Introductory Research Essay

The importance of habitat networks for the grey-sided vole (*Myodes rufocanus*) and the lungwort lichen (*Lobaria pulmonaria*)

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1 Introduction

To describe how patches of suitable habitat for a species are linked in the landscape, a network analysis can be used (Urban and Keitt 2001). Such networks of forest habitat patches for different species has been presented and later utilized with empirical data on a landscape scale (e.g. Bodin *et al.* 2006, Bodin and Norberg 2007). However, knowledge on habitat demands and dispersal potential that are needed to perform this kind of network analysis are uncertain or lacking for many threatened forest species in the boreal region. This essay aims to meet this problem and propose model species. The grey-sided vole (*Myodes rufocanus* Sund.) and the lungwort (*Lobaria pulmonaria* (L.) Hoffm.) are two possible model species from contrasting taxa. The essay concentrates on the ecology of these two species and their spatial distribution in the landscape but also proposes other model species to incorporate and analyse in a network analysis. Further, the essay aims at reviewing current literature for studying networks of forest patches at a regional scale, discuss the major theories involved and how analyzing networks of potential habitats for different species could be used to understand how forest species react to habitat fragmentation.

1.1 Spatiotemporal changes in the boreal forest landscape structure

Human impact on the boreal forest landscape has altered the landscape structure during the last century with suppression of natural processes as an effect (Esseen *et al.* 1997). In the late 19th century the Swedish Forest Service began to survey forests (Östlund *et al.* 1997). The age and type of forest has since then shifted from older, natural forests toward younger even-aged managed forest stands with proportionally less deciduous trees (Östlund *et al.* 1997). The spatiotemporal changes have been pronounced from the 1970s until present and during that time-interval it is possible to follow the shifts in the Swedish boreal forest regions below the mountain timber line with the aid of different sources. Information on how the age of forests and tree-species composition has shifted is readily available through combining sources such as the official yearbooks of forest statistics (Anonymous 1970-2009), aerial photographs from different years and regions (available from Lantmäteriet) and digital maps from *k*NN-Sweden (Anonymous 2005). Forest data from the time-interval 1970-2009 could be linked to the occurrence of the grey-sided vole according to the environmental monitoring programme (Hörnfeldt 2010) and also to data of *L. pulmonaria* occurrence from the Swedish Species Gateway (Anonymous 2009). Anthropogenic disturbance and natural disturbance are causing changes in the composition of forests on a landscape scale and information on the magnitude of these changes may be derived from analysis of time series of maps over landscape composition. Important factors in a species-wise perspective include: (1) Natural fire-frequency for pyrophilus species and species bound to fire-refuges as well as other naturally occurring disturbance regimes (Niemelä 1999); (2) Reduced density and rejuvenation of deciduous trees in the forest landscape with emphasis on aspen (*P. tremula* L., Edenius *et al.* 2008) and goat willow (*S. caprea*, Snäll *et al.* 2005) as well as larger birch (*Betula pubescens* Ehrh., *Betula pendula* Roth.) dominated areas. These kind of shifts are amongst others a concern for species such as woodpeckers and declining epiphytic lichen species; (3) The tree species composition and spatial distribution of forests with more or less old-growth characteristics intact (Kuuluvainen 2002). To maintain and build habitat networks taking these factors into account, information about quantitative requirements for specialized species at individual and population level are needed (Angelstam *et al.* 2004).

1.2 Population decline of the grey-sided vole and the lungwort

A long-term survey on the forest living grey-sided vole (*M. rufocanus*) has been performed from 1971-present (Hörnfeldt 2004, 2010) within the mid-boreal zone (*sensu* Ahti *et al.* 1968) of northern Sweden. Results based on data from the environmental survey have been presented in a series of articles (e.g. Christensen and Hörnfeldt 2003, Hörnfeldt 2004, Hörnfeldt *et al.* 2006, Ecke *et al.* 2006, 2010, Christensen *et al.* 2008). The results indicate that *M. rufocanus* populations are declining in the forest landscape in lowland regions of Västerbotten county with habitat fragmentation as a contributing factor, but still show high numbers with retained cyclicity in the upland mountain region (Fig. 1; Ecke *et al.* 2010). Another declining forest species is the oceanic epiphytic lichen *L. pulmonaria* (Hallingbäck 1986, Gärdenfors 2010). The species was probably much more abundant in the past forest landscape than at present and assumedly one of the dominating species of epiphytic communities (Rose 1988). *L. pulmonaria* has been used as an indicator species of natural forests in large scale Swedish forest inventories (Nitare and Norén 1992, Nitare 2005). Also, an environmental survey in the northernmost Swedish county of Norrbotten has been proposed but not yet undertaken (Carlsson 1996). The aim of that survey would be to monitor *L. pulmonaria* and other epiphytic lichens proposed as good indicator species (Nitare 2005) growing on aspen (*Populus tremula*) and goat-willow (*Salix caprea* L.).

Habitat quality and distance among forest patches are proposed as important explanatory variables for persistence of forest species (Carlsson 1996). Further, threatened epiphytic species are often distributed in accordance with the metapopulation theory (Snäll *et al.* 2005). The short term dynamics of epiphytic species may be predictable by the metapopulation theory (Hanski 1994), and the long term survival at the landscape level is strongly affected by rates of disappearance and re-appearance of suitable habitat (i.e. substrate, goat-willow in particular, Thomas 1994, Thomas and Hanski 1997, Snäll *et al.* 2005, Öckinger and Nilsson 2010). *L. pulmonaria* and *M. rufocanus* belong to different taxa but both react to landscape change processes that may be similar. This is valuable in order to isolate which processes are important for the population dynamics of different groups of threatened species in the same boreal forest ecosystem.

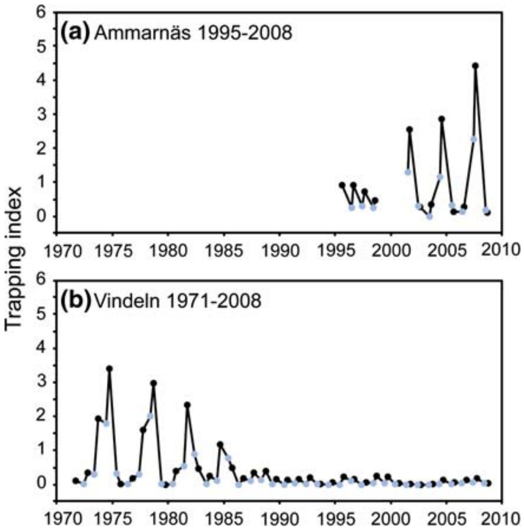


Figure 1. Grey-sided vole dynamics from the ongoing environmental monitoring of small mammals in the Ammarnäs (a) region (1995-2008) and Vindeln (b) region (1971-2008) of Västerbotten county, Sweden (Ecke *et al.* 2010). Trapping index is defined as number of individuals trapped per 100 trap nights.

1.3 Why network analysis of forest patches?

Network based modeling will offer the opportunity to analyse connectivity among a large amount of forest patches as described in Ecke and Bodin (manuscript), where >2200 forest dominated patches were analysed from a species perspective. The species dependent variables will include minimum habitat patch size requirement and maximum dispersal distances. Some boreal forest species have been studied in more detail regarding these factors, such as the long-tailed tit (*Aegithalos caudatus* L., Jansson and Angelstam 1999, Angelstam *et al.* 2004), siberian jay (*Perisoreus infaustus* L., Edenius *et al.* 2004), three-toed woodpecker (*Picoides tridactylus* L., Pechacek 2004) and grey-sided vole (*M. rufocanus*, Christensen *et al.* 2008). Network analysis could be applied to the data presented in these studies for a better understanding of how to manage the landscape from a regional species perspective. Such analyses of species-data will also pinpoint what kind of information is needed in future research to advance the management efforts for declining species at a regional scale.

2 Terminology

2.1 Habitat fragmentation

The concept of habitat fragmentation has been defined in different ways. In this essay it is mainly thought of as the remaining forest patches of a certain type (i.e. age-class, tree-type composition, vegetation) in a landscape, patches which become smaller and more isolated over time (Groom *et al.* 2006). Between the patches lies a more or less hostile matrix utilized differently depending on e.g. dispersal ability of the species in focus. As Christensen (2006) pinpoints, the terminology concerning habitat fragmentation is rather confusing and there is a need for clearer definitions. Franklin *et al.* (2002) presents a flow chart for the three different processes that co-occur during habitat fragmentation (Fig. 2): (1) habitat loss; (2) true fragmentation, i.e. decreased patch area and increased isolation of patches (Andrén 1994, Hanski 1999), which also causes (3) a change in habitat quality with respect to edge effects (Fig. 2; Franklin *et al.* 2002).

