The concept of metapopulation community is still relatively new, and it is not clear if this theory can predict the response of species to habitat fragmentation better than a metapopulation model. Any prediction depends very much on the system in question, as species interactions, spatial structure and dynamics, as well as community interactions are likely to vary in different metacommunities. Furthermore, the metacommunity theory might not be applicable for all communities. Nonetheless, further development could facilitate the explanation of ecological patterns at large scales (Leibold et al. 2004; Holyoak et al. 2005).

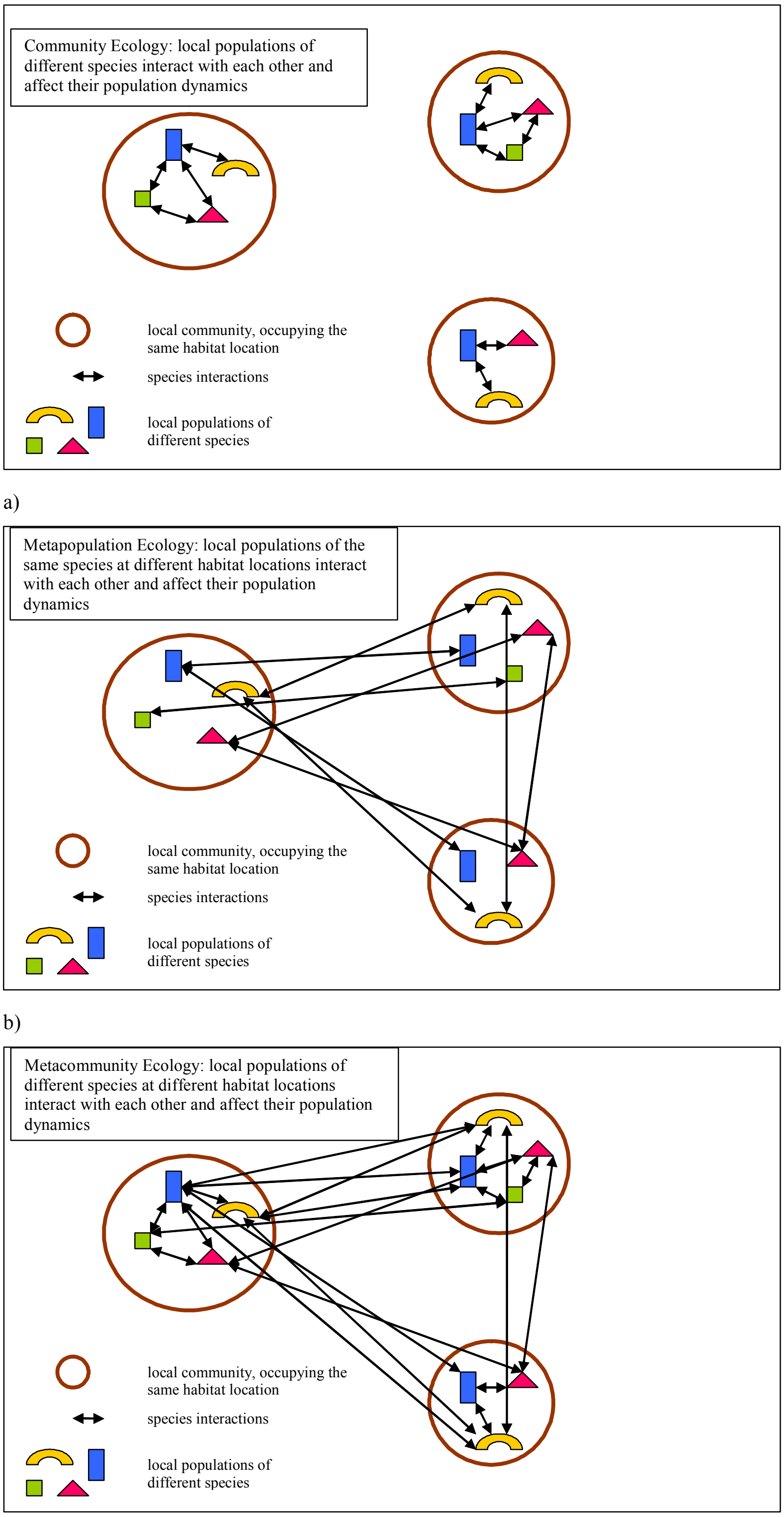

Figure 2. The concepts of community ecology, metapopulation ecology, and metacommunity ecology (after descriptions by Leibold et al. 2004).

