

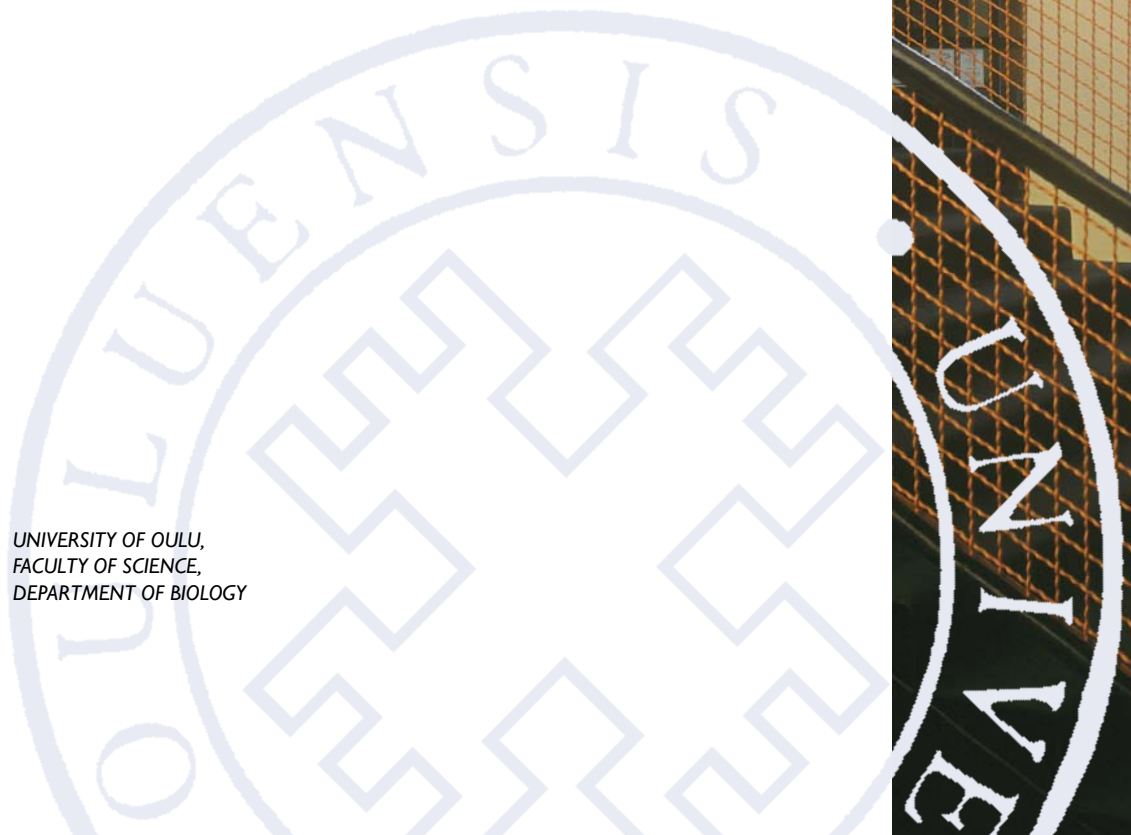
Petri Lampila

POPULATIONS AND
COMMUNITIES IN HUMAN
MODIFIED FOREST
LANDSCAPES

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FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY

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PETRI LAMPILA

**POPULATIONS AND COMMUNITIES
IN HUMAN MODIFIED FOREST
LANDSCAPES**

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Supervised by
Professor Mikko Mönkkönen

Reviewed by
Professor Henrik Andrén
Associate professor Marc Bélisle

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University of Oulu, Faculty of Science, Department of Biology, P.O. Box 3000, FI-90014