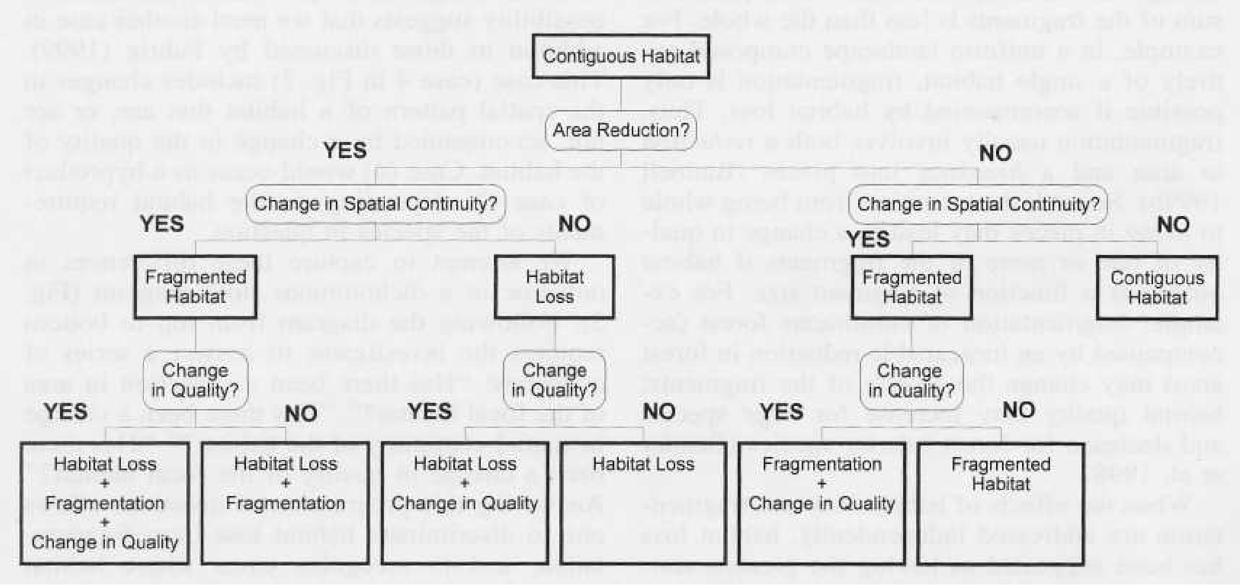


Figure 2. Flow diagram to differentiate between landscapes experiencing habitat loss, habitat fragmentation and changes in habitat quality (Franklin *et al.* 2002).

2.2 Island biogeography and metapopulation theory

The island model could be seen as a good example of how landscape ecology has evolved over the following 40 years since the theory was presented by MacArthur and Wilson (1967). Three broad assumptions are made under the island model concept (Lindenmayer and Fischer 2006): (1) islands (or e.g. forest patches) can be defined in a meaningful way for all species of concern; (2) clear patch boundaries can be defined that distinguish patches from the surrounding landscape, and (3) environmental, habitat and other conditions are relatively homogenous in an island or patch. However, when using the model for explaining landscape dynamics it may fail (Gilbert 1980). The areas between patches are rarely strict non-habitat for all species. Vegetation remnants in the matrix could be secondary habitats for many species or even preferred habitat. MacArthur and Wilson (1967) noted that much of their theory could be falsified when tested with empirical data. The metapopulation theory can be seen as a progress in explaining how species are distributed in the landscape and it has been better accepted than the island model by landscape ecologists (Hansson 1995). The theoretical basis for studies of population dynamics in spatially structured habitats was given by Hanski (2004). In the metapopulation model, the spatial structure of the habitat is considered, but no temporal changes are taken into account (Hanski 1994). By applying network analysis (Urban and Keitt 2001) to time series data on both the spatial landscape composition and species occurrences in accordance with the metapopulation concept, the temporal aspect is taken into account. The important issues that could be handled by applying a species metapopulation approach in a landscape context are summarized by Lidicker Jr (1995):

1. A focal population may utilize more than one community type and may even require more than one
2. Close connection (contiguity) between different community types may have important effects
3. Distances between patches of the same type and presence or absence of connecting corridors may influence the focal population
4. Movements of conspecifics in and out and among habitat patches can affect population dynamics, social behavior, rates of extinction, and genetic composition of populations
5. Different species may respond differently to a given patch array
6. Movements of other species (e.g., predators, parasites, prey) in and out of and among habitat patches can be important to a focal species, and
7. Spatial configurations of patches, including areal proportions, edge-to-area ratios, and orientation to interpatch fluxes, can affect population- and community-level processes.

2.3 Connectedness and connectivity

In fragmented landscapes connectivity is considered important. Connectivity is defined by Merriam (1984) as the resulting landscape property (perceived by individual species) from the interaction between the species' movement capacity (set by physiology and behavior) and landscape structure (set by composition and configuration). A later definition of landscape connectivity is ‘‘the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993). Connectivity in this sense will be a function of threshold size of preferred resource patches and distances among the patches for the focal species. A network of these preferred patches in a landscape is illustrated as nodes with paths between them, paths referring to the dispersal distance for a focal species over a hostile matrix (Fig. 3). These networks are divided into individual components in the landscape. A component becomes isolated when the distance between patches at its periphery is too far (i.e. exceeding the dispersal limit for the focal species) to another component or single patch. The proportion of forest habitat that is included in a component reflects the fragmentation of the forest habitat type that the population depends on in a particular part of the landscape (Bodin *et al.* 2006, Bodin and Norberg 2007).

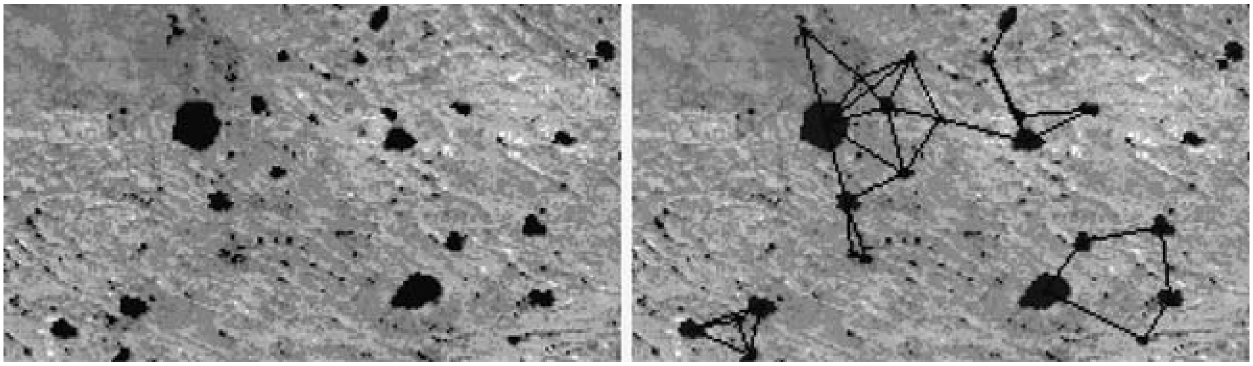


Figure 3. (a) The spatial structure of a subset of forest patches with suitable habitat for ring-tailed lemur (*Lemur catta*), (b) The result of running a graph-theoretical model that revealed five distinct components (Bodin *et al.* 2006).

2.4 Spatial multiscale heterogeneity

Understanding the response of populations to multiscale heterogeneity is important. Multiscale heterogeneity in forest structures can be viewed at branch, tree, tree group, stand, landscape and larger geographic scales (Kuuluvainen 2002). When performing network analysis, the concern is mostly to provide new knowledge on species population dynamics at a landscape or regional scale. When looking at the ecology of particular substrate-depending species it is often more relevant to focus on heterogeneity at a tree or tree-group scale to be able to draw conclusions, for example, concerning the lungwort (*L. pulmonaria*) growing preferably on aspen (*P. tremula*) or goat-willow (*S. caprea*). For other species such as mammals and birds that potentially move longer distances it may often be suitable to focus on heterogeneity at a landscape scale for describing their distribution pattern. Also, it is useful to distinguish between functional and structural heterogeneity. Structural heterogeneity denotes any variability in the system studied without reference to functional effects. Functional heterogeneity means variability in system properties (e.g. species diversity) that affects important ecosystem processes such as productivity and nutrient cycling in boreal forests (Kuuluvainen 2002). Therefore, the concern will mostly be about functional heterogeneity when studying specific species and interactions between species.