Part 2: Applications of metapopulation models

2.1 Introduction

Since Levins developed the metapopulation theory (Levins 1969) there have been many studies of metapopulations, including insect species, mammals, birds, amphibians and plants (e.g. Sjögren Gulve 1994; Hanski et al. 1995; Moilanen et al. 1998; Hanski 1999; Murphy and Lovett-Doust 2004). Some species occur quite obviously in metapopulations as they occupy discrete habitat patches (Hanski 1998), such as the Amerikan Pika (*Ochotona princeps*) (Moilanen et al. 1998) or the Glanville fritillary butterfly (*Melitaea cinxia*) (Hanski et al. 1995). For other species the assumption of a patch network in an unsuitable matrix is a simplification. Some species do not occur in metapopulations at all as the matrix is a sub-optimal habitat, and their population structure is rather continuous in space (Hanski 1998; Murphy and Lovett-Doust 2004).

Metapopulation dynamics have been studied more widely in animal than in plant populations. Some authors (e.g. Murphy and Lovett-Doust 2004) question that plant species occur in metapopulations as for plants a distinction into habitat patch and matrix is often not appropriate. Landscape connectivity plays a different role for plants as they are sessile and their reproductive dispersal abilities depend on e.g. animals or wind as dispersers. However, some plant populations such as epiphytes are clearly confined to certain habitat patches, and can therefore been studied as metapopulations or metacommunities. Their dynamics depend on the dynamics of their patch network (see part 3; e.g. Snäll et al. 2003; Snäll et al. 2005b).

2.2 Examples

2.2.1 Application of the incidence function model to long-term metapopulation dynamics of the American Pika (*Ochotona princeps*).

American Pikas in the Bodie area of California, USA comprise a classical metapopulation (Moilanen et al. 1998). Their local populations occur in distinct habitat patches of broken rock piles within an unsuitable matrix that consists of open sagebrush landscape. Migration movements depend on the varying distance between the habitat patches, there is no “mainland” population, and the size of local populations varies. In general, local population dynamics between patches are assumed to be asynchronous. Patch occupancy data for the American Pika populations have been collected in the Bodie area over 20 years. It became apparent that in one part of the study site the population had declined over this time period while occupancy patterns in the other part remained more or less constant. As no changes in the environment had been observed, Moilanen et al. (1998) used an IFM in order to reveal causes of the decline. The model suggests that regional stochasticity effected colonization-extinction dynamics in the middle and southern parts of the patch network, which decreased the number of occupied patches in these areas. Furthermore, predictions could be made for species performance in particular patch networks. Individual patches were found to contribute differently for long-term persistence of the American Pika metapopulation (Moilanen et al. 1998).

2.2.2 The metapopulation dynamics of the pool frog (*Rana lessonae*)

The metapopulation dynamics of the pool frog (*Rana lessonae*) (Sjögren Gulve 1994) are linked to successional dynamics in the landscape. The pool frog has its northernmost populations in pools of 0.2-2 ha along the Baltic coast in east-central Sweden. Due to the post-Pleistocene land uplift along the Baltic coast new ponds and lakes develop during a time-span of hundreds of years when bays are cut off close to the coast. At the same time shallow inland pools overgrow as a result of natural succession, which leaves larger inland pools isolated. The characteristics of occupied ponds and the pool frog distribution in the landscape suggest that colonization and extinction events can be explained by metapopulation dynamics. Extinctions occur as a result of succession or draining of the pool (deterministic extinctions). It is remarkable that decreasing connectivity due to extinctions of neighbouring pools increased extinction rates even in high-quality habitats. Distance to the next pond as well as warm local climate were found to be important for colonization events, while the presence of predator fish and other chemical water characteristics seemed to have only small or no influence on the distribution pattern of local frog populations. Long-term regional persistence of the pool frog is therefore dependent on patch connectivity as well as on the existence of habitat patches (Sjögren Gulve 1994).

Part 3: Epiphyte metapopulations

Epiphytes are plants or lichens that grow on other living plants. Their habitat patch can be defined as the plant on which they grow. There are obligate and facultative epiphytes. Epiphytic species are not parasitic as they are able to produce carbohydrates by photosynthesis. They need their host plant only as a substrate to attach to. Epiphytes obtain water from the air or from rainwater, and some capture additional nutrients with aerial roots.

