Distribution and Persistence of Epiphyte Metapopulations in Dynamic Landscapes

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Cover: An oak landscape in the county of Östergötland.
    (photo: V. Johansson)

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Abstract

Habitat loss is a major cause of species extinction. Old trees have declined, and this continues because of poor management. Examples are development of secondary woodland in semi-open grasslands, and lack of natural tree regeneration. We therefore can expect that species associated with old tree are declining. The aim of this thesis is to increase the understanding about the habitat requirements, colonization-extinction dynamics and persistence of oak-associated epiphytic lichens with different traits. For species with slow dynamics, data on colonization and extinction events are time consuming to collect. We instead fitted Bayesian incidence function models extended to dynamic landscapes to snapshot data of our study species. The results show that all species were restricted to old trees, but the lower age limit when oaks become suitable differed among species. Colonization rates were generally low and explained by connectivity to surrounding occupied trees, in accordance with metapopulation theory. The colonization rates were higher for species with wide niches (colonizing relatively young trees) and small dispersal propagules than for species with narrow niches (only colonizing old trees) or large dispersal propagules. Stochastic extinctions from intact trees were negligible in all study species, and thus, the extinction rate is set by the tree fall rate, which is low, as oaks become old. By using oak surveys from 1830 and 2009 from a landscape where oaks have declined drastically short after 1830, we show that epiphyte occurrence patterns are better explained by the historical configuration of oaks compared to the present configuration. This indicate non-equilibrium occurrence patterns 180 years after habitat decline, and simulations using the fitted metapopulation models suggest even longer time-lags before new equilibriums are reached. The metapopulation extinction risk increased with decreasing habitat amount, and was highest for species with narrow niches or large dispersal propagules (i.e. low colonization rates). Conservation actions in landscapes with a low density of old oaks had only minor effects on epiphyte persistence, while actions in landscapes with many old but few young trees may increase species persistence. The best conservation approach for the long-term persistence of all species is to assure a constant tree regeneration in landscapes with currently high densities of old oaks.

Keywords: Colonization-extinction dynamics, Connectivity, Extinction debt, Historical landscape, Lichens, Oak, Tree age

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I   Victor Johansson, Tord Snäll, Per Johansson and Thomas Ranius (2010). Detection probability and abundance estimation of epiphytic lichens based on height-limited surveys. *Journal of Vegetation Science* 21, 332-341.

II   Victor Johansson, Thomas Ranius and Tord Snäll (2012). Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology* (in press). http://www.esajournals.org/doi/pdf/10.1890/11-0760.1

III Victor Johansson, Tord Snäll and Thomas Ranius. Estimates of connectivity reveal non-equilibrium epiphyte occurrence patterns almost 180 years after habitat declne (submitted manuscript)

IV   Victor Johansson, Thomas Ranius and Tord Snäll. Epiphyte metapopulation persistence after drastic habitat decline and low tree regeneration: time-lags and effects of conservation actions (manuscript).

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The contribution of Victor Johansson to the papers included in this thesis was as follows:

I   Main author, field work, and analysis. Design and idea together with Tord Snäll, Per Johansson and Thomas Ranius.

II   Main author, field work, and analysis. Design and idea together with Thomas Ranius and Tord Snäll.

III Main author, field work, and analysis. Design and idea together with Tord Snäll and Thomas Ranius.

IV Main author and analysis. Design and idea together with Thomas Ranius and Tord Snäll.

1 Introduction

1.1 Habitat loss and population extinction

Habitat loss has been identified as a major cause of species declines and extinctions (Brook *et al.*, 2003; Fahrig, 2003). Consequently, threatened species are often associated with declining habitats. However, for many organisms we have a very limited knowledge about their habitat requirements and what determines their colonization-extinction dynamics, which are essential to understand for efficient conservation. For species with slow dynamics, colonization and extinction events are rare and therefore time or resource consuming to assess by direct observations. Instead ecologists may have to make inferences from species distribution patterns. However, collecting species distribution data is associated with errors. There is a risk of not detecting the species when it in fact is present (MacKenzie *et al.*, 2002; Gu & Swihart, 2004). This may have conservational implications, but is rarely evaluated. Moreover, in changing landscapes species distributions are likely to lag behind the habitat change, and are hence not in equilibrium with the current landscape structure. Species extinctions after habitat decline may be delayed, which causes an extinction debt (Tilman *et al.*, 1994). This is a major challenge for conservation (Kuussaari *et al.*, 2009), since the species will go extinct even though the current amount of habitat remains. However, if the non-equilibrium condition is detected before species extinction, it is possible to prevent extinction through conservation actions.

One way to detect non-equilibrium conditions and declining populations is to use data on the historical habitat availability of the species (Kuussaari *et al.*, 2009). The distributions of such species should be better explained by the past rather than by the current landscape structure (e.g. Lindborg & Eriksson, 2004; Helm *et al.*, 2006). However, assessing long-term population viability (Beissinger & McCullough, 2002) and testing species persistence in scenarios

of different management (e.g. Morris & Doak, 2002; Roberge *et al.*, 2011) may require simulations of future colonization-extinction dynamics.

1.2   Metapopulations in dynamic landscapes

The concept of metapopulations has during the latest decades become important in population biology (Hanski & Gilpin, 1997; Hanski & Gaggiotti, 2004). A metapopulation consists of a single species inhabiting a network of spatially separated habitat patches that are connected by dispersal. The key idea of the metapopulation concept is that a species can go locally extinct in a habitat patch, but nevertheless persist at the landscape level as it occurs in other patches. The species can disperse and (re)colonize empty but suitable patches. In spatially realistic metapopulation theory, the colonization rate of a patch is determined by its distance to potential dispersal sources, i.e. to surrounding occupied patches (connectivity henceforth; Hanski, 1999), as an effect of restricted dispersal. The extinction rate is determined by patch size, based on an assumption of increasing population size with increasing patch size (Hanski, 1999). Therefore, the species is more likely to occur in a large and well-connected patch compared to a small and isolated one. The colonization and extinction rates can also be determined by other variables affecting dispersal and population size (Moilanen & Hanski, 1998).

The size of the metapopulation (i.e. the number of occupied patches) depends on the amount, size and spatial configuration of the patches in the network and the species' properties (the metapopulation capacity of the landscape; Hanski & Ovaskainen, 2000). The metapopulation extinction risk increases with decreasing metapopulation size (Hanski, 1999), because colonization rates decrease, and also because smaller metapopulations are more sensitive to synchronous stochasticity in colonization and extinction events (Hanski, 1991).

Metapopulation models can be used to increase our understanding of the colonization-extinction dynamics of populations living in fragmented landscapes (Hanski & Gilpin, 1997; Hanski & Gaggiotti, 2004), and to predict the effects of habitat loss and fragmentation (e.g. Morris & Doak 2002). Early metapopulation models were developed for species living in static patch networks (Levins, 1969; Hanski, 1994), where patches do not change over time. However, many species inhabit dynamic patches where the creation and destruction of patches is likely to affect species' colonization-extinction dynamics (Thomas, 1994; Thomas & Hanski, 1997). For some species, local extinctions due to patch-level stochasticity can even be negligible, and only occur deterministically due to patch destruction (Snäll *et al.*, 2003; Jönsson *et*

al., 2008). Theoretical studies have shown that metapopulation extinction thresholds can be more affected by patch duration than by their spatial configuration (Fahrig, 1992; Keymer *et al.*, 2000; Johst *et al.*, 2011), or even overall patch amount (Keymer *et al.*, 2000). We therefore need to account for the dynamics of the patches when studying and making inferences about colonization and extinction rates of these species.

Methods for fitting metapopulation models have been developed for different types of data: occurrence patterns, i.e. data from only a single survey (snapshot data) as in the classical incidence function model (IFM; Hanski, 1994), data on colonizations and extinctions observed by repeated surveys (Sjögren-Gulve & Ray, 1996), or a combination thereof (ter Braak & Etienne, 2003).

1.3 Colonization-extinction dynamics of sessile species

The colonization-extinction dynamics of most sessile species are poorly understood, but several studies have revealed that the dynamics may be affected by the dynamics of their patches (Verheyen *et al.*, 2004; Snäll *et al.*, 2005a; Jönsson *et al.*, 2008). Sessile species are often long-lived and have slow colonization-extinction dynamics (Ouborg & Eriksson, 2004).

1.3.1 Colonizations

Empirical studies of colonization rates are rare, but connectivity to surrounding occupied patches has been shown to be important (Verheyen *et al.*, 2004; Snäll *et al.*, 2005a; Jönsson *et al.*, 2008), suggesting dispersal limitation of many species in accordance with metapopulation theory (Hanski, 1999). These findings are supported by occurrence pattern data (e.g. Johansson & Ehrlén, 2003; Verheyen *et al.*, 2003a; Snäll *et al.*, 2004b), dispersal propagule trapping (e.g. Nathan *et al.*, 2000; Walser *et al.*, 2001), establishment experiments (e.g. Ehrlén & Eriksson, 2000; Sillett *et al.*, 2000) and spatial genetic structuring (Gehring & Delph, 1999; Snäll *et al.*, 2004a; Walser, 2004).

The ability to colonize unoccupied patches can be expected to be affected by species traits (e.g. Verheyen *et al.*, 2003b). Generalists, with wide niches, should occupy more patches in the landscape, compared to specialists with narrow niches (Brown, 1984). This higher number of occupied patches results in higher connectivity for generalist than for specialists and, thus, according to metapopulation theory (Hanski, 1999), a higher colonization rate. Successful colonization depends on three main processes: production, dispersal and establishment of dispersal propagules. The dispersal propagule size is a key trait in explaining the colonization rate in wind dispersed species, but its

relation to colonization rates is complicated. Decreasing propagule size has been suggested to increase the dispersal range (e.g. Okubo & Levin, 1989; Kimmerer, 1991; Löbel *et al.*, 2009), but decrease the establishment or recruitment (Jakobsson & Eriksson, 2000; Löbel & Rydin, 2010). Ground floor vascular plants with small seeds occur more frequently in young forest than large-seeded species which seemingly colonize later (Verheyen *et al.*, 2003b), and forest species with small seeds have higher colonization rates than species with large seeds (Verheyen *et al.*, 2004). Moreover, there is a trade-off between propagule size and numbers (Jakobsson & Eriksson, 2000), suggesting decreasing establishment or recruitment with increasing numbers. However, increasing numbers of dispersed propagules (emigrants) should also increase the colonization rate.