2.5 Extinction debt in a changing forest landscape

In Sweden, the north-eastern coastal region on the Bothnian bay coast and along the large rivers have a long history of human impact due to larger settlements. In northern parts of the country modern forestry practices such as clearcuts have historically been more pronounced at lower altitudes, below the near-mountainous forests. There could be a time-lag in different species' reaction to forestry activities that cause landscape change such as habitat loss. This time-lag is referred to as an extinction debt (Tilman *et al.* 1994). In Fennoscandia, we have limited knowledge on the distribution of many forest-dwelling species before large-scale modern forestry operations began, and as a consequence it is difficult to evaluate the influence of long-term fragmentation of suitable habitat. One way of approaching effects from long term fragmentation on different species groups is to examine reference landscapes that are naturally heterogeneous. Naturally fragmented landscapes have a species pool that might be expected to occur in the same type of recently disturbed landscapes with a similar degree of fragmentation, provided that the species pool has reached its stochastic equilibrium (Berglund and Jonsson 2005). For a species occurring at its local scale, such as a small habitat patch, one main factor involved is how long-lived the species is after it has been cut off from its source pool if treating the population in a metapopulation sense (Hanski 1994). Berglund and Jonsson (2005) investigated whether the richness of epiphytic lichens and wood-inhabiting fungi on dead trees in recently isolated woodland key habitats (WKHs) in a boreal forest region of Sweden diverged from species richness levels in reference forest patches that had been naturally isolated for millennia. Population numbers of crustose lichens were found to be higher than expected in the WKHs compared to the outcome of a modeling scenario. This result could be due to an extinction debt for crustose lichens. I find it reasonable to suspect that many species of epiphytic lichens which are long-lived and growing on a rather stable substrate such as goat-willow or aspen may react slowly to isolation and still survive on their host trees after a long time has passed. They will probably eventually go extinct due to the current fragmentation-grade and as an effect of their dispersal limitations and successive dying off. A larger survey of forest species in Finland estimated that about 1000 forest species were suffering from an extinction debt (Hanski 2000). The same study evaluated the possible survival of different forest species in a future forest management scenario and came to the conclusion that it is probably best to concentrate the efforts of reconstructing or protecting habitats to certain regions to ensure most species to survive. Prominent positive effects came from protecting and reconstructing more forest habitat patches close to larger reserves which could support species pools on a landscape scale.

2.6 Models used for a spatial approach to landscape ecology

Knowledge on whether the local distribution of a rare or declining species is restricted by poor dispersal capacity and/or by habitat requirements will have conservation implications (Niemelä 1997) and be of relevance for the spatial model used. Dispersal-restricted species are usually favoured by an increase in habitat patch area and increased connectivity among patches. A habitat specialist is more favored by creation of new patches and an increase of habitat quality in present patches (Öckinger *et al.* 2005). For many birds, lack of habitat in the landscape seems to be the main restriction (Fahrig 2002), while for epiphytic lichens dispersal and colonization ability may be the main obstacle (Öckinger *et al.* 2005).

2.7 Habitat patch variables and GIS-analyses

Analysis on how spatially separated populations are affected by a changing landscape is usually focused on identifying the most influential variables affecting a species' occurrence across the landscape. Habitat fragmentation and/or habitat loss are usually a problem for many threatened species. There is both a spatial aspect with focus on how the preferred habitat is distributed over a landscape and a temporal aspect that takes into account habitat patch lifespan (Fahrig 1992). These spatiotemporal aspects can be studied in a geographic information system (GIS) using computer software like ArcGIS (Environmental Systems Research Institute 2009). Vegetation vector maps of landcover data and forest land cover types might be combined for a comprehensive vegetation map while studying forest species (Ecke *et al.* 2006). Other relevant forest parameters such as stand age of forests in Sweden could be derived from maps produced from a *k*-Nearest Neighbour (*k*NN) interpolation algorithm on a Landsat-5 TM scene used in combination with forest inventory datasets from the Swedish National Forest Inventory (Franco-Lopez *et al.* 2001, Reese *et al.* 2002, 2003). These types of maps along with data on species occurrence and historical aerial photographs (provided by Lantmäteriet) make up the geographical tools for studying habitat patch changes and distribution of habitat patches in the landscape over time. Habitat fragmentation indices may be calculated by the FragStats software from raster images of landscapes produced by GIS-software as input data (McGarigal and Marks 1995). When treating landscape data from a species perspective one refers to habitat patches in the landscape (Fahrig 1992). The spatial data analysis is best performed if it can cover the whole specific habitat patches within the study area (e.g. Ecke *et al.* 2010). These habitat patches are often connected in the landscape and can be further analysed with a graph theory network analysis method. Graph-theory can be described as a third data structure to represent a landscape, in addition to the vector based information delineating land cover types as polygons and the raster lattices representing the landscape as a grid (Urban and Keith 2001). A graph in this context represents a landscape as a set of nodes (habitat patches) connected by paths that join pairs functionally (by dispersal of an organism). This kind of representation gives the opportunity to analyse landscape data in a more ecological sense. The importance of using a network approach is obvious if the landscape is more or less fragmented, in contrast to consisting of a large continuous habitat patch that dominates the landscape. Also, applying new methods along with graph theory, such as network centric methods (Bodin and Norberg 2007), may reveal important ecological information. These methods are proposed as suitable to (1) identify individual habitat patches that are disproportionally important to preserve organisms' ability to traverse a fragmented landscape, and (2) find internally well-connected compartments of habitat patches that contribute to a spatial compartmentalization of species' populations (Bodin and Norberg 2007). The network analysis methods may be seen as the final stage to analyse spatial data of habitat patches, where a software such as JMatrixNet (Bodin 2006) is suitable to use.

3 Grey-sided vole (*Myodes rufocanus*) ecology

3.1 Suitability as model species

The documented long-term decline, the occurrence linked to large forest patches, the availability of long-term landscape data around the sampling plots for the grey-sided vole argue for the potential use of this vole as a model species to study (Christensen and Hörnfeldt 2003, Hörnfeldt 2004, Hörnfeldt *et al.* 2006, Ecke *et al.* 2006, 2010, Christensen *et al.* 2008). When using *M. rufocanus* as a model species in a future network study, the minimum focal forest patch of about 80 ha (coniferous forest >60 yr) reported by Ecke *et al.* (2010) could be used as the minimum habitat patch size requirement. To follow up this threshold estimate, a landscape study on a large regional scale focusing on the occurrence of *M. rufocanus* in forest patches of different size and quality in different kind of protected areas will be crucial, by testing whether there is a general such threshold that may limit the occurrence of the species (see also Christensen *et al.* 2008, Ecke *et al.* 2010). This will contribute to the science of landscape ecology and to the study of small mammal dynamics by adding knowledge on the effects from a rapidly changing forest landscape.

3.2 Habitat selection and demography

In Fennoscandia, grey-sided voles are primarily forest dwelling (Siivonen 1968, Kaneko *et al.* 1998). When occurring in upland forest regions the species prefers meso- and eutrophic birch and spruce forests, while in lowland regions preference is directed toward boulder terrain and pine forests with *Vaccinum myrtillus* L. and *Empetrum nigrum* L. in the forest layer (Siivonen 1968, Henttonen *et al.* 1992, Ecke *et al.* 2006). A high quality habitat may be seen as a source habitat. To distinguish a source habitat, demographic data in addition to vole density data needs to be incorporated (Christensen 2006). Occurrence of reproductive females was proposed as a good indicator of a high quality habitat in addition to vole density data. This is because a high quality habitat for a species doesn't necessarily have a positive relationship with the species' density data alone (Van Horne 1983). Christensen and Hörnfeldt (2006) recently analysed habitat preferences of reproductive grey-sided vole females at the microscale around trap-stations in boreal Sweden. They identified four preferred vegetation types: (1) forest/mire complexes rich in dwarf-shrubs, (2) coniferous forests of the moist dwarf shrub type or (3) of the myrtillus type, and (4) coniferous forest mixed with deciduous trees of wet/hydric dwarf-shrub type. In the Ammarnäs mountain region, Ecke *et al.* (2003) identified birch and coniferous forest of heath type as the preferred habitat types, when all grey-sided vole categories were pooled. An important feature in *Myodes* spp. is their territorial behaviour of females, limiting the number of potential territories and hence number of individuals per unit area (Viitala 1977, Löfgren 1989). Viitala (1977) reported that maturation of female grey-sided voles ceased when all habitable space where occupied. Generally, demography changes with phase (and hence density) of the vole cycles, in *Myodes* spp. as well as other voles. The reproductive season, for example, is longest and most intense in the increase phase and becomes successively shorter throughout the cycle (Kalela 1957, Krebs and Myers 1974, Nyholm and Meurling 1979, Stenseth *et al*. 1985, Kaneko *et al.* 1998). In contrast, body size and aggression vary in a more or less opposite way being highest at the peak (Krebs 1970, Boonstra and Krebs 1979). Andreassen and Ims (1990) concluded that female breeding activity was affected by the quality and quantity of food and that malnutrition caused delayed sexual maturity in females. The high level of aggression of female grey-sided voles associated with peak phase populations (Boonstra and Krebs 1979) could be connected to a low food supply and malnutrition (Andreassen and Ims 1990).