Epiphytic species can form metapopulations as their local populations live on discrete habitat patches that are separated from each other by an unsuitable matrix. A local epiphytic population can be defined as all single plants or thalli of the same species occupying the same habitat patch (tree). This is in agreement with the definition by Hanski and Gilpin (1991) (section 1) in which a local population includes all individuals that are likely to interact with each other. Several epiphytic species usually occur on the same habitat, which allows us to classify them as communities (e.g. Lobarion community on *Populus tremula* and *Salix caprea*). Furthermore, the metapopulations of these species within a region can be categorized as a metacommunity (see section 1.4).

As it has been shown in other metapopulations, habitat patch occupancy depends on colonization and extinction rates of the species, which in turn depend on species interactions, dispersal ability of the species, habitat connectivity, habitat patch size, habitat patch quality, and stochastic events. However, an epiphyte metapopulation differs from other above described metapopulations as colonization and extinction events are coupled with habitat patch succession such as tree growth, bark fissure development, bark scaling, and tree death. Because of the link between metapopulation dynamics and habitat patch dynamics epiphytic metapopulation systems are more complex than classical metapopulations. The processes characterizing such an epiphytic patch-tracking metapopulation are shown in Figure 3 (Snäll et al. 2003).

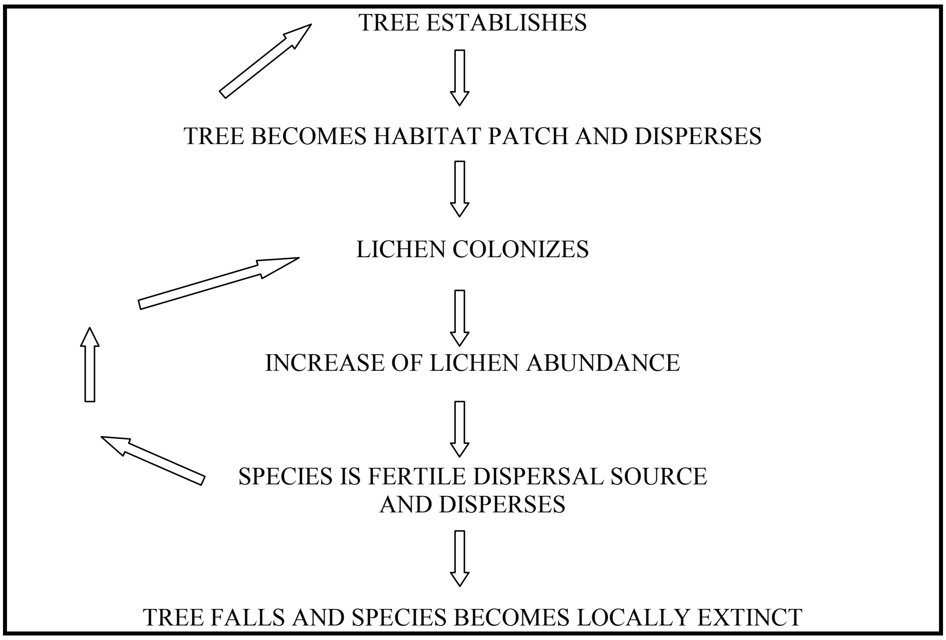

Figure 3. Patch tracking model of a tree-epiphyte system (Snäll et al. 2003).

Epiphytes just as other plant species can be expected to interact with each other in different ways. They compete for habitat space (Kuusinen 1994a), and some species may also alter the habitat so that it becomes more or less suitable for other species (Schöller 1997). However, Löbel et al. (2006) that studied spatial epiphyte structure in bryophytes and lichens found no negative effect on species richness due to the presence of another bryophyte or lichen species.

Reproduction and dispersal in plant or fungi species often depend on wind or animals as dispersers. Size and weight of seeds, spores, or other reproductive propagules are important variables for wind dispersed plants, while food source or attachment to an animal are essential for plants that disperse with the help of animals (Silvertown and Charlesworth 2001). Epiphytic bryophytes and lichens can disperse vegetatively or sexually (e.g. Honegger 1996; Schöller and Mollenhauer 1997; Hedenås et al. 2003; Snäll et al. 2004a; Walser 2004). Sexual dispersal occurs by spores, while asexual dispersal is by asexual fragments or by specialized propagules such as gemmae in bryophytes and soredia and isidia in lichens. Sexual dispersal in lichens has the further complication that lichens are symbiotic. Their spores are derived from the fungal partner (mycobiont), which means that the symbiosis between photobiont(s) and mycobiont needs to be re-established after sexual dispersal (Honegger 1996; Walser 2004).