1.3.2 Extinctions

Local extinctions of sessile organisms can either result from demographic and environmental stochasticity in intact patches, or from destruction of the patches (Snäll *et al.*, 2003). Stochastic extinctions have been shown to be negligible in predicting the metapopulation dynamics of a bryophyte (Snäll *et al.*, 2005a) and of wood-decaying fungi (Jönsson *et al.*, 2008). Instead, local extinctions were driven by deterministic patch destruction. In contrast, stochastic extinctions are relatively common in other sessile organisms (Zartman & Shaw, 2006; Laube & Zotz, 2007; Öckinger & Nilsson, 2010; Caruso *et al.*, 2010; Fedrowitz *et al.*, 2012; Zartman *et al.*, 2012). Evidently, the importance of local stochasticity in determining the extinction rates of sessile organisms varies, and may depend on the stability of the patch.

1.3.3 Modeling slow metapopulation dynamics

A key problem in studying colonization-extinction dynamics of sessile species is their slow dynamics. Data on colonization and extinction events from repeated surveys are, thus, time or resource consuming to collect. Therefore, a model that can be fitted using data from one point in time (snapshot data) is useful. Snäll *et al.*, (2005b), having snapshot data on an epiphyte whose patches are trees, fitted a metapopulation model by simulating the past landscape and metapopulation dynamics, and then selected the set of parameters that best reproduced the current spatial structure of the landscape and the epiphyte. However, this approach requires empirical data on the past dynamics of the landscape. Verheyen *et al.*, (2004) instead extended the incidence function model (IFM; Hanski, 1994) to be applicable on dynamic landscapes by including the age of the patches. This meant adding a temporal dimension to the model, a feature that was lacking in the original IFM. The

model was successfully used to assess colonization-extinction rates of forest plants.

1.4 The tree-epiphyte study system

Epiphytes are sessile organisms (e.g. lichens and bryophytes) that grow upon other living organisms (e.g. trees) without taking nutrients and water from them. The tree-epiphyte system is a good model system to explore dispersal and metapopulation processes of sessile species living in dynamic landscapes (Snäll *et al.*, 2005a; Löbel *et al.*, 2006, 2009; Fedrowitz *et al.*, 2012), as trees are easily defined dynamic patches that emerge, grow and fall, surrounded by an inhospitable matrix (Fig. 1). For other sessile species, such as vascular plants, suitable patches may be more difficult to identify and delimit (Ouborg & Eriksson, 2004; Alexander *et al.*, 2012), which is one of the major criticisms for using the metapopulation framework for these species (Freckleton & Watkinson, 2002).
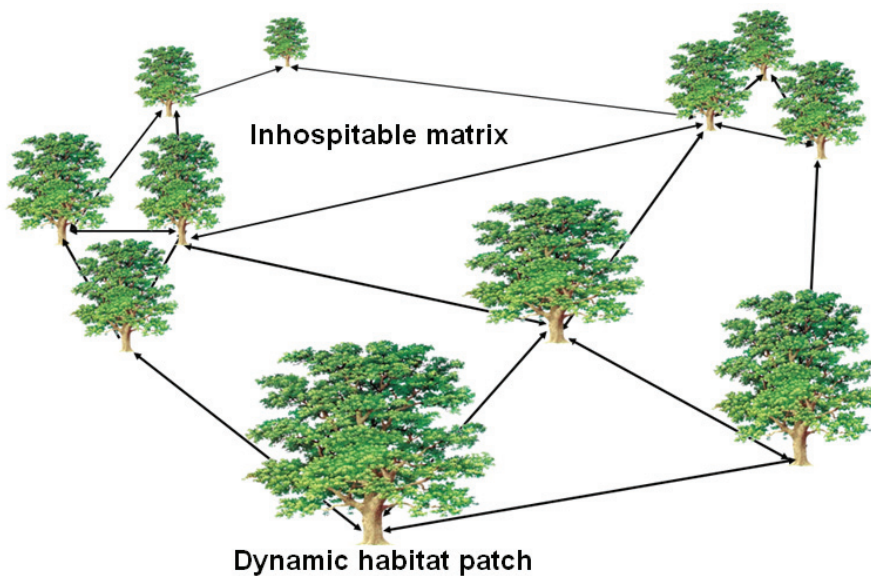

Figure 1. A network of trees (dynamic patches) that emerge, grow and fall, surrounded by an inhospitable matrix. Dispersal is possible between all trees but the number of arrows has been reduced for simplicity.

However, all trees are not suitable patches - epiphytes are often more or less associated with one or a few tree species (Nitare, 2000), and the suitability may also be affected by the surrounding environment and tree specific characteristics (e.g. Snäll *et al.*, 2004b; Löbel *et al.*, 2006). Tree age, or

characteristics correlated to age, has been shown to be very important for explaining the occurrence probability and abundance of many epiphytes (e.g. Gustafsson *et al.*, 1992; Gu *et al.*, 2001; Johansson & Ehrlén, 2003; Ranius *et al.*, 2008b; Fritz, 2009); some species are only found on very old trees, while others may occur also on younger trees. As the tree ages, the abiotic conditions and the substrate suitability changes, and tree age may therefore be a suitable, relatively easily measured niche proxy for many epiphytes.

The lower limit of the niche breadth for an epiphyte can be determined by the age at which its host tree species becomes suitable for colonization. For species that have no upper limit defined by tree age, the lower limit can be used as a proxy for the breadth on one niche dimension. The lower age limit differs among species, and will determine the species-specific number of suitable trees in a network of trees. A specialist, colonizing only old trees (i.e. with a narrow niche), has fewer suitable trees in a landscape compared to a generalist, colonizing also young trees (i.e. with a wide niche), which may affect their colonization rate (1.3.1). Another trait that may affect the colonization rate is dispersal propagule size (1.3.1). Epiphytic lichens and bryophytes may form both sexual (spores) and asexual (fragments or specialized structures) dispersal propagules, of which the latter is generally bigger (Löbel *et al.*, 2009).

Local extinctions of epiphytes may occur stochastically from standing trees or deterministically as trees fall (Snäll *et al.*, 2003; Öckinger & Nilsson, 2010; Fedrowitz *et al.*, 2012), but for some species extinctions from standing trees may be negligible (Snäll *et al.*, 2005a).

1.4.1 Epiphyte surveys

Epiphyte surveys are, for practical reasons, most often restricted to the lowest 2 m of the trunk (e.g. Dettki & Esseen, 1998; Johansson *et al.*, 2007; Nordén *et al.*, 2012). For protruding and easily identified species, this is sometimes complemented by a survey of the rest of the tree using binoculars (Hedenås & Ericson, 2000; Öckinger *et al.*, 2005; Fedrowitz *et al.*, 2012). However, for many species it is unlikely that all occurrences will be detected if only the lowest 2 m of the tree is surveyed (Fritz, 2009). Before interpreting species occurrence patterns from height-limited surveys, knowledge about their vertical distribution is important to judge how well the lowest 2 m represent the whole tree. Species associated with the rough bark of old trees are likely to occur on the lower (oldest) parts of the trunk, while earlier successional species may only be found higher up in the canopy (Hedenås & Ericsson, 2000).

1.4.2 Epiphytes in changing landscapes

Old trees have declined and are still declining due to forest management and changes in agricultural practices (e.g. Nilsson, 1997; Fischer *et al.*, 2010). Consequently, species associated with old trees have declined and are expected to decline in the future (Berg *et al.*, 1994). Today a large proportion of the very old trees are mainly found in remnant old-growth forests and wooded grasslands, and poor management of these fragments may lead to further declines. One example is development of secondary woodland in wooded grasslands, due to abandoned management. This has negative effects on several species and even the vitality of the trees themselves (Kirby *et al.*, 1995; Jönsson *et al.*, 2011; Paltto *et al.*, 2011).

Another widely recognized management problem is the lack of natural tree regeneration due to intensive browsing (Kirby *et al.*, 1995; Harvey & Haber, 1998; Kouki *et al.*, 2004) or the absence of forest-fires (Abrams, 1992). This will eventually decrease the number of old trees, and even if the regeneration would increase there would still be significant gaps in the tree age structure (e.g. Russell & Fowler, 1999; Fischer *et al.*, 2009; Ranius *et al.*, 2009) that species dependent on old trees have to bridge.

Many epiphytes can be expected to have low extinction rates, as trees are relatively long-lived and local extinctions mainly occur by tree fall (patch-tracking metapopulations; sensu Snäll *et al.*, 2003). Therefore, in landscapes where the number of trees has declined recently, epiphyte occurrence patterns will not be in equilibrium with the current landscape structure - species will be more frequent than expected given the landscape structure. Relationships between current epiphyte occurrence patterns and the historical landscape structure have suggested more than century long time-lags (Ellis & Coppins, 2007) in agreement with other sessile species (e.g. Reitalu *et al.*, 2009). However, these studies are based on snapshots of the historical habitat configuration, and hence, we do not know how long time-lags that can be expected before a new equilibrium is reached after habitat decline. Moreover, we do not know how much habitat that is required to support viable populations of species with different traits in the long term. This poses a challenge for their conservation.

1.4.3 Old oaks and crustose lichens

Pendunculate oak (*Quercus robur*) is a key substrate for many epiphytes, fungi and insects (Niklasson & Nilsson, 2005) because it lives longer than most other tree species in Northern Europe (Drobyshev & Niklasson, 2010), and can become over 500 years old.

In Sweden, oaks (including the southwesterly associated *Q. patrea*) were owned by the state from the mid 16th to the beginning of the 19th century (Eliasson, 2002). During this period farmers were not allowed to cut oaks on their own land, which lead to a high density of oaks. However, oaks declined drastically on farmland during the 19th century (Eliasson & Nilsson, 2002). Nevertheless, from a European perspective, Sweden still has rather many old oaks, even though oaks are climatically restricted and almost only occur south of *Limes Norrlandicus*. One of the most oak-rich counties in Sweden is Östergötland (9979 km^2, Fig. 2), which currently has approximately 19 000 oaks with a diameter exceeding 1 m (Claesson & Ek, 2009).