3.3 Habitat properties of the landscape

Age of the forest, proximity and access to old pine forest seem to be variables that can partly explain the decline of the grey-sided vole in the county of Västerbotten, in northern Sweden (Hörnfeldt 2004, 2010, Christensen 2006, Ecke *et al.* 2006, 2010, Hörnfeldt *et al.* 2006). In addition, results that emerged from analysing environmental monitoring data on the occurrence of grey-sided vole on permanent sampling plots along with those from a field study on temporary plots also highlighted the importance of a patch perspective approach when studying the species' decline in relation to forest fragmentation (Christensen *et al.* 2008). Forest patch size and quality are considered to be important parameters for explaining the decline of *M. rufocanus* (Christensen *et al.* 2008). It is probably a combination of local habitat, focal forest patch size and quality as well as habitat properties in the surrounding landscape (the matrix) that together explain the local abundance (Christensen and Hörnfeldt 2006, Christensen *et al.* 2008). *Myodes rufocanus* seems to be positively affected by the occurrence of older forests (>60 years old) and a high proportion of old-growth pine forests in the landscape (Christensen *et al.* 2008).

3.4 Dispersal potential in the forest landscape

For a measure of dispersal ability of the grey-sided vole it is possible to use the distance of around 0.2 km reported by Saitoh (1995) for natal dispersal and the long-range dispersal of about 3 km for adults in the increase phase of the vole cycle reported by Oksanen *et al.* (1999). A calculation based on relationships between home range size and dispersal distance as found by Bowman *et al.* (2002), and using a home range size of 0.135 ha for reproducing grey-sided vole females (Löfgren 1995), gives a median dispersal of 0.26 km and a maximum dispersal of 1.47 km (according to two different formulas in Bowman *et al.* (2002)).

Depending on local density and phase of the vole cycle, individuals are more or less prone to undertake long-range dispersal. Oksanen *et al.* (1999) studied grey-sided vole dynamics in a low arctic tundra landscape of northernmost Fennoscandia. The landscape is characterized by a pronounced fragmentation of productive habitats with unproductive heaths dominating the surrounding landscape. Populations of *M. rufocanus* make up the largest part of the microtine rodent fauna in that landscape with highest density in productive habitat patches. The estimated dispersal rates were dependent on survival rate of the dispersing animals and also on the frequency of trappings (trapping grids and dispersal path ways are shown in Fig. 4). Despite contrasting patterns in numerical fluctuations in productive and unproductive sub-areas the areas were connected by long-range dispersal and especially presaturation dispersal (*sensu* Lidicker 1975).

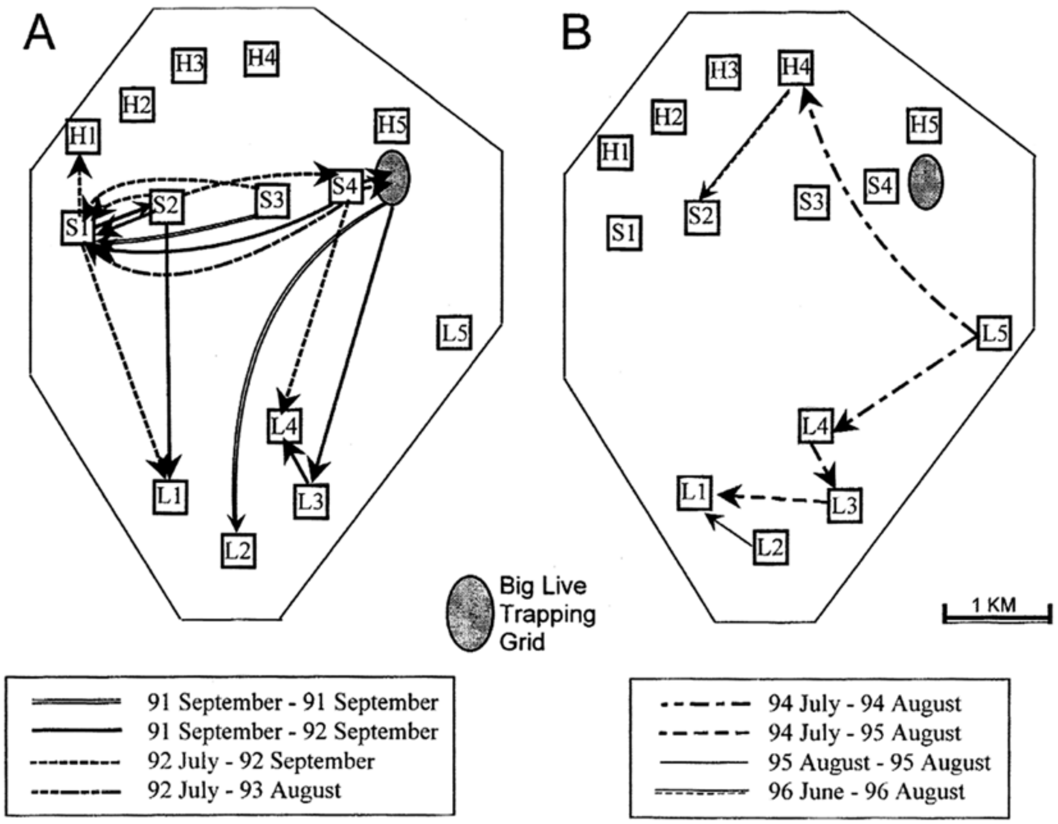


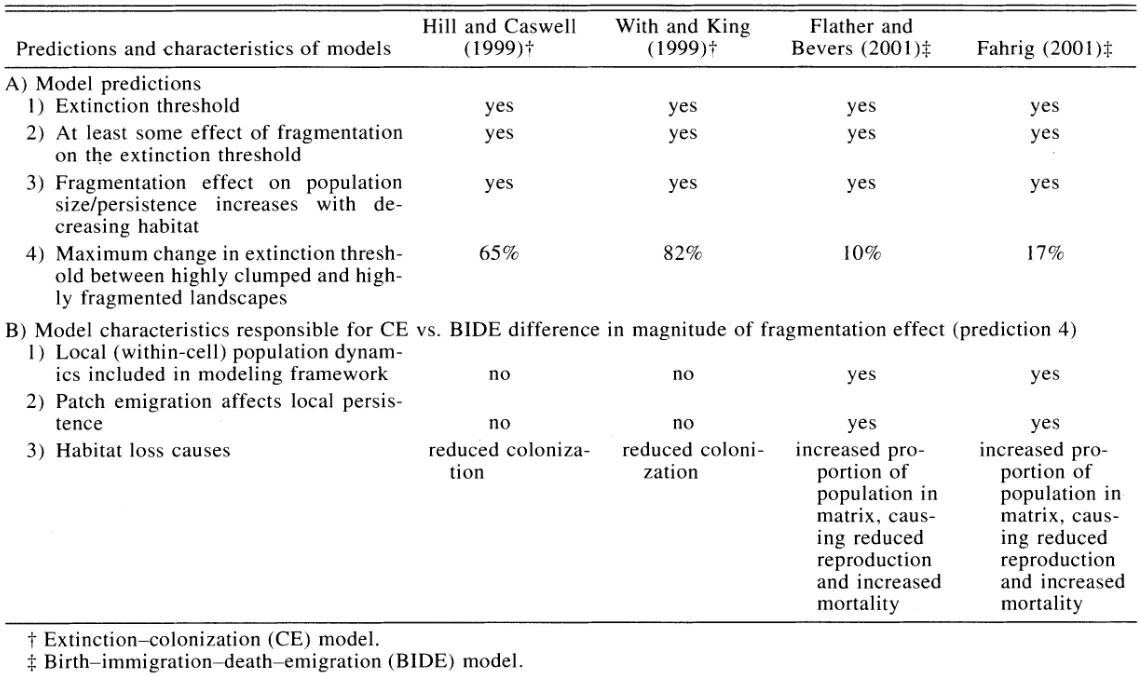
Figure 4. Recorded cases of between-grid dispersal of grey-sided voles. A: cases recorded during the increase phase 1991-1992. B: cases recorded during decline and low density phases 1994-1996 (Oksanen *et al.* 1999)

The occurrence of long-distance dispersal up to approximately 3 km is an interesting aspect to take into account, especially as it was reported to be connected to a period of rapid population growth for *M. rufocanus* by Oksanen *et al.* (1999). Dispersal ability is probably very much dependent on the amount of suitable habitat in the landscape. However, long-distance movements between habitat patches may be hard to track in homogenous landscapes without distinct dispersal corridors. Studying the grey-sided vole in a network of forest patches, a range of dispersal distances would probably be suitable to use with an upper distance of approximately 3 km for complete isolation of a habitat patch. To complement the dispersal measures currently available, I suggest a “homing study” by using the vole’s behaviour to return to its home range after being translocated to various distances. Such a study may reveal maximum dispersal ability for different sexes and ages of the voles and during different phases of the vole cycle.