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Abstract

Alteration of natural habitat usually has two kinds of effects on the populations living in the area. No single organism is able to survive or reproduce without its habitat, so it is very easy to understand and predict direct habitat loss effects. Moreover, fragmentation effects can enhance the effects of pure habitat loss, and in some cases, the effects of fragmentation can exceed the effects of habitat loss. In addition, harvesting by humans has significantly shaped wildlife populations and done so probably well before any other human activity. Different types of anthropogenic change in nature often happen simultaneously and their separate effects are not necessarily easily disentangled. I studied the effects of forest fragmentation on bird populations and communities on different levels, as well as the effects of harvesting on grouse populations. My results suggest that in natural systems there is always a multitude of factors influencing the population distribution and abundance. This complexity makes it difficult to discern and predict the consequences of human activities, and any additional human activity, such as habitat fragmentation or harvesting, can cause seemingly unexpected population consequences. My results also suggest that considering protected areas in isolation of the matrix is not sufficient to understanding species distribution and abundance within the conservation network. All management practices in commercial forests affect the landscape where protected areas are embedded, but simultaneously, conservation actions also influence the management planning. Therefore, an integrated approach is needed to sustain forest biodiversity. Finally, I showed that there are marked differences in responses to fragmentation among regions and among ecologically different species, which are partly associated with the evolutionary history of the biota in different regions. Therefore, patterns and processes in one region may not be transferrable to other regions. Moreover, disentangling the fragmentation effects on bird species requires careful consideration when selecting for research a combination of life-history variables that can distinguish among the underlying demographic mechanisms, because the mechanisms and the variables susceptible to these mechanisms may vary among regions.

Keywords: birds, conservation biology, forest fragmentation, harvesting

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Tiivistelmä

Eliön habitaatin muokkaamisella on yleensä kahdentyyppisiä seurauksia. Habitaatin hävittämisen seuraukset ovat suoraviivaisia, koska yksikään laji ei pysty säilymään elossa tai lisääntymään ilman lajityypillistä habitaattiaan. Pirstoutumisvaikutukset puolestaan voivat voimistaa habitaatin hävittämisen vaikutusta ja olla joissakin tapauksissa jopa niitä voimakkaampia. Lisäksi metsästyksellä on muokannut eläinpopulaatioita luultavasti ensimmäisenä ihmistoiminnan muotona. Erilaiset ihmistoiminnan vaikutukset ovat usein yhtäaikaaisia, eikä niiden vaikutuksia ole aina helppoa erottaa toisistaan. Tutkin väitöskirjatyössäni metsien pirstoutumisen vaikutuksia lintu- ja nisäkkäipopulaatioihin ja – yhteisöihin sekä metsästyksen vaikutuksia kanalintu- ja nisäkkäipopulaatioihin. Tulosteni mukaan luonnonoloissa on aina useita tekijöitä vaikuttamassa populaation kokoon ja levinneisyyteen. Tämä tekee ihmistoiminnan vaikutuksista hyvin vaikeasti ennustettavia. Niin ikään tulosteni mukaan suojelualueiden lajiston levinneisyyttä ja runsautta ei voi ymmärtää, mikäli ympäröivien alueiden ominaisuuksia ei oteta huomioon. Osoitin myös, että vasteissa pirstoutumiseen on huomattavia eroja maantieteellisten alueiden ja ekologisesti erilaisten linturyhmien välillä, mitkä osaltaan johtuvat eri alueiden erilaisesta evoluutiivisesta historiasta. Tästä syystä vasteita pirstoutumiseen ei voida välttämättä yleistää alueelta toiselle. Tulosteni mukaan pirstoutumisvaikutusten erottelu vaatii huolellista tutkimuksen suunnittelua, jotta lajeihin vaikuttavat demografiset tekijät voidaan tunnistaa, koska näissä voi olla huomattavaa alueellista vaihtelua.

Asiasanat: linnut, luonnonsuojelubiologia, metsien pirstoutuminen, metsästyks

To my parents

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It seems like an eternity ago when I shyly knocked on Mikko Mönkkönen's door and asked if he had any vacancies for PhD students. He immediately had a number of ideas and topics enough for 3–4 PhD theses. From those, the first plan of my PhD was soon formed – a plan which was to change a number of times. Mikko must be one of the most energetic living things on this planet, and his stunningly brilliant comments on manuscripts always arrive sooner than expected. Besides his professional abilities, he is also a nice chap and congress trips with Mikko have been very enjoyable (perhaps excluding some mornings...). Mikko's move to Jyväskylä was certainly a great loss for me personally and also for the University of Oulu.