Several crustose lichens depend on the characteristic coarse bark of old oaks (Thor & Arvidsson, 1999). For several of these lichens, a large proportion of the global occurrences have been recorded in south-eastern Sweden (*Global biodiversity information facility*, 2012). Today old oaks are mainly restricted to remnant wooded grasslands and appropriate management of these is therefore essential for the persistence of these lichens. However, several areas with high density of old oaks currently have a poor oak regeneration (Ranius *et al.*, 2009). Moreover, many old oaks are today surrounded by secondary woodland (~15% in a large oak survey in a county in south-eastern Sweden), which show a strong negative relationship to the occurrence of several oak dependent lichens (Paltto *et al.*, 2011). However, these trees have the potential to become suitable patches if the secondary woodland is removed, which is a common restoration action (Read, 2000; Claesson & Ek, 2009).

2 Thesis aim

The general aim of this thesis is to increase our understanding of the habitat requirements, colonization-extinction dynamics and persistence of epiphytic lichens associated with old trees. The specific questions addressed in each paper are:

I   What is the detection probability, and how much is the total abundance underestimated, when lichen surveys are restricted to the lowest 2 m of the trunk? What explains the vertical distribution of epiphytes?

II Are the colonization-extinction dynamics of epiphytic lichens explained by metapopulation theory, i.e. are colonizations explained by connectivity, and are extinctions explained by local population processes or patch dynamics? Are colonization rates explained by species traits (here niche breadth and dispersal propagule size)? What is the relative importance of stochastic and deterministic extinctions?

III Are epiphytic lichens associated with old oaks in equilibrium with the current habitat distribution? Are the epiphyte occurrence patterns best explained by the historical or the present landscape structure? Are species with low colonization rates better explained by the historical landscape structure than species with higher rates?

IV How is persistence of epiphytes with different species traits affected by habitat decline, low tree regeneration and different conservation actions? How long time-lags in epiphyte occupancy can be expected after habitat decline? What are the extinction risks of species with different traits after drastic habitat declines or low tree regeneration? Can conservation actions increase epiphyte persistence?

3 Methods

3.1 Study sites and data collection

The field work was conducted 2007-2009 at three study sites in the county of Östergötland, south-eastern Sweden (Fig. 2).
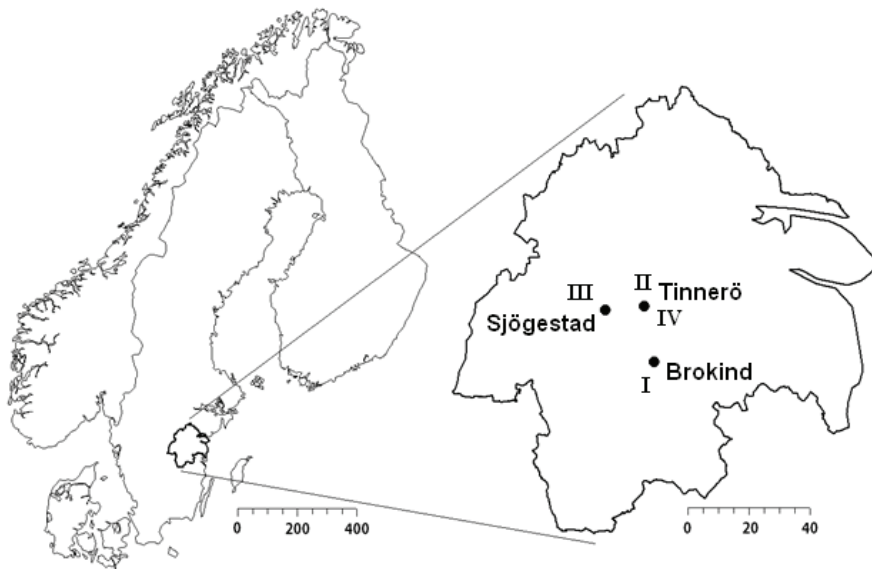

Figure 2. The three study sites in the county of Östergötland, south-eastern Sweden, where the four studies (roman numbers) were conducted. Scale in kilometers.

For Paper I we choose "Brokinds skolhage" (58°12′ N, 15°39′ E), which is a nature reserve with widely spaced oaks, of which a high proportion is old. At this site we randomly selected 35 oaks of varying age (40-435 years). Each tree was divided in vertical segments by attaching ropes from a height of 6 m down

to the ground. These ropes were marked every meter, where each marking constituted corners of plots (Fig. 3), giving a total of 24 plots per tree that covered the whole trunk surface 0-6 m. For each plot we recorded abundance of each study species and potential explanatory variables (Table 1).
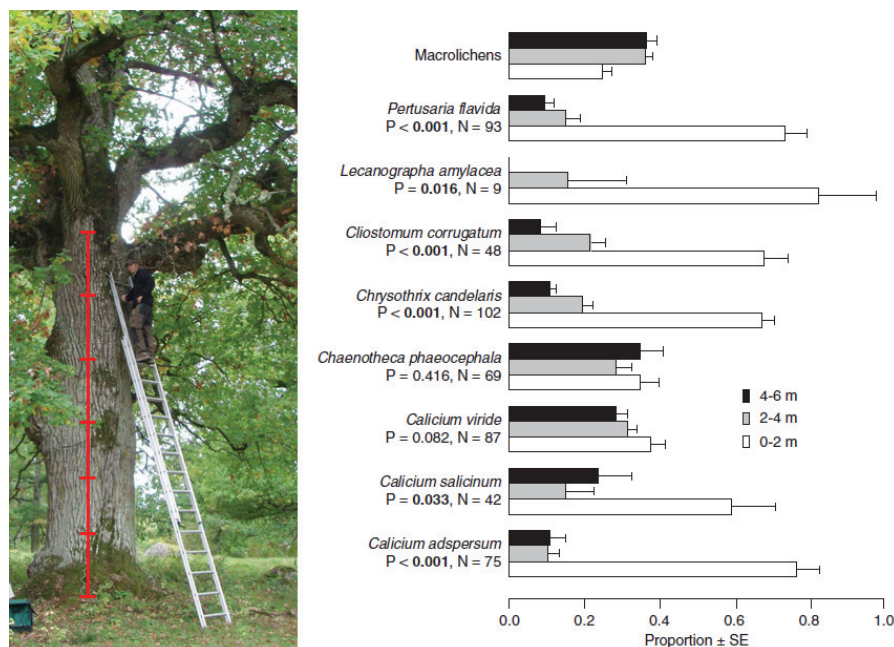

Figure 3. Sampling design (the photo) in Paper I and proportional abundance at different heights for the eight study species and macrolichens as a group (the bar plot). The lower 6 m of the trunk was divided into four vertical segments (only one is shown), which were further divided into six horizontal segments, at every meter, giving a total of 24 plots per tree. Photo: Dennis Jonason.

The field work for paper II and IV was conducted at "Tinnerö eklandskap", (58°22´ N, 15°36´ E) which is an oak rich nature reserve. The area was an important hay producer from the beginning of the 17th century until about 1960, with a high proportion of oak-rich wooded meadows (Anonymous, 2006). We choose this study area because of the known high current and historical oak density (Anonymous, 2006). Another reason was that the current age distribution of potentially suitable trees suggests that the system is in regeneration and mortality equilibrium. Within an area of 2.1 km^2, all potentially suitable oaks were mapped using GPS (Fig. 4). For each tree (in total 2083), we also measured tree and environmental variables that were hypothesized to affect lichen metapopulation dynamics or were correlated to tree age (Table 1). On all trees within the area, and within a buffer zone around the area, we recorded the occurrence of each study species. The ages of all

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trees were either measured using increment cores or estimated based on tree and environmental characteristics.
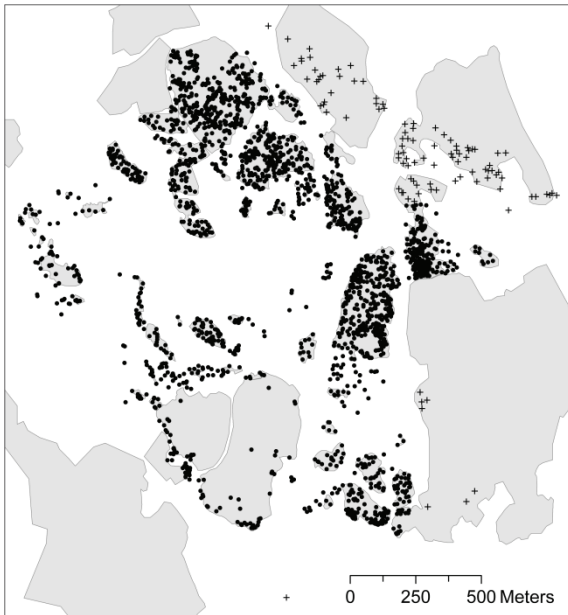

Figure 4. The study landscape in Paper II and IV with the 2083 study oaks (black dots) on a mix of clay-rich agricultural fields or lays (white), or wooded pastures or woods on moraine (grey). Black crosses represent oaks in a 400 m buffer zone around the study area that were occupied by any of our study species.