3.5 Extinction threshold

Extinction thresholds imposed by habitat restrictions are valuable to estimate for different species in contrasting landscape surroundings and also important to apply when performing a network analysis. Species extinction of at least birds, and possibly other taxa, on a landscape scale is closely connected to the remaining habitat in the landscape (see below). Different models for estimating habitat fragmentation include colonization-extinction models and birth-immigration-death-emigration models (Fahrig 2002). Two models from each of these types were reviewed by Fahrig (2002) with respect to their predictions on the effect of population extinction thresholds (Table 1). The colonization-extinction models predict that the pattern of the habitat patches is an important issue for extinction thresholds (see A4 in Table 1). In contrast, the birth-immigration-death-emigration models predict that habitat loss rather than the spatial pattern of habitat patches are important for the species persistence (see B3 in Table 1). According to Fahrig (2002), extinction thresholds may be very different depending on the adaptability of the studied species to utilize the matrix. Living in the matrix may be triggered by habitat loss and increase as a direct effect of continuing habitat loss. The part of the population living in the matrix should theoretically become more susceptible to decreased reproduction and increased mortality (Fahrig 2002). Empirical studies on birds have emphasized that their abundances are more affected by habitat loss than by the pattern of habitat patches in the landscape (Table 1). These empirical studies support the usage of birth-immigration-death-emigration models that take into account that loss of habitat will increase the proportion of the population that spends time in the matrix (Fahrig 2002). This effect would be interesting to test with the grey-sided vole as a model species and poses these three questions in accordance: (1) In which different matrix types do the voles occur if they can survive in the matrix? (2) To what extent do voles reproduce when being forced to live in different matrix types? and; (3) To which degree does mortality increase or decrease in different kind of matrices? In a conservation management sense, research on these issues could be built into the management plans for species persistence on a landscape scale and extinction thresholds for different regions may be calculated. Management objectives that focus on halting the habitat loss primarily according to the birth-immigration-death-emigration models will become more efficient. One should also take into account that if the overall reproduction rate is too low relative to mortality, for example due to pollution or competition with other species, this is the largest factor influencing extinction thresholds. In such a scenario there are simply too few individuals to inhabit the suitable habitat patches present (With and King 1999, Fahrig 2001, 2002). No amount of habitat will then be sufficient for population persistence and the extinction threshold will not be ruled by habitat amount. The landscape could contain 100% suitable habitat and still the population would be declining in such a scenario.

Table 1. Comparison of four spatial models that predict the landscape-scale effect of habitat fragmentation and habitat loss on the population extinction threshold (Fahrig 2002).



Predictions and characteristics of models	Hill and Caswell (1999)†	With and King (1999)†	Flather and Bevers (2001)‡	Fahrig (2001)‡
A) Model predictions				
1) Extinction threshold	yes	yes	yes	yes
2) At least some effect of fragmentation on the extinction threshold	yes	yes	yes	yes
3) Fragmentation effect on population size/persistence increases with decreasing habitat	yes	yes	yes	yes
4) Maximum change in extinction threshold between highly clumped and highly fragmented landscapes	65%	82%	10%	17%
B) Model characteristics responsible for CE vs. BIDE difference in magnitude of fragmentation effect (prediction 4)				
1) Local (within-cell) population dynamics included in modeling framework	no	no	yes	yes
2) Patch emigration affects local persistence	no	no	yes	yes
3) Habitat loss causes	reduced colonization	reduced colonization	increased proportion of population in matrix, causing reduced reproduction and increased mortality	increased proportion of population in matrix, causing reduced reproduction and increased mortality

† Extinction–colonization (CE) model.
‡ Birth–immigration–death–emigration (BIDE) model.

4 The lungwort (*Lobaria pulmonaria*) ecology

4.1 Suitability as model species

The lungwort (*L. pulmonaria*) and also *L. scrobiculata* (Scop.) DC. are threatened epiphytic lichens that depend on goat-willow or aspen as substrates (occasionally birch, spruce or mountain ash). They both have a distribution which includes the boreal forest region in Sweden (Gärdenfors 2010) and their substrate dependence makes the description of suitable habitat rather different than for more mobile species with home-ranges such as birds and mammals. In an evaluation of different inventory methods Carlsson (1996) proposed that a reasonable approach would be to concentrate the efforts on sampling good-quality aspen trees and goat-willows rather than the *Lobaria*-lichens themselves. Important results from the pilot study of Carlsson (1996) included the positive dependence of *L. pulmonaria* occurrence on trees with an increasing diameter at breast height (DBH; Table 2). The frequency (%) of goat-willows with *L. pulmonaria* were rather low and the total numbers would possibly be too low for handling in a statistical analysis. The species is well known for many people working with forestry management in Sweden as an indicator species indicating high natural values (Nitare 2005). Hence, it would be instructive to model this species in order to use the analysis results for conservation management purposes on a regional scale. Current species data (December, 2009) from the Swedish species gateway includes 3851 reports of *L. pulmonaria* from Västerbotten and 1769 reports from Norrbotten (Anonymous 2009). I assume that the data is probably biased and collected preferably from high quality forest patches in protected areas or WKHs. With this bias in mind, the lungwort reports could be used to recognize preferred vegetation type, tree-type composition and environmental variables for a preliminary network analysis of the spatial distribution of lungwort.

Table 2. Observed number of goat-willows of different BHD*-classes in a forest stand close to Norrmyrberget in Norrbotten, Sweden in 1995, and number and frequency (%) of goat-willows with *Lobaria pulmonaria* according to a pilot study on inventory methods for epiphytic lichens (see Carlsson 1996).

BHD (cm)*	No. goat-willows	No. goat-willows with *L. pulmonaria*	% of all goat-willows (*N* =58) with *L. pulmonaria*	% goat-willows with *L. pulmonaria* per BHD-class
< 20	33	3	5	9
≥ 20 - < 30	18	6	10	33
≥ 30 - < 40	4	3	5	75
≥ 40	3	2	3	67
Total	58	14	24	

* BHD = tree diameter at breast height

4.2 Habitat selection of epiphytic *Lobaria* lichens

Habitat selection and occurrence of *L. pulmonaria* in different populations seem to depend on a number of factors which according to Carlsson (1996) include:

- The grade of isolation. The *Lobaria spp.* seem to prefer late fire-succession forests. Fire-dependent species usually have a good dispersal capability. The black fire beetle *Melanophila acuminate* DeG., for example, can sense a forest fire from long distance and spread over tens of kilometers (Nilsson *et al.* 2001). However, the current *Lobaria* species that occur on old host trees in late fire-succession forest stands have originally established in a less fragmented landscape with shorter distances between potential host trees. They are not adapted for long range dispersal in the same manner as the beetle. Isolation of potential habitats would thus become a problem for the lichens.
- The orientation and shape of the habitat stand. A slim and long forest patch will have larger edge-influence than a circular patch, in the sense of a longer edge and larger area facing towards the surrounding matrix.
- *L. pulmonoria* reacts negatively to pollution and fertilizilation. In boreal forest regions in Sweden, an important issue these days is intensive energy forest harvesting with increased fertilization. The potential negative effects on *Lobaria*-lichens may be important to consider and affect their habitat quality.

According to Gustafsson and Eriksson (1995), the local occurrences of epiphytes on aspen are primarily correlated with light conditions, thickness of aspen stands, ground vegetation and the cation content of the ground layer. The influence of these various variables on *L. pulmonaria* occurrence means that the trees in a stand that act as hosts are usually in much lower numbers than the available number of aspen and goat willow trees (see Table 2).