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As with almost every thesis published by our department, I want to thank the loyal 9 a.m. coffee team, which sometimes, during the most uninspiring winter months, was my biggest source of motivation to force myself to go to the university. In its daily meetings, all imaginable things (and then some) were discussed. On rare occasions, work-related issues were also discussed. And on even more rare occasions, it was something else than complaining about how bad things are nowadays. Having spent far too many years in the department, I realise that dozens of individuals in that group have come and gone, and it is impossible to remember all the regular members. Current active members include at least Laura Kvist, Tuija Liukkonen, Pauliina Louhi, Kaisa Huttunen, Emma Vatka, Tuomo Jaakkonen, Jukka Forsman & Juhani Karvonen. In a group of rare guests and immigrants are e.g. Robert Thomson, Denzil Dexter, Juli Broggi, Ahti Putaala, Juha Markkola, Antti Rönkä + many more. Thank you all! I would also like to thank all those fellow birdwatchers with whom I have spent a lot of time in the field. Those moments have very effectively taken me away from the worries of the work (well, sometimes even too effectively...). So thanks to Markus Keskitalo, Panu Kuokkanen, Pirkka Aalto, Aappo Luukkonen, Samuli Lehikoinen, Harri Taavetti, Toni Uusimäki *et al.* And special thanks to Jari Ylönen, who has taken me a number of times to the remote island of Ulkokrunni. Even though I have sometimes tried to disguise these trips as work, they have been very important in balancing the stress from the work.

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And finally, my wife Satu. This thesis would never have been finished without her unconditional love and support. I am not much of a poet, so I'll just say thank you, my darling wife, for everything!

List of original publications

- I Lampila P, Mönkkönen M & Desrochers A (2005) Demographic responses by birds to forest fragmentation. *Conservation Biology* 19: 1537–1546.
- II Lampila P, Mönkkönen M & Rajasärkkä A (2011) Bird communities in old forest fragments are more dense but less diverse than in continuous forest. Manuscript.
- III Lampila P, Ranta E, Mönkkönen M, Lindén H & Helle P (2010) Grouse dynamics and harvesting in Kainuu, NE Finland. *Oikos* 120: 1057–1064.
- IV Lampila P, Mönkkönen M & Rajasärkkä A (2009) Ability of forest reserves to maintain original fauna – why the Chiffchaff (*Phylloscopus collybita abietinus*) has disappeared from eastern central Finland? *Ornis Fennica* 86: 71–80.

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1 Introduction

1.1 Human – dominant species of the earth

The effects of human activity are clearly to be seen in any ecosystem of the world. One staggering indication of this is the human use of net primary production (NPP_0), which is estimated to be 23.8% of the global terrestrial NPP_0 (Haberl *et al.* 2007). The figure is even higher in many industrialised countries and can reach up to 90% in intensively cropped regions (Haberl *et al.* 2004). The effects of human activities take many forms. Land transformation, e.g. cutting the trees for forestry purposes or the transformation of wetlands for cultivation, usually has the most profound effect on organisms. Up till now, habitat loss resulting from human land use has caused the vast majority of species extinctions and loss of biodiversity. As the forests (especially tropical and subtropical evergreen forests) probably hold more species than all other habitat types together, forestry has had the most dramatic effect on biodiversity loss. For example, nearly two-thirds of all bird species are found in forests, mainly in the tropics, and many can live nowhere else (BirdLife International 2008a).

The alteration of natural habitat usually has two kinds of effects on the populations living in the area. No single organism is able to survive or reproduce without its habitat. Therefore it is very easy to understand and predict the effects of direct habitat loss. However, from a human point of view it is not always easy to distinguish habitat from non-habitat. Moreover, fragmentation effects can enhance the effects of pure habitat loss. In practice, the effects of habitat loss and fragmentation are very difficult to separate from each other. In some cases, the effects of fragmentation can exceed the effects of habitat loss, although habitat loss probably usually has more significance (Fahrig 1997, Bender *et al.* 1998). The key issue here is that fragmentation effects can make the response by populations to habitat alteration non-linear and far less predictable (Andrén 1994, Mönkkönen & Reunanen 1999)

Harvesting by humans has significantly shaped wildlife populations probably well before any other human activity. For example, the well-known end-Pleistocene megafaunal mass extinction was undoubtedly partly influenced by the hunting of the humans, although other factors (like climate) probably had an effect, too (Brook & David 2002, Alroy 2001). Among the most drastic early examples of the effect of harvesting on bird populations is the prehistoric

extinction of as many as 2000 bird species from Pacific Islands (a majority of which were species of flightless rails) (Steadman 1995). Again in this case, the effect of other anthropogenic factors (e.g. habitat loss, alien predators) is evident, hunting still probably being a major factor. Typically, harvesting is linked simultaneously with other potentially harmful effects, which is why its exact role in extinctions (local or global) may not be easy to detect. However, hunting has been implicated as a factor in the extinction of at least 50 bird species in the past 500 years, and hunting for food and trapping for the cage-bird trade have been identified as threats for over 400 globally threatened birds (BirdLife International 2008b).