For Paper III we used a study landscape (32.9 km^2 study area and a 1.8 km buffer zone surrounding it, Fig. 5), that consists of the parish of Sjögestad (58°22' N, 15°22' E) and some adjacent villages. We choose this study landscape because of the good documentation of the historical oak densities. This occurs due to a high proportion (~72%) of the land owned by farmers, for which oak surveys were conducted around 1830 (Eliasson, 2002). To compare the historical oak density with the current, we counted all oaks with a diameter at breast height (dbh, henceforth) exceeding 48 cm (150 cm in circumference) in the study landscape (1386 oaks), and in a buffer zone of 1.8 km around the area (953 oaks). We surveyed the study species and measured explanatory variables (Table 1) on 104 of these trees. They were selected to be of approximately the same age and as spatially dispersed as possible.
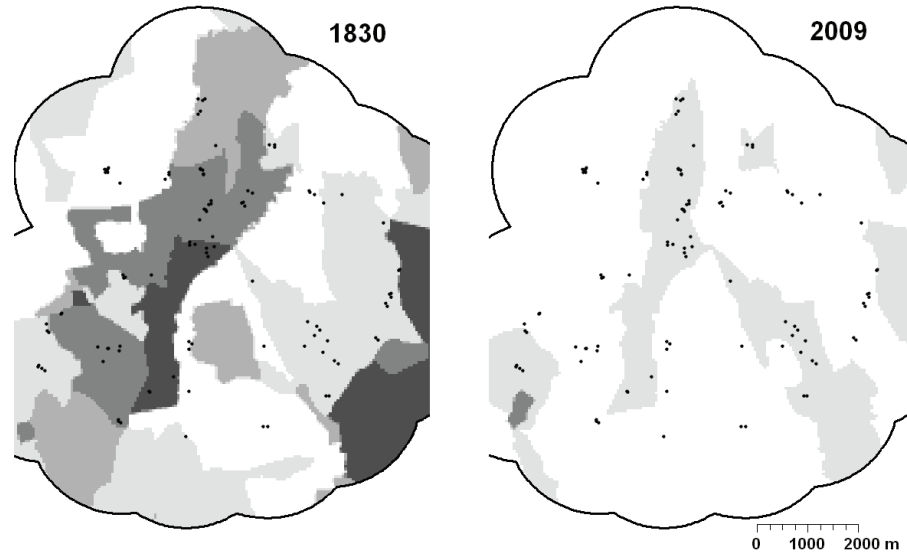
Figure 5. The study landscape in Paper III. Black dots represent the 104 study trees, and the grey scale shows the number of oaks in 50 x 50 m cells (increasing from light to dark) based on oak densities in 1830 and 2009, in 63 villages. The black line indicates the outer margin of a 1.8 km buffer zone.

Table 1. *Tree and environmental characteristics recorded for each tree in paper I-III.*

Variable	Paper
Tree age	I, II
Bark fissure depth	I, II, III
Diameter at breast height	I, II, III
Shade	III
Wind exposure	III
Openness	II
Bush cover	III
Moss cover	I, III
Macrolichen cover	I, III
Inclination (Inclination of the centre of the trunk 0-2m from the ground)	I, II, III
Tree condition (Proportion dead branches)	II
Ground properties (Proportion wooded pasture, compared to agricultural field within a 15 m radii buffer surrounding the tree)	II

3.2 Study species

In total we studied ten crustose lichen species with different species traits and that differ in frequency and abundance on oaks (Table 2, Fig. 6). Six of them mainly occur on old oaks, of which four are red-listed (Gärdenfors, 2010). In

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Paper II and IV we only used species of conservational concern. We also wanted species that were more or less strictly associated with old oaks (Table 2), which increase the possibility to find all potential dispersal sources in the landscape. *Chaenotheca phaeocephala* may occur on other old deciduous trees (Nitare, 2000). However, apart from oaks we only found it on two old *Sorbus intermedia* in the study landscape. In paper III, we added *Chrysothrix candelaris*, which also may occur on other deciduous trees. However, in the landscape studied, occurrences on oaks should dominate. In Paper I, the association with old oaks was less important and we included also species that are relatively common on other trees.

Table 2. *Characteristics of the study species.*

Species name - Authority	Main dispersal mode[1]	Lower oak age limit[2]	Redlist category [3]	Mainly oaks	Paper
Buellia violaceofusca - G.Thor & Muhr.	Soredia	100-200	NT	X	II,III,IV
Calicium adspersum - Pers.	Spore	>100	LC	X	I,II[4],III
Calicium salicinum - Pers.	Spore	>100	LC		I
Calicium viride - Pers.	Spore	>100	LC		I
Chaenotheca phaeocephala - (Turner) Th. Fr.	Spore	>100	LC	X	I,II,III, IV
Chrysothrix candelaris - (L.) J.R. Laundon	Soredia	>100	LC		I,III
Cliostomum corrugatum - (Ach.:Fr.) Fr.	Spore/conidia	100-200	NT	X	I,II,III, IV
Lecanographa amylacea - (Ehrh. ex Pers.) Egea & Torrente	Spore	200-300	VU	X	I,II,III, IV
Pertusaria flavida - (DC.) Laundon	Isidia/soredia	>100	LC		I
Schismatomma decolorans - (Turner & Borrer ex Sm.) Clauzade & Vĕzda	Soredia	200-300	NT	X	II,III,IV

1. According to Smith et al. (2009). Generally the size of soredia/isidia>spores>conidia
2. Based on knowledge before any of the papers - Ranius et al. (2008b) and field experience
3. LC = Least concern, NT = Near threatened, VU = Vulnerable
4. *Calicium adspersum* was surveyed, but removed from the analysis

Figure 6. Three of the study species - *Cliostomum corrugatum* in the left photo, *Lecanographa amylacea* (white) and *Chrysothrix candelaris* (yellow) in the right photo. Photos: Victor Johansson.

3.3 Analysis

In this thesis we use several different analysis methods. In paper I and III we use generalized (non)-linear models (GLMs: McCullagh & Nelder, 1989), while in paper II we use a Bayesian non-linear model (Gelman *et al.*, 2004). Paper IV is based on simulations using the model developed in paper II.

In paper I we used linear regression models to test (i) the relationship between species abundance and height above the ground, (ii) the relation between total abundance and tree age related characteristics and, (iii) whether the proportion of the total abundance recorded above 2 m increased with tree age. We also developed GLM:s to predict the total abundance on the tree (0-6 m) based on abundance data and tree characteristics from the lowest 2 m. Finally, we used ordinal regression (Agresti, 2002) to test whether the vertical distributions of lichens were related to the vertical distribution of tree characteristics.

In paper II we used the Bayesian framework to fit an incidence function model (IFM henceforth: Hanski, 1994), that has been extended to be applicable for dynamic landscapes (Verheyen *et al.*, 2004), to snapshot data on five species. To incorporate patch dynamics, Verheyen *et al.*, (2004) added a temporal dimension to the IFM by solving for the conditional probability that a patch is occupied at an arbitrary age,

$$J_i(age) = \frac{C_i - C_i(1 - C_i - E_i)^{age - \psi}}{C_i + E_i}.$$

This extension also facilitates the solving for colonization (C_i) and extinction (E_i) rates, which may otherwise be difficult, as very different rates can lead to

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similar patterns of species occupancy. We further extended the model by adding the parameter Ψ, which defines the age at which a patch (here tree) becomes suitable for colonization. This parameter estimates the breadth of the niche – a species colonizing also young trees (i.e. a generalist) has a wider niche than a species colonizing only old trees (i.e. a specialist). In the code for fitting the model, age-Ψ was set to 0 if age<Ψ. Thus, J_i(age) = 0 if age<Ψ. We modeled the colonization probability (C_i) as a function of connectivity (S_i) as

$$
C_i = 1 - \exp\left(-\left(\underbrace{\Xi + \Phi \sum_{i \neq j} p_j \left(\frac{\alpha^2}{2\pi} \exp\left(-\alpha \times r_{ij}\right) \right)}_{S_i} \right) \right).
$$

This connectivity measure (S_i) assumes that propagules are dispersed from unknown background sources at long distance with the rate Ξ, or from local (within the area) occupied patches according to a dispersal kernel, where α regulates the dispersal range and r_{ij} is the distance in meters between tree i and j. The variable $p_j = 1$ if tree j is occupied by the species, otherwise $p_j = 0$. The colonization parameter Φ includes the rate of emigration of dispersal propagules from occupied patches, and the propagule establishment ability ("the force of infection" using epidemiological terminology). For testing the relative importance of local stochastic extinctions on metapopulation dynamics, we compared metapopulation models where we estimated the extinction rate, E, with models where the extinction rate was fixed at 0. We used uninformative prior distributions for all model parameters. Models were built based on the Deviance Information Criterion (DIC; Spiegelhalter *et al.*, 2002), which is an information-theoretic approach with properties similar as Akaike's Information Criterion (Burnham & Anderson, 2002).

In paper III we modeled species occurrence based on tree characteristics, environmental conditions and habitat connectivity, using GLM:s with binomial distribution and a logit link function (logistic regression). Connectivity was calculated based oak density, in 1830 and in 2009, in 50 x 50 m cells that were distributed over the whole study landscape (Fig. 5) as:

$$
S_i = \sum_{i \neq j} e^{-\alpha \times d_{ij}} A_j,
$$

where α is a parameter regulating the spatial scaling, and d_{ij} is the distance in meter between the centre coordinate of the cell i where the focal oak is located, and the centre coordinate of cell j. A_j is the number of oaks in cell j in 1830 and

in 2009, for the historical and current connectivity, respectively. Model selection was based on AIC that was calculated as -2 log-likelihood + 2k, where k is the number of model parameters. When calculating AIC, we accounted for the fact that both connectivity variables included two parameters – the "slope parameter" and α. We also estimated approximate 95% confidence interval for the parameter α, based on the deviance profile (Hudson, 1971), which is rarely done in ecological studies.

In paper IV we used the fitted Bayesian incidence function models (Paper II) to project epiphyte metapopulation dynamics into the future. We investigated differences in persistence of five lichens with different traits in 11 scenarios (Table 3) of habitat decline, low tree regeneration rate and conservation actions. First, we investigate the effect of drastic habitat decline on species persistence. These simulations also reveals the time-lags until a new equilibrium is reached. We decreased the number of trees in the study landscape to 10% and 40% of the reference level (i.e. the current number of oaks in the study landscape) and investigated how likely it is that the extinction risks are higher than in the reference landscape. Second, we investigated the effect of conservation actions in landscapes where the oak density has decreased to 10% and 40% of the oak density in the reference landscape. Specifically, we estimate how likely it is that species persistence is improved by actions such as creating 15% more old trees (simulating clearing of bushes and small trees, which may make the old trees suitable), or increasing the tree regeneration rate so that the tree density of the reference landscape is obtained. Third, we investigated how likely it is that a low tree regeneration rate affects species persistence by decreasing the rate to 10% in the reference landscape. Forth, we investigated how likely it is that conservation actions after 100 years of low tree regeneration, i.e. in a landscape with a gap in the tree age structure, increased species persistence. We investigated effects of (i) setting the regeneration rate to that of the reference landscape, (ii) creating 15% more old oaks (simulating e.g. clearing around old trees) in combination with the regeneration rate of the reference landscape, or (iii) doubling the regeneration rate during 100 years after the age gap.