For metapopulation dynamics the rate and distance of dispersal as well as successful establishment are important as these affect the ability of a metapopulation to survive in the long-term. Measures of the distance of different dispersal strategies and of the genetic variability of epiphytic species within a forest stand and within a landscape might reveal the dispersal ability of a species. This can help in predicting future occupancy and dispersal rates of the species in a landscape.

Walser (2004) showed limited dispersal of vegetative propagules in *Lobaria pulmonaria* and suggested that long-distance dispersal will depend on sexual reproduction. Werth et al. (2006) emphasize that colonization of epiphytic species is the result of two processes, dispersal and establishment. They suggest that the lichen *Lobaria pulmonaria* is not dispersal limited but instead limited by ecological factors at the stand level (establishment limitation). Dispersal limitation has also been suggested for the epiphytic bryophytes *Orthotrichum speciosum* and *O. obtusifolium* (Snäll et al. 2004a), and shown for *Neckera pennata* (Snäll et al. 2005b). Hedenås and Ericson (2000) studied patterns of epiphytic macrolichens in *Populus tremula* stands of different age. They concluded that epiphytic lichens on aspen differed in their dispersal strategy depending on time of colonization. Sexual dispersal strategies dominated among early colonizers while late colonizers dispersed mainly asexually. Hedenås et al. (2003) compared the spatial distribution of sexual and asexual dispersed epiphytes in a forest stand and showed that asexually dispersed species were more common than sexually dispersed species. Furthermore, the spatial pattern of asexually dispersed species reflected the spatial pattern of their host trees, while spore-dispersed species occurred more aggregated than their host trees. The authors suggested that the local distribution of the epiphytes can be explained by their dispersal strategies, and that environmental factors can be neglected in describing their spatial distribution pattern (Hedenås et al. 2003).

Epiphytic species have specific requirements regarding moisture content, acidity, and nutrient conditions in the tree bark (e.g. Kuusinen 1994a; Gustafsson and Eriksson 1995; Löbel et al. 2006) that lead to restrictions to specific host tree species (Schöller 1997). In addition to chemistry and microclimate of the bark, bark structure (including bark fissure depth and roughness) plays also an important role as epiphytes need to attach to the bark (e.g. Kuusinen 1994a,b; Gustafsson and Eriksson 1995; Hedenås et al. 2003; Snäll et al. 2004b; Löbel et al. 2006). Bark structure, in turn, depends on tree species, tree age, and tree diameter. Tree inclination influences moisture content and light conditions on the bark (e.g. Barkman 1958; Kuusinen 1994b). Furthermore, it has been suggested that tree inclination decreases the probability of diaspore flush-off (Snäll et al. 2004b), and increases the abundance of competitive bryophyte species (Snäll et al. 2005b). Branches from neighbouring trees that touch the host tree might affect bark properties due to percolating rain water (Gustafsson and Eriksson 1995). Moreover, local environmental factors such as level of air pollution, soil chemistry, and shading may affect the bark properties of the individual tree, as well as the epiphytes (e.g. Gustafsson and Eriksson 1995; Konttinen 1998; Snäll et al. 2003). Tree diameter and tree age reflect the time available for colonization and the area of available substrate (e.g. Snäll et al. 2003; Snäll et al. 2004b; Snäll et al. 2005b). However, tree diameter is not always positively correlated to species richness (Hedenås and Ericson 2000; Löbel et al. 2006). As described above there are many factors that can contribute to a variation in tree properties within the same species, and it is therefore not surprisingly that microhabitat heterogeneity has been found to explain epiphytic species diversity on trees (Kuusinen 1994b).

Local extinctions have been described to occur frequently in metapopulations as a result of environmental, genetic, or demographic stochasticity, or caused by extrinsic factors such as habitat loss, fragmentation, and species competition (Hanski 1998). It has been suggested that successional changes of the host tree, such as change of bark properties with the ageing of the tree, alters the epiphytic community on the tree over time (Löbel et al. 2006). Bark scaling is thought to be a disturbance factor which increases habitat heterogeneity (Kuusinen 1994b). Different tree species vary in quantity and rate of bark scaling. Trees with a high scaling rate have a relatively species-poor epiphytic flora compared to trees with a more stable bark. It has been suggested that some scaling can lead to high biodiversity as strong competitors are removed and fast colonizers replace them (Kuusinen 1994b). However, the only study on extinction events of an epiphytic species showed that tree mortality was the main reason for local extinctions (Snäll et al. 2005b). This implies that stochastic events which usually result in local extinction events in classic metapopulations, followed by new colonizations (Hanski 1998), can possibly be neglected in the long-term prediction of epiphytic patch-tracking metapopulations (Snäll et al. 2005b).