1.2 Birds as model organisms in fragmentation studies

For various reasons, birds have always been popular study organisms among ecologists. Birds are mostly diurnal and relatively easily detectable and identifiable animals. Birds have also adapted into various habitats, and the number of species is fairly high in most areas. Furthermore, birds' functional scale is similar to human activities. Birds are also relatively large animals, and consequently they live in fairly large territories. Therefore they do not necessarily respond to very small-scale patterns in landscapes, but to changes in larger scale landscape composition. The operational units in forest management are known as forest stands, which correspond in size to territories of e.g. many passerine species. Therefore, birds may be an ideal taxon to study the effects of forest landscape change.

Birds, however, may not react very well to all aspects of habitat loss and fragmentation, and their use as primary study subjects can be criticised. Birds have the ability to move great distances, especially during seasonal migration, and one might argue that birds are perhaps among the poorest indicators of forest fragmentation effects, a view supported by the meta-analysis of Watling *et al.* (2010). This is, however, only partly true. There are a number of indications that especially long-distance migrants suffer from fragmentation (Hobson & Bayne 2000, Askins 1995, Lampila *et al.* 2005). Looking at the ability to move might be misleading, and it cannot be directly linked with dispersal ability. Somewhat paradoxically, long-distance migrants may actually be poorer dispersers than residents and short-distance migrants. This is because long-distance migrants are very time-limited in their breeding and have a very short period of time during which they can look for a suitable breeding habitat, which has apparently also led

to population decline due to climate change (Both & Visser 2001, Moe *et al.* 2008).

1.3 Boreal and temperate forests as habitats for birds

The forests in the northern latitudes are most of all characterised by strong seasonality. Winter is generally the limiting season for any species, and therefore various strategies have been evolved to cope with these challenges. For birds, the most common solution is migration to more benign conditions. There is evidence that at least some of the migratory birds actually have their origin in the Tropics (recent summary by Bruderer & Salevski 2008), and they visit boreal and temperate latitudes in order to benefit from short-term yet plentiful food resources. Resident birds often need to cope with subzero winter temperatures and especially with diminishing food resources. In fact, food is by far the most important limiting factor, as the bird's plumage has much better isolation properties compared with the mammalian fur.

There are only a very few places in the Western Palaearctic region where the natural dynamics of boreal forests still prevail. Most forests in the Western Palaearctic have been altered with intensive land use for agriculture and other purposes, in Central and Southern Europe since thousands of years ago. Furthermore, European forests shrunk to small refugia during the last Ice Age, perhaps resulting in the loss of most fragmentation-sensitive fauna (Mönkkönen & Welsh 1994).

In the Nearctic region, the patterns are somewhat contrasting. There the Ice Age refugia were relatively continuous and the anthropogenic fragmentation also has a fairly short history. In other words, Nearctic birds are facing fragmentation for the first time in at least >10 000 years (Mönkkönen & Welsh 1994). Based on this, Nearctic birds are expected to be less adapted to habitat changes (anthropogenic or natural) and respond to them more easily than their Palaearctic counterparts.

1.4 Forest grouse – birds under pressure from habitat alteration and heavy harvesting

Forest grouse species (capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, hazel grouse *Bonasa bonasia* and willow grouse *Lagopus lagopus*) have had to face not

only the drastic change in landscape and lately in climate, but also the relatively high and increasing hunting pressure. The number of hunters in Finland has increased from c. 100 000 in 1960 to 310 927 in 2010, and grouse are among the most popular game (Suomen Metsästäjäliitto 2010). Summing up all these changes in the environment, it is not surprising that recent decades have witnessed a drastic decline in the grouse population in Finland. For example, capercaillie populations diminished by 60% between the early 1960s and the late 1980s. The respective decline is 40%, 30% and 50% for the black grouse, hazel grouse and willow grouse (Helle *et al.* 2002, Helle *et al.* 2003, Ludwig 2006). These changes have often been attributed to anthropogenic changes in forest landscapes, i.e. habitat loss, fragmentation and degradation, and to the corollary increase in the numbers of small to medium sized mammalian predators (e.g. Kurki & Linden 1995, Kurki *et al.* 2000, Kurki *et al.* 1997, Aaberg *et al.* 1995), Borchtchevski *et al.* 2003, Storch 2000). The numbers of small to medium sized mammalian predators have apparently further increased due to so-called mesopredator release (Soule *et al.* 1988), a possible consequence of the overhunting of large carnivores (bears, wolves etc.). For example, the appearance of the lynx (*Lynx lynx*) is shown to have an indirect positive impact on the abundance of the mountain hare (*Lepus timidus*) via a mesopredator, the red fox (*Vulpes vulpes*) (Elmhagen *et al.* 2010). Global climate change may also be associated with the decline of grouse as shown by Ludwig *et al.* (2006) for a black grouse population. However, we still lack the final understanding about the reasons for grouse population decline (Ranta *et al.* 2003).