The statistics software R versions 2.6.2 - 2.14.1 (R Development Core Team, 2008-2012) was used for analyses in papers I, III and IV. The Bayesian models in Paper II were fitted using OpenBUGS 3.0.2 (Thomas *et al.*, 2006).

Table 3. *The simulated scenarios in paper IV. "Constant reg." means a regeneration rate that maintains the initial tree age structure. "Clearing" means creating 15% more old oaks than the initial conditions, simulating a situation when unsuitable shaded oaks immediately become suitable due to clearing of bushes and young trees around them. "High reg." means a regeneration rate that in the long run reaches the number of trees of the reference landscape (i.e. "Normal reg." in the reference landscape). "Low reg." is 10% and "Double reg." is 200% of the regeneration rate that keep the tree age structure constant.*

Scenario	Initial tree numbers[1]	Description
Constant reg.	100%	Stable conditions (reference landscape)
Constant reg.	10%	Drastic habitat decline to 10% of the reference level
Constant reg.	40%	Drastic habitat decline to 40% of the reference level
Clearing & constant reg.	10%	Clearing in a low (10%) density landscape
Clearing & constant reg.	40%	Clearing in a low (40%) density landscape
High reg.	10%	Increased reg. in a low (10%) density landscape
High reg.	40%	Increased reg. in a low (40%) density landscape
Low reg.	100%	Low reg. (10%) in a high density landscape (100%)
Normal reg.	100%	Increased reg. after 100 years of low regeneration
Normal reg. & clearing	100%	Increased reg. and clearing after 100 years of low reg.
Double reg.	100%	Double reg. during 100 years after 100 years of low reg.

[1]The proportion of oaks >100 years in the current study landscape that was used to set the condition at year 0

3.4 Statistical inference – Frequentist versus Bayesian

Frequentist statistics is by far the most widely used branch for statistical inference among ecologists, but in recent years Bayesian statistics has gained increasing support (Ellison, 2004). There are some fundamental differences between these two branches. Frequentist methods give point estimates of parameters, and inference is based on estimating the probability of falsely accepting the hypothesis (H_1), i.e. incorrectly rejecting the null hypothesis (H_0). In contrast, Bayesian methods give probability distributions (degree of belief) of parameters, given the available data and the prior distribution (see below). Inference is made by estimating credible intervals (Bayesian confidence intervals), from which the probability of the parameter being within a certain interval, e.g. 95%, can be assessed. An analogous frequentist 95% confidence interval only says that if the experiment would be repeated, and new intervals calculated each time, the true parameter value is within these intervals 95% of the times. Therefore, Bayesians can make statements like: "there is a 95% probability that the true parameter value is within this interval"

or "there is a 80% probability that the true parameter is larger than 0", while frequentists cannot. Another important difference is that Bayesian methods can utilize prior information about a parameter, based on other independent data or expert opinions. Moreover, simulations based on Bayesian posterior distributions of model parameters can reflect natural variability and uncertainty, while simulations based on parameters estimated by frequentist methods do not (Fig. 7).
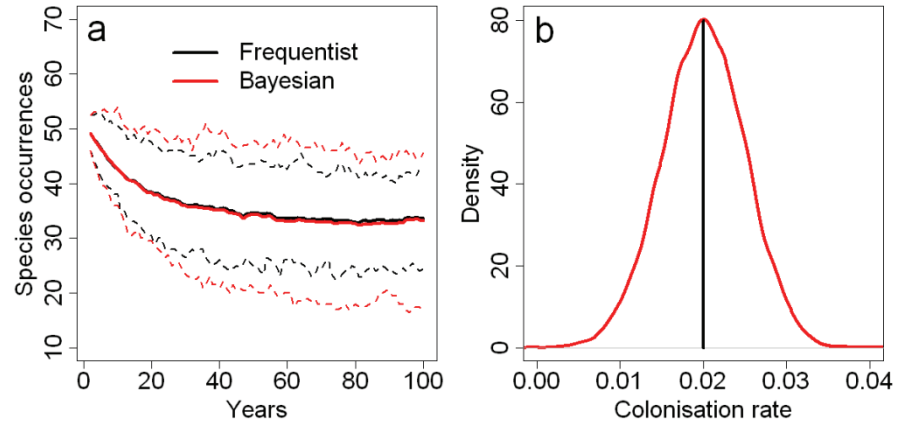

Figure 7. Mean (continuous lines) and 95% confidence limits (broken lines) of the number of species occurrences among 100 patches projected over 100 years from simulations of colonizations and extinction with frequentist and Bayesian methods (Fig. 7a). The model assumes stochastic colonization and extinction events with rates that are identical among patches and over time. In the Bayesian projection, the colonization rate is sampled from a posterior distribution, here created with 10000 values from a normal distribution with a mean of 0.02 and a standard deviation of 0.005 (Fig. 7b), while the frequentist projections only uses the mean of this distribution (0.02). The extinction rate is fixed at 0.04 in both projections.

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4 Results and Discussion

Epiphytes associated with old trees (Paper I, II) have low colonization and extinction rates that depend on species traits and patch dynamics (Paper II). This results in slow responses to changes in the landscape structure and non-equilibrium occurrence patterns long after habitat decline (Paper III, IV), which poses both conservational challenges and opportunities for their long-term persistence (Paper IV).

4.1 Colonization and extinction dynamics

The colonization rates of the study species were generally low, and strongly related to connectivity to surrounding occupied patches (Paper II). This agrees with metapopulation theory (Hanski, 1999) and with earlier studies of sessile species (Verheyen *et al.*, 2004, Snäll *et al.*, 2005a, Jönsson *et al.*, 2008). This is most likely a result of restricted dispersal ability, which has also been suggested by occurrence pattern data (e.g. Johansson & Ehrlén, 2003; Verheyen *et al.*, 2003a; Snäll *et al.*, 2004b), establishment experiments (e.g. Sillett *et al.*, 2000; Ehrlén & Eriksson, 2000) and spatial genetic structuring (e.g. Gehring & Delph, 1999; Snäll *et al.*, 2004a; Walser, 2004). However, our results also suggest a background deposition of dispersal propagules from unknown sources, indicating frequent long-distance dispersal events in epiphytes (Paper II). This has also been suggested for vascular plants (e.g. Nathan, 2006), and may be important for their metapopulation dynamics and long-term persistence (Mildén *et al.*, 2006; Meulebrouck *et al.*, 2009).

The colonization rates were related to species traits, and we show for the first time for sessile species, that they are higher for species with wide niches (with many suitable patches) and small dispersal propagules, than for species with narrow niches or large dispersal propagules (Paper II, Fig. 8a, Fig. 9). This implies that species with more patches (Fig. 8b, Fig 9b) in the landscape occur more frequently than species with fewer patches (Brown, 1984), which

result in higher connectivity, and thus, higher colonization rates in accordance with metapopulation theory (Hanski, 1999). In addition, the colonization rate was affected by dispersal propagule size, and was lower for species with large propagules, which agrees with findings from forest plants (Verheyen *et al.*, 2004). Our models suggest that species with high colonization rates have long dispersal, high propagule production or high establishment capacity. However, it is rather difficult to disentangle the independent effects of these processes on the colonization rate using our models. Decreasing propagule size has been suggested to increase the dispersal range (e.g. Okubo & Levin, 1989; Kimmerer, 1991; Löbel *et al.*, 2009), which should increase the colonization rate. Moreover, there is a trade-off between propagule size and numbers (Jakobsson & Eriksson, 2000); species with small propagules produce more propagules (emigrants), which should also increase the colonization rate. High establishment capacity is less likely for species with small propagules, as it has been shown to increase with increasing propagule size (Löbel & Rydin, 2010).
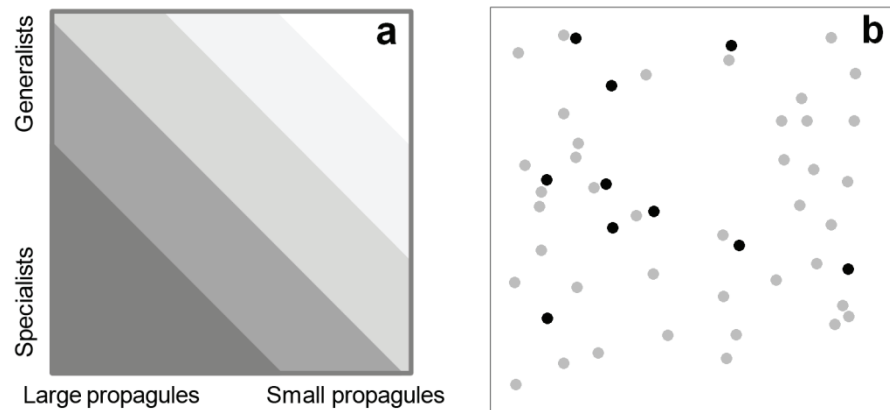

Figure 8. Conceptual model (a) for the relationship between niche breadth, propagule size and colonization rates in sessile species. The colonization rate increases from dark to light. Conceptual landscape (b) for a species with a wide niche (utilizing both grey and black dots) and a species with a narrow niche (utilizing only black dots).