Several factors affecting epiphytic species interactions (e.g. Kuusinen 1994a; Schöller 1997), species specific reproduction, and dispersal strategies (e.g. Schöller and Mollenhauer 1997; Hedenås et al. 2003; Snäll et al. 2004a; Wagner et al. 2006), and abiotic habitat requirements (e.g. Barkman 1958; Kuusinen 1994b,b; Gustafsson and Eriksson 1995; Schöller 1997; Hedenås and Ericson 2000), have been studied empirically for some time. However, the dynamics of epiphytic metapopulations and metacommunities have not been studied widely (but see Snäll et al. 2005b).

Since the patches for epiphytes are dynamic, epiphyte metapopulations require formation of new habitat patches for their long-term persistence. In a natural forest system pioneer trees establish after disturbances due to fire, windfall, or other gap dynamics. Studies of forest stands of different age suggest a change in the epiphytic community over time (Hedenås and Ericson 2000). Different light conditions during forest succession have been suggested to explain these patterns. Many pioneer lichens can be assumed to be adapted to high light intensities, while late-successional species prefer shady habitats (Hedenås and Ericson 2000). This is of importance for metapopulation dynamics as it has been observed that some late-successional species do not colonize younger trees very frequently, even if the dispersal distance is short (Hedenås and Ericson 2000). For a species to persist in a patch-tracking metapopulation, in general, the moment of its maturity for dispersal must co-occur with the availability of a patch at a suitable successional stage at a reachable distance. It can be assumed that slow growth and dispersal rates of epiphytic species means that they do not tolerate short rotational periods and large distances between suitable habitats. Epiphytic species might have reached their extinction threshold already in many landscapes, and currently only occur as part of an extinction debt. This could be the case if there are no new or suitable habitat patches in proximity for an epiphytic species to colonize, as colonization of new patches is more likely the closer a habitat patch lies to a possible dispersal source (e.g. Snäll et al. 2005b). Under such a scenario the species disappear from the last forest stand once the last occupied trees dies. Forest management practices influence the long-term survival of epiphytes as they determine the diversity of tree age and tree species (e.g. broad-leaf vs. coniferous) in the forests. Grazers and browsers like roe deer and moose might also negatively effect the establishment of tree habitat patches such as the keystone species *Populus tremula* and *Salix caprea* in boreal forest landscapes.

To summarize, based on previous research several assumptions can be made for epiphytic metapopulations: (1) Colonization and extinction events of epiphytic local populations are coupled with habitat patch dynamics, (2) local environmental factors, species dispersal and establishment abilities, and connectivity to occupied habitat patches affect colonization rates of habitat patches, (3) patch destruction (natural or anthropogenic), not stochasticity related to small local population size, is the main factor affecting local extinction rates.

The main focus of prior studies on epiphytes was on the pattern, not on the dynamics of epiphytic species, with the exception of Snäll et al. (2005b). Important questions to answer now are how previously studied variables affect the dynamics of epiphytic species. These variables include dispersal distance of epiphytic species, their growth rate and age of reproductive activity, environmental factors that affect local extinction and colonization rates, species interactions within the metacommunity (e.g. competition and facilitation), effects of other species on epiphyte dispersal, and genetic variability of the epiphytes within a region. It is also of interest whether environmental factors or dispersal factors are most important for colonization as this will influence possible conservation measures. Further research could focus on revealing some of the factors that affect local extinction and colonization rates. Moreover, establishment probabilities under different environmental conditions, growth rate, and age of reproductive activity, need to be tested in the field. Studies on species interactions within epiphyte metapopulations and metacommunities could add useful information. Furthermore, genetic analysis of epiphyte species within a region could be used to estimate their dispersal kernel. Further modelling of epiphyte dynamics in relation to the patch dynamics of their host trees could give insight to species extinction risks under different forest management scenarios on different time scales, and therefore contribute to the long-term conservation of these species.

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