The effects of hunting on grouse population dynamics and abundance are not very well known. Hunting is often thought to be of marginal importance, and some authors have considered the effects of hunting negligible with respect to the recent well-documented decline in grouse populations in Northern Europe (Storch & Willebrand 1991, Helle *et al.* 2002, Ranta *et al.* 2008). The key issue in harvesting any natural population is whether the mortality caused by hunting is additional or compensatory. Ideally, ecologically sustainable harvesting should be compensatory, although harvesting mortality is probably always at least partially additional. Usually compensatory mortality is associated with a strong density dependence in the population, and harvested individuals are assumed to make way for the remaining ones. This view is not supported by (Pedersen *et al.* 2003), who found the mortality of willow grouse to be weakly compensatory despite strong density dependence. In an experimental study, Lindén & Sorvoja (1992) found signs of partially compensatory hunting mortality. If hunting mortality is at

least partially compensatory, populations should increase faster after heavy hunting mortality because reduced population density should enhance reproductive success.

There are various recommendations on how natural populations should be harvested. Lande *et al.* (1997) demonstrated the effects of four different easily applicable harvesting strategies with a modelling approach. They showed that the so-called proportional threshold harvest (a certain proportion of the population is harvested above a threshold population size) resulted in the largest cumulative hunting bag in the long run and also in the lowest risk of extinction of harvested populations. Other hunting strategies, such as constant harvest, threshold harvest without proportionality, and proportional harvest without threshold, resulted in larger risks of extinction and in reduced long-term harvest yield. Likewise, Lindén & Sorvoja (1992) suggested, based on long-term empirical data, that cyclic grouse populations should be hunted with varying relative hunting pressure depending on the phase of the population cycle: large and increasing populations could be harvested proportionately more than small and declining populations; see also (Jonzen *et al.* 2003). Thus, both theoretical and empirical studies suggest that for optimal sustainable yield, hunting pressure should be reduced when populations are declining, and no or very little hunting is optimal at the low ebb of population fluctuations.

There are many ways for hunting authorities to restrict grouse hunting in Finland if population densities based on monitoring counts suggest that this is necessary. Game management districts may shorten or even close the hunting season, which according to hunting law is between September 10 and October 31. Local authorities and hunting clubs on private land are able to set regulations. Selling hunting licences to state-owned land also has to follow the decisions made by game management districts, and licences are sold in relation to grouse density. Recommendations for quota, i.e., how many birds can be hunted by a hunter, are also given, but there is no data available on how well recommendations are being followed.

1.5 Aims of this study

Changes in bird populations and in the structure of their communities may obviously stem from many alternative mechanisms. Only comprehensive research that disentangles the reasons for these changes from many different perspectives

can provide understanding on the underlying mechanisms. This thesis deals with the effects of human-induced landscape transformation (habitat loss and fragmentation due to forestry) and harvesting on bird populations and communities. The effects of these factors are inevitably coupled with the effects of climate change. For example, the destruction of forests enhances climate change by releasing greenhouse gases and, on the other hand, warming climate may turn large areas of tropical forest into more arid vegetation types like savannah. In addition, habitat change and climate change can have significant interactions (Warren *et al.* 2001, Root *et al.* 2003, Thomas *et al.* 2004), potentially complicating the picture as shown by Warren *et al.* (2001) in British butterflies. Likewise, the negative effects of population harvesting may be exacerbated by habitat loss and climate change, and levels of harvesting that were previously sustainable may turn into over-harvesting under the current conditions. Further, the effects of anthropogenic changes on populations are often non-linear, which makes them difficult to predict (Andrén 1994, Mönkkönen 1999). Understanding and predicting the effects of these changes is crucial when trying to preserve earth's biodiversity.