4.3 Different types of dispersal and their limitations

Dispersal by soredia was proposed as the main type of dispersal for the common lichen species *Hypogymnia physodes* (L.) Nyl. by Armstrong (1990). In his experiment soredia and thalli fragments were trapped on adhesive strips at different sites during a 36 day period. Dispersal by soredia was more common than by thalli-fragments. Further, survival and colonization were enhanced if the surface of the bark was rough and heterogeneous rather than smooth and homogenous. Dispersal of *L. pulmonaria* is mainly vegetative (i.e. by soredia or thalli fragments, Hallingbäck 1986), although this species can also reproduce and disperse by spores. Vegetative dispersal is mediated by releasing soredia, isidia or parts of the thalli for transport through the landscape. Spore dispersal is very unusual because of the low production of fruiting bodies (Hallingbäck 1986). Overall, dispersal capacity in lichens is poorly studied, as it is difficult to study. Sometimes conclusions on dispersal have to rely on what the lichen population structure looks like. Dettki *et al.* (2000) compared the number of thalli found in second growth forest stands (35-78 years old) to the number of thalli in old-growth stands (122-298 years old), where the latter were thought of as propagule sources. They found a negative effect on number of thalli in five of six groups of lichens with increased distance from the old-growth stands. The result indicated that dispersal distance capacity is an important factor explaining low numbers of epiphytic lichens in young forests. In a study in southern Sweden, local distribution of *L. pulmonaria* was investigated at 12 sites in 1992 and 2001 (Öckinger *et al.* 2005). By comparing trees with a successful colonization in 2001 and their nearest neighboring trees occupied by *L. pulmonaria* in both 1992 and 2001 a mean distance of dispersal was calculated to 35 m with a maximum dispersal distance of 75 m. At least 18 new trees were colonized by the lichen. All these trees were found at sites where the lichen was already present on other trees in 1992. There were no new colonizations at sites where the lichen was absent in 1992. These results support the hypothesis that dispersal capacity is the main factor limiting the distribution of *L. pulmonaria* and short-range dispersal is the main form of dispersal in the landscape (Öckinger *et al.* 2005). On a local spatial scale, short-range dispersal may be sufficient to support a viable population, but at a landscape or regional scale it is probably very difficult to survive and recolonize new trees for this kind of species and dispersal. A comparative study on the occurrence of *L. pulmonaria* in fragmented managed forest and in non-fragmented old-growth forest indicated a more clumped distribution in the fragmented stand (Wei-Dong *et al.* 2001). The authors suggested that a higher continuity of suitable habitat containing host trees was present in the old-growth stand. The spatial pattern of the lichen's occurrence was in line with an hypothesis assuming that tracking of host trees by the lichen could be interrupted in a managed, fragmented landscape because of discontinuity in the distribution of host trees (Wei-Dong *et al.* 2001).

4.4 Availability of substrates in a dynamic forest landscape

In the boreal biome, generalist species, which survive in a wide range of habitat conditions, dominate (Kuuluvainen 2002). A smaller number of species, such as the lungwort (*L. pulmonaria*), are specialist species that are dependent on specific substrates (Kuuluvainen 2002). Lungwort is especially bound to late succession forests after a fire where the preferred substrate species, viz. older goat-willow and aspen trees with a coarse bark structure, has had the ability to grow in a moist climate. These late succession forests are a mix of deciduous/coniferous forest containing deciduous trees with a pH above ~5.5 on the bark and a light and moist microclimate (Hallingbäck 1986). Old deciduous trees are an important component of functional heterogeneity in boreal forests. An old *Salix caprea* tree may host a number of specialist species of lichens including *Lobaria pulmonaria, Lobaria scrobiculata, Nephroma bellum* (Spreng.) Tuck., *Nephroma parile* (Ach.) Ach. and *Nephroma resupinatum* (L.) Ach. (Nitare 2005). In southern Sweden presence of *L. pulmonaria* has been positively correlated to the presence of other Red-listed epiphytes and also to Red-listed beetles dependent on hollow trees (Nilsson *et al.* 1995). Epiphytic lichens are perhaps the single most important species group depending on trees as physical growing surfaces (Kuusinen 1996, Kuuluvainen 2002). Goat-willow is probably the most important substrate for lungwort, but little has been published on the ecology of goat willow. Field experiments suggest that its life history parameters resemble those of aspen (Snäll *et al.* 2005). There are records of goat willows up to 200 years old in northern Finland (T. Wallenius, unpubl.). Both aspen and goat-willow have declined in density in the boreal forest landscape in the last decades (Snäll *et al.* 2005). For aspen in Sweden there has been a decline in rejuvenation rate since the beginning of the 1970s, while the volume is rising (Edenius *et al.* 2008). An important factor explaining the increase in aspen volume, estimated to about 70% during the last 20 years, is reduced cutting (Edenius *et al.* 2008).

4.5 Planning area units for analysis of *L. pulmonaria* occurrence

An estimation of the area that would cover a population of *L. pulmonaria*, appropriate for planning field studies on a landscape scale, has been proposed by Angelstam *et al.* (2004): "Assume that a 100-m buffer zone of old forest around a suitable habitat patch would allow protection for blow-down of trees at the edge and also the maintenance of a moist local climate in a 1-ha area including about 500 trees. This corresponds to a stand size of ca 5 ha. Further, assume that such stands cover about 2% of the landscape as Swedish key biotopes do (Hansson 2001), and that the suitable window in time in the succession is 20% of the rotation of 100 yr, the area needed for a population is ((5/0.02)/0.2) = 1250 ha = 12.5 km^2".

In parts of a landscape the proportion made up of suitable habitat patches of currently protected areas may be higher or lower than the above mean value of 2%. Identifying such contrasting areas is important. The habitat patches in these contrasting areas are expected to be separated by different distances which may cause difficulties, when also adding dispersal capacity for *L. pulmonaria*, to the calculation of the area needed to cover a population of the lichen. Öckinger *et al.* (2005) showed that occurrence of *L. pulmonaria* is mainly restricted by dispersal distance (see 4.3 above).

5 Understanding spatially separated populations of threatened forest species

5.1 Background to network analysis

Metapopulation models are often used to describe how different sub-populations of a species are distributed in the landscape (Hanski 1994). In these models it is common practice to use species-specific dispersal distances in order to predict how the exchange of individuals among habitat patches are in a fragmented landscape (Hein *et al.* 2004). The ability for an organism to disperse through a hostile matrix to any suitable patch is usually ignored, but from a species persistence perspective this may be very important. Hein *et al.* (2004) simulated such a scenario with factors such as patch number, movement pattern and dispersal mortality. The network theory combines metapopulation theory with these types of ecological scenarios of species moving in the landscape into a model. However, it is preferable to adopt a permeability value for moving through a more or less hostile matrix, instead of considering the matrix between patches as completely hostile for settling in temporary habitats (Urban *et al.* 2009). The graph theory is informative for management planning of species conservation because of its graphical output (see Fig. 5 and Bodin 2006). Further, the output could be supplied with actual values on fragmentation indices (McGarigal and Marks 1995) that may be analysed individually for each species model.

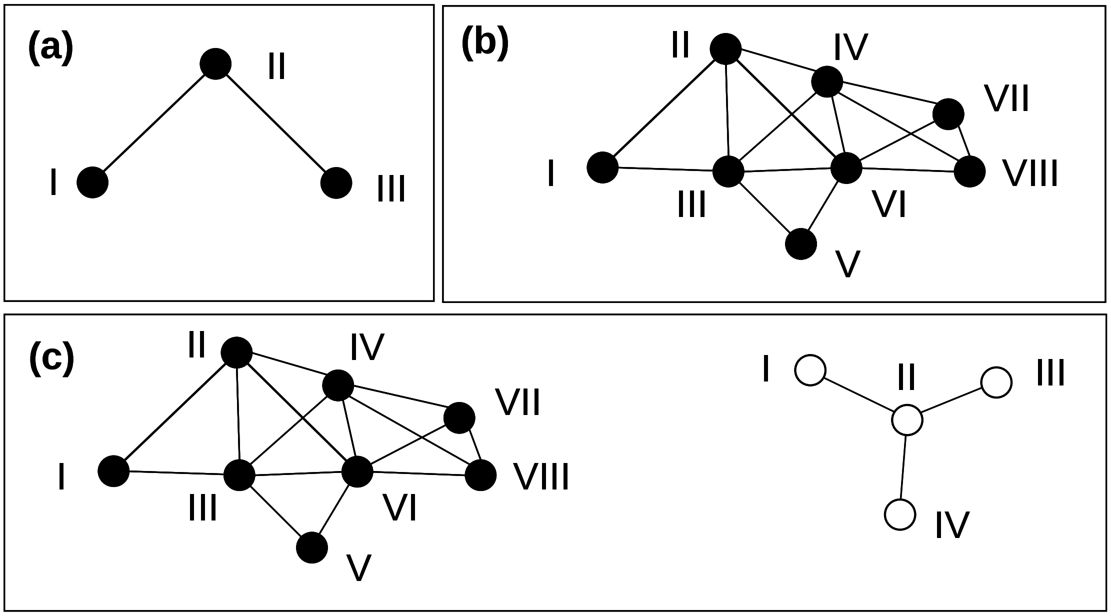


Figure 5. Schematic illustration of the network theory concept (Ecke and Bodin *Manuscript*). Two patches (*syn*. nodes, represented as circles) are considered as connected or linked (illustrated by the black lines) if they are located within a certain threshold distance, i.e. patches I-II and II-III but not I-III in (a). A network component consists of inter-connected patches (b). The diameter in (b) equals three, i.e. the shortest distance between the most separated patches (patches I and VIII) equals three links. The network in component (b) also provides alternative pathways among the patches. For example patch V can be reached from patch I via patch III. However, patch V can also be reached from patch I via the patches II-III or II-IV-VI. The network in (c) consists of two components (represented by black and white patches, respectively). The network is fragmented since the two components are separated by a longer distance than the defined threshold distance.