Extinctions from standing trees seem rare for our study species (Paper II, Fig. 9). This implies that when an epiphyte has established on a tree it is unlikely to go extinct until the tree dies. Stochastic extinctions are negligible and the extinction rate is driven by tree fall rates (Snäll *et al.*, 2003). This result agrees with results from an epiphytic moss (Snäll *et al.*, 2005a; Roberge *et al.*, 2011) and wood-inhabiting fungi (Jönsson *et al.*, 2008), but contrasts results from studies of other sessile organisms living in dynamic patches (Zartman & Shaw, 2006; Laube & Zotz, 2007; Öckinger & Nilsson, 2010; Caruso *et al.*,

2010; Fedrowitz *et al.*, 2012; Zartman *et al.*, 2012). Explanations for this difference could be the stability of the patch or the life-form of the organism. When the organism lives closely attached or even inside a stable substrate (Paper II, Snäll *et al*., 2005, Jönsson *et al*., 2008) the stochastic extinction risk may be low. In contrast, when the organism lives on the surface of a substrate that is more unstable, e.g. growing, decomposing or even moving, stochastic extinctions become more frequent. Examples are leaves (Zartman & Shaw, 2006, Zartman *et al*., 2012), decomposing stumps (Caruso *et al*., 2010) or branches (Laube & Zotz, 2007). It should be noted, though, that we have studied oak pastures that are grazed by cattle; local extinctions may increase for our study species if the management of these wooded pastures is abandoned (Paltto *et al*., 2011, Nordén *et al*., 2012).
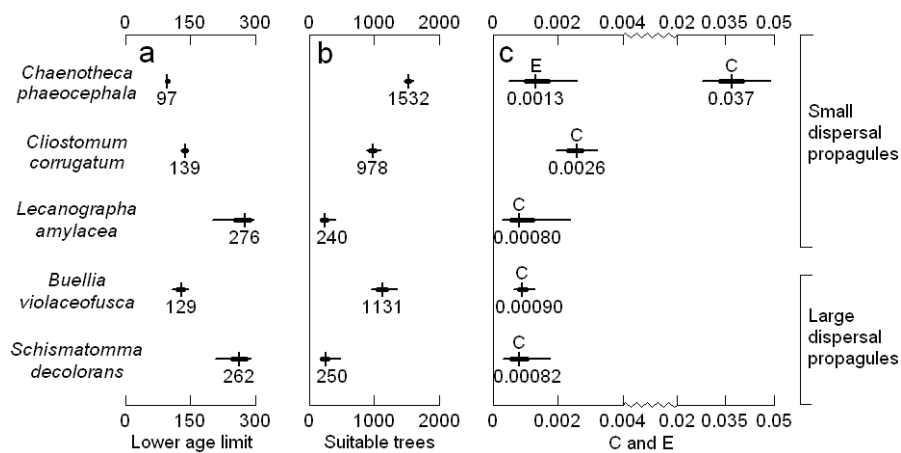
Figure 9. (a) The age at which the trees become suitable for lichen colonization, (b) the number of suitable trees for each lichen species, (c) the mean lichen colonization (C) and extinction rate (E) per year among suitable trees. For four species the stochastic extinction rate was 0. Modes (short vertical lines) and 50% (thick horizontal lines) and 95% (thin horizontal lines) highest posterior density intervals (Bayesian confidence intervals) of the parameters in the best model in Paper II for each species are shown. Propagule size according to Smith *et al.,* (2009) - small = spore or conidia and large = soredia.

4.2   Species distribution in changing landscapes

Simulation of the future metapopulation dynamics based on the models fitted in Paper II showed that after habitat decline the number of occupied trees continued to decline (Paper IV). This agrees with metapopulation theory, as decreasing number of patches decreases connectivity, and thus, also decreasing the colonization rate which leads to fewer colonizations (Hanski, 1999). However, there were time-lags of at least 250 years before new equilibriums

were reached after habitat decline (Fig. 10, Paper IV). This agrees with Paper III, where we show that our study species are better explained by the historical landscape structure 180 years ago, compared to the current landscape structure. Our findings also agree with earlier studies of epiphytes (Snäll *et al.*, 2004b; Ellis & Coppins, 2007), wood-inhabiting fungi (Paltto *et al.*, 2006; Ranius *et al.*, 2008a) and vascular plants (e.g. Lindborg & Eriksson, 2004; Helm *et al.*, 2006; Reitalu *et al.*, 2009). However, we show time-lags in species occurrence patterns of almost 180 years after a change in the landscape structure, which never has been shown for organisms other than vascular plants before (e.g. Reitalu *et al.*, 2009), and the result from paper IV suggest that the time-lags can be even longer.
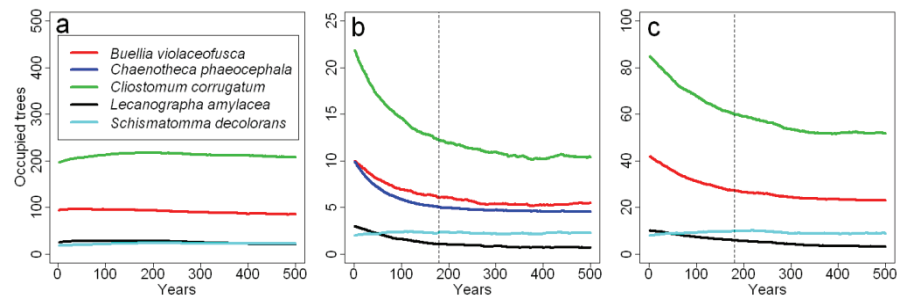
Figure 10. Mean number of occupied trees over time for five lichen species in (a) the study landscape, and in landscapes where the oak density at year 0 declined to (b) 10% and (c) 40% of the density in the study landscape (Paper IV). For *Chaenotheca phaeocephala* the minimum number of occupied trees in the 10%-landscape ranged 15-71, and since all other scenarios were less severe, we decided to exclude it from further simulations (see Paper IV). For improved visualization, the number of trees occupied by *C. phaeocephala* is divided by 10. Vertical broken lines show that occurrence patterns are not in equilibrium after 180 years, i.e. in landscapes where oaks declined drastically short after 1830 (Paper III).

The observed long time-lag in Paper III and Paper IV most likely result from slow colonisation-extinction dynamics. The study species have very low extinction rates, as they rarely go extinct from standing trees (Paper II), and oaks may be suitable patches for these species for up to several hundred years (Drobyshev & Niklasson, 2010). This means that the local extinction rate is similar for different species, which explains the rather similar length of the time-lags until reaching new equilibriums (Paper IV). Our results indicate that occurrences of species with low colonization rates are better explained by the historical landscape structure in 1830, compared to species with higher rates (Paper III). As the trees studied most likely have been colonized after the oak decline, all species should be most common in areas which had high oak densities (many dispersal sources) in 1830. The reason is that these areas contain the highest number of occupied remnant trees, which can act as

dispersal sources for the colonisation of new trees. Species with low colonization rates may almost only be found in such areas, while species with higher rates may also occur in areas which had a lower oak density in 1830. Hence, how well the spatial structure of the historical landscape explains species occurrence may depend on species-specific colonization rates (Paper III). However, species with similar extinction rates have similarly long time-lags before reaching a new equilibrium (Paper IV).

4.3 Population persistence after drastic habitat decline or low tree regeneration

The metapopulation extinction risks differed among species and scenarios of drastic oak declines, low tree regeneration and conservation actions (Paper IV). The metapopulation extinction risks increased with decreasing oak density (Fig. 11). The extinction risk was higher for species with narrow niches or large dispersal propagules (i.e. low colonization rates) compared to species with wide niches and small propagules (i.e. high colonization rates). In landscapes where the habitat has declined, the colonization rates of most species decrease, but the species with already low rates are the ones most likely to cross the threshold where colonizations cannot compensate extinctions (Hanski, 1999; Hanski & Ovaskainen, 2002). Moreover, species with narrow niches are likely to have smaller metapopulations compared to species with wide niches, making them more sensitive in synchronous stochasticity of local extinctions (Hanski, 1991), which further increase their metapopulation extinction risk.
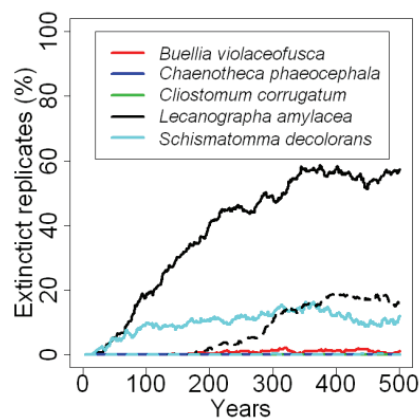

Figure 11. The metapopulation extinction risk (i.e. percentage of replicates with zero occurrences) for five lichens over time in landscapes where the oak density at year 0 declined to 10% (continuous lines) and 40% (broken lines) of the density in the reference landscape.

Conservation actions had only minor effects on species extinction risks in the landscapes where the oak density had declined to 10% and 40% of the current density in the study landscape (i.e. the reference landscape). Increasing the tree regeneration rate may have the potential to recover species that have been lost from a landscape if the background (long distance dispersal) is high enough (see 4.1). However, for decreasing species' short-term extinction risks this strategy may be poor, especially for species dependent on very old trees (i.e. with narrow niches) due to the long delivery time (i.e. the time it takes for trees to become suitable). In contrast, the currently common conservation action of clearing bushes and trees around old oaks (Claesson & Ek 2009) is assumed to increase the number of patches without a long delivery time. However, our results show only minor positive effects on species persistence, as the potential restoration objects (based on a mean for the county of Östergötland) are so few, only increasing the number of old trees with 15%.

Low tree regeneration resulted in a decrease in the long term number of occupied trees and increased the extinction risks. However, there were considerable time-lags before the number of occupied trees declined. Our results show that many epiphytes can bridge gaps in the tree age structure in landscapes where the regeneration has been low during 100 years, which have currently high old tree density, if the tree regeneration increases again (Fig. 12). This is a positive message for conservation – it is not too late to act in systems with many old trees, but few young as a consequence of too intense browsing (e.g. Kirby *et al.*, 1995; Harvey & Haber, 1998; Kouki *et al.*, 2004) or the absence of forest fires (Abrams, 1992), even if the gaps in the tree age structure are rather wide (e.g. Russell & Fowler, 1999; Fischer *et al.*, 2009; Ranius *et al.*, 2009). The reason is that landscapes with high old tree densities potentially harbor large metapopulations, which as a result of long time-lags may not decrease much before the new suitable trees are delivered. Species that rarely go extinct from standing trees (Snäll *et al.*, 2005a, Paper II) can persist in the landscape during long periods of low regeneration, and after the age gap provide dispersal sources for new suitable trees. However, for species with narrow niches, age gaps may constitute bottlenecks with increased extinction risk even in landscapes with high densities of old trees. Moreover, for species associated with trees that have shorter life-spans (e.g. Snäll *et al.*, 2005a), or for species with considerable stochastic extinction rates (Öckinger & Nilsson 2010; Fedrowitz *et al.*, 2012), gaps of 100 years in the tree age structure may have much severer impacts on the population persistence compared to our study species.
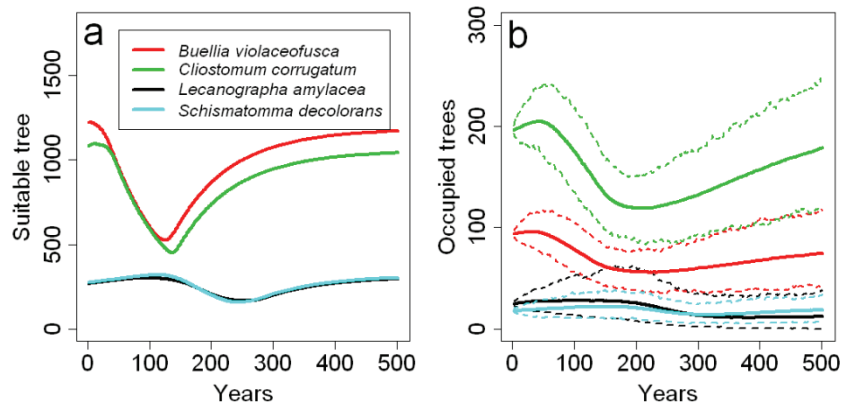
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Figure 12. Mean (continuous lines) number of suitable (a) and occupied trees (b) for four lichens in a landscape with a normal regeneration after 100 years of low (10% of normal) regeneration. 95% confidence limits for the number of occupied trees are shown as broken lines.

4.4 Habitat quality and vertical distribution of epiphytes

Understanding the habitat requirements of an organism is essential for defining its patch, understanding its colonization-extinction dynamics and determining where species surveys should be conducted. These are all important factors for efficient conservation.

Tree age, or characteristics correlated to age, seems to be a very important variable in explaining the occurrence probability of our study species (Ranius *et al.*, 2008b; Johansson *et al.*, 2009; Paper I; II; III), and of many other epiphytes (e.g. Snäll *et al.*, 2004b; Fritz, 2009). There may be several possible reasons for this. First, young trees are not suitable patches - the quality of the bark changes with the tree ageing, e.g. bark structure, chemistry and microclimate change (Barkman, 1958; Ranius *et al.*, 2008b). Second, old trees have been available for colonisation for a longer time, compared to young trees (Rose, 1992; Gu *et al.*, 2001; Snäll *et al.*, 2003). For species with low colonisation rates it may take long time for a suitable tree to become colonized. Our results suggest a combination of these two factors, as we show species-specific age thresholds for when trees become suitable patches, and that epiphytes may have very low colonization rates (Paper II). Another potential explanation could be that epiphyte abundance increases with tree size (e.g. Johansson & Ehrlén, 2003; Snäll *et al.*, 2004b), and old (large) trees therefore harbor larger populations, which are less prone to extinction (Hanski, 1999). However, as extinctions from standing trees seem rare for our study species (Paper II) this is an unlikely explanation. For other epiphytes the stochastic

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extinction rate has been shown to both increase (Öckinger & Nilsson, 2010) and decrease (Fedrowitz *et al.*, 2012) with tree diameter.

The association with old bark substrate makes height-limited surveys of the lowest (oldest) 2 m of the trunk, which is common for epiphytes (e.g. Dettki & Esseen, 1998; Kantvilas & Jarman, 2004; Johansson *et al.*, 2007), a suitable method for collecting occurrence data of our study species (Paper I). We show that when using this method, the detection probability was high (>96%) for seven out of eight species. Species abundance generally declined with height (Fig. 3), for five species >69% of the total abundance (0-6 m) was recorded on the lowest 2 m. However, the proportion of the total abundance present above 2 m increased with tree age for three species. This suggests that the vertical distribution of late successional species is determined by gradients in substrate age, i.e. the species establish on the lowest (oldest) parts of the trunk and expand upwards as the tree ages. However, early successional species may instead move upwards (i.e. disappearing from the lowest parts) with tree age (Hedenås & Ericson, 2000), making height-limited surveys less suitable for these. Therefore, before interpreting data from height-limited surveys, knowledge of species vertical distribution and how it changes with tree age is important.

Several lichens found on oaks are associated with sun exposed and dry bark (Rose, 1974). However, we found indications for this only for one species, *Chaenotheca phaeocephala*. This species showed a negative relationship with the bush cover near the trunk and a positive relationship with wind exposure (Paper III), and its vertical distribution also indicates that it is not negatively affected by exposure (Paper I). Exposure is related to the microclimate on the bark, suggesting that this species tolerates sun-exposed and dry bark. Another possible explanation is that its dispersal is promoted in open environments. It should be remembered that our studies have been performed in rather open and well-managed areas. Paltto *et al.*, (2011) have shown that the occurrence probability of several of these species has a negative relationship with the development of secondary woodland around the tree, which may be a result of higher extinction rates and lower colonization rates in unmanaged sites (Nordén *et al.*, 2012).

4.5 Summarized answers to the questions in thesis aims

I For most species the detection probability is high and a fairly large proportion of the total abundance can be recorded if only the lowest 2 m of the trunk are surveyed. The vertical distributions seem to be mainly

determined by a gradient of substrate age (age decreases with increasing height).

II Epiphyte colonization rates are explained by connectivity, in accordance with metapopulation theory. The extinction rates are explained by patch dynamics, and stochastic extinctions seem negligible. This is consistent with the concept of patch-tracking metapopulations, and do not conform to the classical view were extinctions are purely stochastic. Colonization rates are explained by species traits - niche breadth and dispersal propagule size.

III Epiphytes are not in equilibrium with the current landscape structure. The occurrence patterns are better explained by the spatial configuration of oaks 180 years ago than by the present configuration. Species with low colonization rates are better explained by the historical landscape structure, compared to species with high rates.

IV The number of occupied trees decreases after drastic habitat decline, but there may be at least 250 years long time-lags before new equilibriums establish. Low oak regeneration also leads to species declines. Extinction risks increase with decreasing habitat and is highest for species with narrow niches or large dispersal propagules. Conservation actions in landscapes with a low density of old oaks has only minor effects on epiphyte persistence, while actions in landscapes with many old but few young trees may increase species persistence.

5 Conclusion and implications for conservation

Epiphytes associated with old trees have slow colonization-extinction dynamics that may depend on species traits, connectivity and patch dynamics. After habitat loss, species with low extinction rates will display long time-lags in species occupancy. Therefore, in landscapes where the number of old trees has declined recently, species occurrence patterns will provide an over-optimistic view of the size of metapopulations that can be harbored in the landscape in the long term. The long time-lag is most likely because many epiphytes rarely goes extinct from standing trees (Snäll *et al.*, 2005a; Paper II), and oaks can live for more than 500 years (Drobyshev & Niklasson, 2010). This suggests time-frames of up to a few hundred years before inhabiting species go extinct, and consequently, cease to act as dispersal sources for colonization of new trees. We can therefore expect future declines and extinctions in many agricultural and forest landscapes where old trees have declined during recent decades (Nilsson, 1997; Fischer *et al.*, 2010). On the other hand, this also offers a positive message for conservation: low extinction rates give an opportunity to improve long-term population persistence by increasing and restoring habitat before species extinction (Snäll *et al*., 2004b).

The success of the conservation actions may differ among species with different traits and depend on the current old tree density. Our results suggest that long-term persistence of species with low colonization rates requires a continuity of high old tree densities at a rather small spatial scale. It is therefore important where the new habitat is created (Hanski, 2000). Conservation actions may be inefficient in landscapes with currently low densities of old trees, especially for species with narrow niches (i.e. those only colonizing very old trees). Conservation efforts should instead focus on protecting and restoring stands with currently rich epiphyte floras, as well as promoting regeneration of trees in the near vicinity. Our results suggest that more than

1600 oaks of an age exceeding 100 years within an area of 1.8×1.8 km are needed for the long-term persistence of all our study species. However, at present many areas with high old tree densities have poor tree regeneration (e.g. Kouki *et al.*, 2004; Fischer *et al.*, 2009; Ranius *et al.*, 2009), resulting in gaps in the tree age structure even if regeneration increases. This may constitute bottlenecks for the persistence of many species. However, our results suggest that in landscapes with many old but few young trees, epiphytes may persist if conservation actions quickly address the need to increase tree regeneration rates, as long as the number of old trees at present can harbor viable metapopulations.

Successful conservation of lichens associated with old oaks requires long-term management plans that strive to achieve a balance of light availability and protection against browsing, which is necessary for successful oak regeneration (Bakker *et al.*, 2004). Fencing parts of pastures (Pigott, 1983), faster grazing rotation or planting oaks (Fischer *et al.*, 2009), may be necessary to assure the long-term persistence of several rare and red-listed oak-associated species.

6 Acknowledgements

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Populärvetenskaplig sammanfattning på svenska

Många arters habitat (livsmiljöer) har minskat på grund av det moderna jord- och skogsbruket. Denna minskning har haft och kommer att ha en negativ effekt på många arters utbredning och vissa arter har försvunnit från regioner eller riskerar att försvinna i framtiden. För de allra flesta arter vet vi väldigt lite om vad som begränsar deras habitat och om vad som påverkar kolonisation (nyetablering) och utdöenden (försvinnanden) från habitatytor. Detta är dock viktig kunskap för att kunna föreslå naturvårdsåtgärder som ökar chansen att bevara arterna på lång sikt.

Metapopulationsteori har under de senaste årtiondena fått en ökande betydelse inom ekologin. En metapopulation är ett nätverk av en arts lokala populationer, som binds samman genom spridning. Grundtanken är att en art kan försvinna lokalt (i en habitatyta) men ändå finnas kvar i nätverket inom andra ytor. Arten kan sprida sig och återkolonisera lämpliga habitatytor där arten saknas. Sannolikheten för kolonisation är större om det finns många spridningskällor i närheten och sannolikheten för att arten försvinner lokalt minskar med ökad storlek på den lokala populationen. För många arter kan lokala utdöenden även äga rum genom att habitatytan helt försvinner. Ju mer habitat det finns desto mindre är risken att arten försvinner helt från landskapet (dvs. risken att hela metapopulationen dör ut). Metapopulationsmodeller bidrar till att öka förståelsen för arters kolonisations- och utdöendedynamik. De kan även användas för att simulera framtida lokala kolonisationer och utdöenden och på så sätt användas för att förutsäga arters överlevnad efter en habitatminskning. Man kan även utvärdera effekten av olika naturvårdsåtgärder.