5.2 The importance of using a network approach for understanding species dispersal

Graph models are a robust framework for studying connectivity patterns on a landscape level. Especially interesting is the idea to establish different degrees of dispersal permeability among habitat patches depending on the surrounding matrix. The species specific dispersal distance could be treated either as a straightforward Euclidean distance between edges or centroids of nodes in a patch network or as functional distance weighted to reflect navigability or matrix permeability (Urban *et al.* 2009). The functional distances in a GIS are computed as ‘least cost paths’ over a ‘cost surface’. The cost surface is the matrix between patches. The matrix is assigned different degrees of permeability depending on whether hostile habitat or physical barriers such as roads or streams are present or not. These ideas have existed for some time but it is only recently that it has become computationally feasible to compute least-cost links for a large graph of hundreds of nodes in a GIS (Urban *et al.* 2009). The computational process for building landscape networks with functional connections between patches in a GIS environment has been described as a user guide to functional connectivity modelling by Theobald *et al.* (2006). Although it is possible to perform these modeling approaches, a computational limitation still exists with very large graphs networks. Often the models used only calculate one least cost path between two patches. However, alternative paths with comparable costs may also exist. There are some graph theory models that encounter this problem and extend the least cost approach (Urban *et al.* 2009). Two of these models using multiple dispersal routes were applied to a real landscape by Pinto and Keitt (2009). They simulated habitat destruction which caused existing dispersal routes between patches to become narrower and eventually disappear. To describe species’ dispersal abilities it is probably important to incorporate the option of alternative least cost pathways for dispersal in complex landscapes (McRae *et al.* 2008).

6 Applied network analysis using model species from different taxa

6.1 A literature review of an array of forest species possibly suitable for network analysis

A recent study of five bird species: lesser spotted woodpecker (*Dendrocopus minor* L.), white-backed woodpecker (*Dendrocopos leucotos* Bech.), three-toed woodpecker (*P. tridactylus*), long-tailed tit (*A. caudatus*) and siberian jay (*P. infaustus*) concentrated on information suitable to use in a network analysis (Angelstam *et al.* 2004; Table 3). These five species all have shown declining population trends in Sweden that may be interesting, in a conservation sense, to relate to time-series of forest landscape changes. Further, I propose some specialized species from contrasting taxa as suitable to use when studying the functionality of habitat networks of protected areas for species persistence (Table 4). The species proposed occur in the forested areas of northern Sweden. The dispersal potential of the comparatively rare shrews *Sorex caecutiens* Laxm., *S. isodon* Turov and *S. minutissimus* Zimm. in Table 4 has not been studied as far as I know. For these species, habitat selection data is probably the only relevant information available for network analysis purposes at present (Hanski and Kaikusalo (1989) after Ivanter (1981); Table 5).

Table 3. Parameters for habitat suitability modeling (1-2) for five potential focal bird species in the northernmost landscape region of boreal Sweden (the counties Västerbotten and Norrbotten), and estimates of the minimum area (rounded to the nearest 1000 ha) hosting a local breeding population of 100 females in a landscape with pure habitat (3) or minimum amount of required habitat (4). Unpublished expert knowledge provided by ornithologists is denoted with the symbol ≈ (after Angelstam *et al.* 2004).

Species	1. Habitat area requirements for one pair or social unit[1] (ha) (HAB_PATCH)	2. Required minimum landscape-scale proportion % (HAB_PROP)	3. Area requirement (ha) of a "population" of 100 breeding females in "pure-habitat" landscapes[2]	4. Area requirement (ha) of a "population" of 100 breeding females with minimum HAB_PROP
Lesser spotted woodpecker	40	0.2	8000	40000
White-backed woodpecker	100	0.1	50000	500000
Three-toed woodpecker	100	≈0.1	30000	≈330000
Long-tailed tit	10	0.15	2000	11000
Siberian Jay	50	0.5	10000	20000

[1.] Note that this area does not need to be a single patch but may rather be a network of interconnected patches within the home range.

[2.] A pure-habitat landscape is defined as a planning unit where suitable habitat make up the whole landscape, i.e. HAB_PROP = 1.

Table 4. Estimates on habitat size requirement and dispersal capacity (distance) for seven bird species, two epiphytic lichens, four insects and five small mammals. I propose these species as suitable to include in a network analysis of the functionality of habitat networks. The selection represents species occurring in the boreal forest region. Both rare specialist and more common generalist species are included.

Species	**Minimum habitat area requirement[1] (ha)**	**References**	**Dispersal distance (km)**	**Reference**	**Swedish Redlist status[2]**
Birds					
Crested tit *Lophophanes cristatus*	?		?		
Long-tailed tit *Aegithalos caudatus*	5-15	Jansson and Angelstam 1999 Angelstam *et al.* 2004	0.2 ~3	Gaston 1973 Oksanen *et al.* 1999	
Siberian jay *Perisoreus infaustus*	50-150	Edenius *et al.* 2004	1-2.4	Uimaniemi *et al.* 2000	NT
Middle spotted woodpecker *Dendrocopos medius*	75	Pettersson 1985	14	Pettersson 1985	RE
Three-toed woodpecker *Picoides tridactylus*	109	Pechacek 2004	6.35[3]	Pechacek 2006	NT
Capercaillie *Tetrao urogallus*	80-220	Angelstam *et al.* 2004	5-20	Keith and Gareth 1998	
Hazel Grouse *Bonasia bonasia*	?		5.7[3](m)[4] 4.8[3] (f)[4]	Fang and Sun 1997	
Lichens					
Lobaria pulmonaria	Dependent on substrate [5]		0.035	Öckinger *et al.* 2005	NT
Lobaria scrobiculata	Dependent on substrate [5]		?		NT
Insects					
Calathus micropterus	?		?		
Platynus mannerheimii	?		?		NT
Tachinus elegans	?		?		NT
Lycaena helle	0.60-0.90	Bauerfeind *et al.* 2009	0.235-0.287	Bauerfeind *et al.* 2009	EN
Small mammals					
Common shrew *Sorex araneus*	~ 0.6[6]	Hanski 1986	?		
Taiga shrew *Sorex isodon*	?		?		NT
Grey-sided vole *Myodes rufocanus*	80[a, 7] 0.135[b, 6] 0.03[c, 6]	[a] Ecke *et al.* 2010 [b] Löfgren 1995 [c] Viitala 1977	0.2[a, 3] ~3[b] 0.257[c, 8]	[a] Saitoh 1995 [b] Oksanen *et al.* 1999 [c] Bowman *et al.* 2002	
Bank vole *Myodes glareolus*	0.424[a, 6] ~3[b, 9]	[a] Löfgren 1995 [b] Hanski 1986	<1[a] 0.4[b] 0.456[c, 8]	[a] Szacki and Liro 1991 [b] Dickman and Doncaster 1989 [c] Bowman *et al.* 2002	
Wood Lemming *Myopus schisticolor*	?		?		