För många arter tar det troligen lång tid från en habitatminskning till dess att arten helt försvinner i landskapet. Detta innebär att gamla förekomstmönster dröjer sig kvar. Det kan då se ut som om de klarar sig bättre i dagens landskap

än vad de i själva verket kommer att göra på längre sikt. För de allra flesta arter vet vi dock inte hur lång denna fördröjning är och hur mycket habitat arterna behöver för att överleva på lång sikt.

Gamla träd utgör en viktig livsmiljö för många organismer, men har minskat kraftigt i det moderna skogs- och jordbrukslandskapet. Ett exempel är gamla ekar som i Sverige minskade radikalt i början av 1800-talet, när ekarna på bondemark övergick från statlig till privat ägo. Vi kan därför förvänta oss att många organismer som är beroende av ek har påverkats negativt. Idag återfinns gamla ekar främst i hagmarker. Skötseln av dessa är därför mycket viktig för den långsiktiga överlevnaden av många arter. Igenväxningen av hagmarker är ett stort naturvårdsproblem, eftersom den har en negativ påverkan både på själva träden och på ljuskrävande arter som lever på dessa träd. Ett annat omfattande naturvårdsproblem är dålig föryngring, dvs. att det är få unga träd som på sikt kan ersätta de gamla träd som finns idag, ofta på grund av för hårt betestryck. Även om föryngringen skulle öka, kommer det alltså på många håll att finnas ett trädåldersglapp, som arter beroende av gamla träd måste ta sig över.

Jag har studerat epifytiska (i detta fall trädlevande) lavar som är mer eller mindre strikt knutna till gamla ekar, av vilka flera är rödlistade (eftersom de har små eller minskande populationer i Sverige). Varje lämpligt träd kan hysa en lokal population och eftersom det sker spridning mellan träden utgör de lokala populationerna inom ett landskap tillsammans en metapopulation (Fig. 1). För att öka kunskapen om dessa arters habitatkrav och kolonisations- och utdöende-hastigheter har jag studerat förekomstmönster och utvecklat metapopulationsmodeller.

Resultaten visar att alla våra studiearter är beroende av gamla träd, men den ålder då träden blir lämpliga för kolonisation varierar mellan olika lavarter. Detta leder till att antalet lämpliga träd i ett landskap också varierar mellan arter. Kolonisationshastigheten är generellt låg och starkt påverkad av avståndet till potentiella spridningskällor (dvs. andra träd där laven finns), vilket tyder på spridningsbegränsningar. Arter som bara kan nyttja väldigt gamla träd har lägre kolonisationshastighet jämfört med arter som även kan kolonisera yngre träd. Detta beror på att en art med mer habitat förekommer mer frekvent i landskapet jämfört med en art som har mindre habitat, vilket leder till fler spridningskällor och därav en högre kolonisationshastighet. Dessutom tycks kolonisationshastigheten påverkas av hur stora spridningsenheter (t.ex. sporer) de olika arterna har. En art med små spridningsenheter kan troligtvis sprida sig längre och producera fler spridningsenheter jämfört med en art som har stora spridningsenheter, vilket leder till en högre kolonisationshastighet.

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Resultaten visar också att när lavarna väl har etablerat sig på ett träd, så sitter de kvar tills trädet dör. Därför kan lavarna finnas kvar i landskapet under lång tid, eftersom ekar kan bli gamla - ofta närmare 500 år. Detta gör att det blir en lång fördröjning från det att mängden gamla träd minskar till dess att arterna börjar försvinna från hela landskapsavsnitt. Genom att använda historiska ekinventeringar från 1830, dvs. strax innan ekarna minskade drastiskt, visar jag att dagens förekomstmönster förklaras bättre av mängden ek i det historiska landskapet för 180 år sedan jämfört med dagens ekmängd. Jag simulerar även effekten av minskad ekmängd med hjälp av mina metapopulationsmodeller och visar att fördröjningen troligtvis är ännu längre - över 250 år.

Genom att simulera framtida kolonisationer och utdöenden har jag också bedömt om arter med olika egenskaper kommer att klara sig på lång sikt givet olika scenarier av ekminskning, låg nyetablering av ek och olika naturvårdsåtgärder. Antalet koloniserade träd minskade och risken att metapopulationen dog ut ökade med minskande mängd habitat, vilket stämmer överens med metapopulationsteori. Arter som bara kan nyttja väldigt gamla träd och som har stora spridningsenheter (dvs. arter med låg kolonisationshastighet) hade generellt högre utdöenderisk än arter som kan nyttja något yngre träd och som har små spridningsenheter (dvs. arter med hög kolonisationshastighet). I landskap med en nuvarande hög täthet av gamla träd men låg nyetablering var minskningen långsam och den skedde med en lång tidsfördröjning.

Effekten av olika naturvårdsåtgärder i landskap med låg ektäthet var ganska liten. Att öka trädföryngringen (dvs. nyskapandet av träd) hade bara en liten positiv effekt på den långsiktiga överlevnaden av de mest känsliga arterna. Detta beror på att dessa arter hinner dö ut innan nya lämpliga träd hinner uppkomma, vilket kan ta mer än 200 år. I landskap med en nutida hög ektäthet men dålig trädföryngring kunde en ökad föryngring dock öka den långsiktiga överlevanden, även för de mest krävande arterna. Lavarna verkar kunna överbrygga 100-åriga glapp i trädåldersstrukturen. Detta är positivt för naturvården, eftersom åldersglapp är vanligt förekommande.

För att bevara rödlistade lavar knutna till gamla träd krävs långsiktig naturvårdsplanering. Naturvården bör satsa på att bevara ektäta områden och se till att det finns en konstant föryngring av ek i dessa områden för att på sikt ersätta dagens gamla träd. Även i områden som har haft dålig föryngring och där alltså en framtida nedgång av gamla ekar förväntas, kan naturvårdsåtgärder som ökar nyskapandet av unga ekar vara lyckade. Ett minskat betestryck eller plantering av ek kan komma att krävas om rödlistade lavar knutna till gamla träd ska överleva på lång sikt i dessa områden.

Tack!

Stort tack till alla som har hjälpt och stöttat mig under dessa år som doktorand, utan er hade det inte gått! Först och främst vill jag tacka mina fyra handledare…

Thomas – Det är fantastiskt att ha en så entusiastisk forskare som sin huvudhandledare, som dessutom är Östgöte! Tack för att jag fick chansen att prova på forskning och för allt ditt stöd under denna resa. Du tar dig alltid tid att diskutera och ger alltid snabb respons på texter (ofta inom ett dygn). Jag har lärt mig mycket av dig och jag ser fram emot vårt arbete under kommande år!

Tord – Du har också dragit ett tungt lass, tack! Du är en klippa på statistik och modellering - både frekventistiskt och Bayesianskt. Vårt "bollande" av framförallt Paper II (den så kallade "Verheyen-studien"), där otaliga pappersversioner bytte ägare via din postlåda och bilruta, har utvecklat mitt skrivande. Jag hoppas att jag nu skriver lite mer "stringent"!

Per – Vi har ju inte setts så många gånger, men pratat desto mer i telefon. Tack för alla långa samtal när jag har varit ute i fält! Du har alltid funnits där om jag behövt snacka lavar.

Lena – Det känns oerhört tryggt att veta att du finns några dörrar bort. Även om vi inte har behövt ha så mycket kontakt under min doktorandtid, så har du alltid funnits där i bakgrunden och hållit ett vakande öga över oss alla. Tack!

… jag tror inte att det går att få ett bättre gäng och jag hoppas på fortsatt kontakt och samarbete!

Det finns även en värld utanför ekologiinstitutionen, tro det eller ej ☺. Även där är det många som förtjänar ett tack!

Fältassistenterna – Henrik och Niclas, tack för alla hundratals träd ni har borrat, trots att borren ofta trilskats i de hårda och ihåliga ekarna. Hedvig och Anna, tack för alla träd ni har mätt och räknat! Anton, se nedan.

Per Milberg och Karl-Olof Bergman, tack för att ni lät oss prova på ett lite mer "forskningslikt" ex-jobb i Linköping. Innan dess hade jag inte en tanke på att doktorera.

Sist men inte minst, de nära och kära!

Närmsta vännerna - Anton och Therese, ni är inte bara mycket goda vänner till mig och Emilia, ni har även varit excellenta fält- och GIS-jobbare! Anton, tack för fältsäsongen 2008! Du gjorde att tre månader i Tinnerö blev riktigt kul. Fästingar (ca 150 st gemensamt), kor och Torssons ljuva toner i en härlig symbios. Theres, tack för att du fixade alla historiska kartor - det sparade mycket tid! Tack också för att jag fick bo hos er under fältjobbet! Ellen, Elle, Daniel och Alve, tack för alla trevliga middagar i Uppsala och Viksta under de senaste åren. Det är en av veckans höjdpunkter! Anneli och Egon (Dennis har ju redan nämnts, men har också varit delaktig här ☺), tack för allt kul vi haft i Uppsala och senare i Örsundsbro. Härligt med lite Östgötar att hänga med i Uppland! Jocke, Dan, Patrik, Micke, Jonas och Anna, vi har haft mycket kul ihop (och tillsammans med ovan nämnda), och jag hoppas att vi fortsätter ha det! Tack för att ni finns!

Familjen – Mor och Far, tack för en trygg uppväxt nära naturen! Storebror och Syster-yster, tack för att ni har varit så snälla mot er lillebror! Nu kan ni äntligen se vad jag pysslat med under de senaste åren!

Emilia – Min blivande fru! Tack för att du har stått ut med mig under de senaste sju åren och för att du följde med mig till Uppsala, fast du fick lämna din fina lägenhet i Linköping och bo med mig i en liten sunkig stuga på 20 kvadrat. Du sätter fart på mig! Utan dig skulle jag inte få mycket gjort och aldrig komma ut i världen! Tack också för att du illustrerade figuren i paper I ☺ och för att du har varit så förstående under slutspurten. Du betyder allt!