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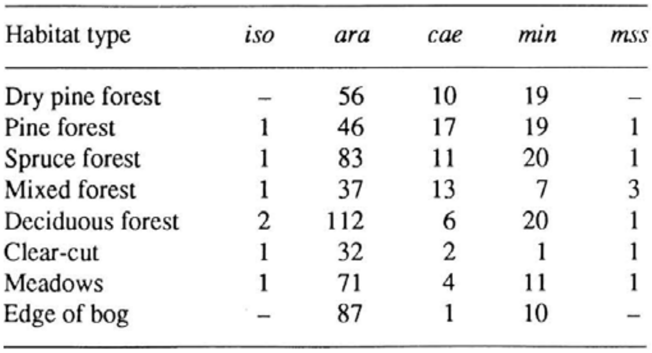
[1] If the area is dominated by preferred habitat. **[2]** Gärdenfors 2010 (NT = Near threatened, EN = Endangered, RE = Regionally Extinct). **[3]** Natal dispersal **[4]** m = male, f = female. [5] Preferably aspen (*Populus tremula*) or goat-willow (*Salix caprea*) [6] Home range [7] Minimum forest patch size [8] Calculation on median dispersal distance using home range size estimated by Löfgren (1995) [9] Minimum island size to sustain a viable population of the species in an island archipelago. **[a,b,c]** Refer to the source article for area requirement or dispersal capacity.

Table 5. Habitat selection of *Sorex* shrews in Soviet Karelia. Number of individuals per 100 trap-nights. The species are *Sorex isodon, S. araneus, S. caecutiens, S. minutus* and *S. minutissimus* (Hanski and Kaikusalo 1989 after Ivanter 1981).



Habitat type	*iso*	*ara*	*cae*	*min*	*mss*
Dry pine forest	–	56	10	19	–
Pine forest	1	46	17	19	1
Spruce forest	1	83	11	20	1
Mixed forest	1	37	13	7	3
Deciduous forest	2	112	6	20	1
Clear-cut	1	32	2	1	1
Meadows	1	71	4	11	1
Edge of bog	–	87	1	10	–

6.2 Multispecies approach to network analysis of the functionality of habitat patches

Depending on different habitat area requirements, landscape studies of different species have to be carried out on different scales. Before performing a network analysis of the functionality of habitat patches to preserve a focal species it is essential to first estimate the size of proper planning units on a landscape scale.

Angelstam *et al.* 2004 estimated the size of planning units (habitat networks) to preserve a number of forest-dwelling species listed in the EC Birds directive on a landscape scale in Sweden. The estimated minimum planning units for these bird-species were estimated to about 40 000 ha where suitable habitat dominated the landscape but to 250 000 ha on average in landscapes with minimum amount of habitat (Angelstam *et al.* 2004). Consequently, the estimated size of the planning unit will vary across the landscape according to the proportion made up by conservation areas. The amount of habitat in the landscape has been proposed as the most important factor for the distribution and abundance of birds rather than patch configuration and fragmentation (Fahrig 2002).

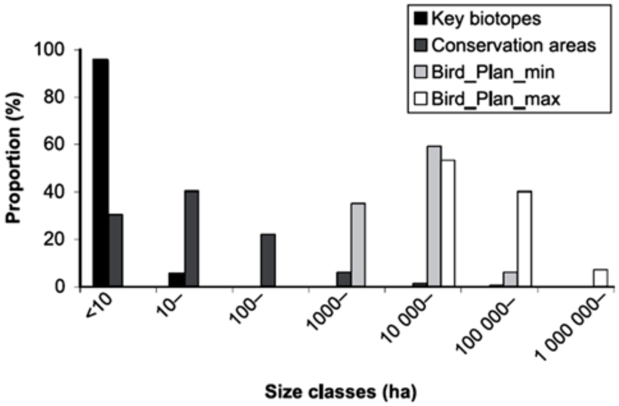


Figure 6. Distribution of the size of conservation areas (40071 woodland key habitats and 3407 protected areas) in Sweden 2004, and distribution of estimated sizes of planning units required for the maintenance of 17 forest bird species based on the minimum estimate, and of 15 species based on the maximum estimate (Angelstam *et al.* 2004).

6.3 Management tools and recommendations for forest management authorities

Illustrating networks of protected areas, more or less suitable for preserving threatened species, on digital maps will allow for applying network analysis in the planning process to locate new protected areas. The main information that may be used is (1) what kind of habitats for threatened species are currently lacking in a landscape, and (2) where are the dispersal routes too few to allow individuals to move effectively among habitats patches. I propose that mapping networks of protected areas should be undertaken to create an infrastructure for helping analysing what is missing and need to complemented with to maintain population numbers of different threatened species. More than 400 of the threatened species in Sweden have an action programme worked out for management purposes (Anonymous 2008). These action programs contain information on how large a singles species' population should be in order to be self-sustainable and which kind of habitats are preferred by the species. However, it is a difficult task to identify which suitable habitat patches that should be protected. Identifying these by network analysis will hopefully become a commonly used management tool for many species. Also, forming an infrastructure of protected areas in nature for these kind of analyses to improve the network functionality for different forest species will hopefully advance adopting similar types of network planning for species in many taxa and also in other ecosystems, for example in limnic ecosystems.

The management options for sustaining biodiversity on a landscape scale by applying network analysis tools for species in many different taxa may be summarized as follows:

- Identify where networks of suitable habitat for the target species exist and what kind of management is needed, i.e. improving the connectivity among protected areas or increasing the amount of habitat.
- Distinguish between future prospects for different threatened species and answer the management question: Which species are the most effective ones to direct the management efforts towards to ensure their future survival in a particular landscape?
- Evaluate the value of creating new natural forest protection areas in different parts of the landscape and integrate this planning with forest companies and private forest owners.
- Building the infrastructure for scientific studies by producing distribution maps for different species and parts of Sweden, in collaboration with management authorities that work out action plans for threatened species. Future updated versions of such distribution maps may also be supplemented with information of available habitat amounts.

7 Conclusions

In order to analyse spatial data of species' distribution in an ecological sense a network analysis offers new possibilities. When viewing the landscape from a species' perspective, single habitat patches or nodes are joined with neighboring patches by links. These links are a representation of the species' dispersal capacity (Urban and Keitt 2001, Bodin and Norberg 2007). The effects from the surrounding landscape on dispersal permeability are important to incorporate into a network model, which can be done by applying a 'cost surface' (Urban *et al.* 2009). In such a cost surface, different vegetation types will affect the species dispersal permeability through the landscape. The cost surface also accounts for physical barriers such as roads or streams.

Working with a multispecies approach to network analysis, it is necessary to address variation among species in their dispersal ability and means of dispersal. The contrasting dispersal ability of the grey-sided vole (*Myodes rufocanus*) compared to that of the epiphytic lichen lungwort (*Lobaria pulmonaria*) illustrates this problem. While the grey-sided voles disperse by moving actively, the lungwort's dispersal is passive and dependent on the physical environment of the air, in terms of wind and moisture conditions. For example, a favorable wind direction might carry soredia propagules from lungwort to new host trees. It has been shown that the lungwort is limited by dispersal capacity (Öckinger *et al.* 2005). However, the shortage of potential host trees, supplying suitable substrate is probably the most acute threat to the future survival of lungwort in a long term perspective in the Swedish boreal forests.

The grey-sided vole has been monitored since the beginning of the 1970s in the middle boreal forests of Sweden and there has been a pronounced population decline during recent decades (Hörnfeldt 1994, 2004, 2010). Forestry has caused a drastic change of the boreal forests in northern Sweden since the early 1970s, fragmenting potentially high quality grey-sided vole habitats (Ecke *et al.* 2006). Also, the vole's decline has recently been connected to changes of the forest landscape (Christensen *et al.* 2008, Ecke *et al.* 2010). An important research aim regarding the current grey-sided vole situation is to explore whether available habitat patch sizes compared to home range size or dispersal capacity sets the limits to the species' distribution on a regional scale. The prerequisites for a successful prediction of a species' spatial distribution using network analysis include access to high quality data on home-range size and dispersal capacity. Reliable such data have been presented for the grey-sided vole on home range size (Löfgren 1995) and dispersal capacity (Saitoh 1995, Oksanen *et al.* 1999). However, there is a need for complementary studies to explore whether dispersal distance differs depending on which matrix type the vole has to disperse through.

Other forest species, declining or threatened or not, that could be interesting to study using network analysis include: other small mammals than the grey-sided vole, bird species such as the three-toed woodpecker, long-tailed tit and the siberian jay and specialist insect species with emphasis on carabid beetles. The ability to recognize species affected by habitat fragmentation will have conservation implications for forest management practices. Planning networks based on individual species' habitat requirements and dispersal ability could be used to improve the spatial arrangement of the protected areas by creating new such areas to bridge critical gaps. These planning networks may also be thought of as an attempt to start creating a network infrastructure with wider species functionality. Establishing realistic networks for a few indicator species with variable habitat demands and dispersal abilities can help in promoting the landscape's suitability for a multi-array of other species from different taxa but with similar habitat demands as the indicator species.

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