In this thesis I examined the effects of fragmentation on bird populations of different scales, ranging from continental scale (Original publication I) to local landscape scale in communities (II). I also studied the effects of hunting mortality on forest grouse living in fragmented landscapes to see if population harvesting has an impact on bird population densities (III) in addition to landscape changes that have been addressed in many earlier studies (summarised in Moss *et al.* 2010). Finally, I explored potential reasons for the drastic collapse of one example species (IV) to exemplify the variety of mechanisms behind bird population changes.

In Paper I the aim was to identify, on the basis of published literature, the most sensitive species and stages of birds' life cycles to habitat fragmentation. When the most sensitive elements of the life cycle are known, it is possible to deduce which mechanisms are mostly responsible for the fragmentation effects (see Table 1 in I). The results might also help to plan more effective experiments in the future as different components of fecundity vary considerably in terms of the difficulty of measuring them. I was also interested to see whether the different fragmentation history of the Nearctic and Palaearctic regions reflects responses by birds to forest fragmentation.

In Paper II the focus is on a large-scale "natural experiment" conducted in Eastern Finland and in adjacent areas in Russian Karelia, which made it possible

to compare bird communities in a fragmented and a non-fragmented landscape. Based on earlier theoretical work, I hypothesised that forest fragments should lack some species (especially old-forest specialists) compared with the continuous forest due to disturbed dispersal into forest fragments. With respect to the total density of birds, one might expect either negative or positive fragmentation effects. Negative effects arise if species dispersal is disturbed and other species do not compensate for the lack of fragmentation-sensitive species in remnant old-forest fragments. Positive effects may prevail particularly under strong effects from the surrounding matrix on birds in remnant old-forest fragments (e.g. increased productive energy at the landscape scale).

In Paper III, the motivation was to find out whether hunting mortality has strong enough potential to hide landscape effects on grouse populations. If hunting mortality is a strong determinant of grouse population sizes, it may homogenise population densities across the landscape, so that the responses of populations to human-induced landscape transformation are ostensibly weak. I also wanted to see if the harvesting has been carried out in a sustainable way and following the recommendations of (Lande *et al.* 1997, Lindén 1991), according to which e.g. cyclic populations should be harvested less in the decreasing stage than in the increasing stage, and small populations should be harvested less intensively than large populations.

Paper IV is a case study of one species which evidenced an exceptional and unexpectedly apparent bird population crash. My aim was to explore the reasons behind this population decline and to find out whether this could tell us something general about the effects of fragmentation on populations.

The combined results of the four papers measures the effects of different human activities on bird populations in different geographical scales and aims to add our knowledge of these.

2 Methods

2.1 Definitions and terminology

Fragmentation effects have been the most popular single topic among conservation biologists during past decades. The wide range of studies concentrated on fragmentation has led to difficulties in defining the term; to such a degree that Lindenmayer (2007) called it “panchestron”, a term used so widely that it has practically lost its significance. He also justifiably called for a better definition of fragmentation. I shall provide a general definition of habitat fragmentation and other key terms in Table 1.

More specifically, in Papers II, III (to the extent that it is referred to) and IV, I define fragmentation as an anthropogenic change in forest age composition resulting in a mosaic-like structure of mostly young and even-aged tree groups dotted by small patches of old-growth forest, of which roughly half are situated in protected areas. Thus, from the perspective of a species tightly associated with old-growth forests, human-induced landscape change may be perceived as habitat fragmentation and loss, but for more generalist species it merely appears as redistribution of alternative habitat types and may even have resulted in reduced-level fragmentation for some species. In Paper I, I review the demographic responses by birds to habitat fragmentation, and here I have accepted the definition of fragmentation by the original authors of the papers included in our review. However, fragmentation had to have a measurable effect on some demographic variable in order to be included into review.

Table 1. Some key terms used in this thesis and their brief definitions.

Term	Definition
Habitat loss	Loss of habitat (usually) through human activities (Fahrig 1997).
Habitat fragmentation	Resulting from habitat loss; shattering of originally continuous habitat into smaller patches surrounded by more or less inhabitable matrix (Andrén 1994, Lindenmayer 2007)
Connectivity	Spatial continuity of a habitat type across a landscape. Connectivity includes both the physical structure of the landscape and species ability to traverse the landscape of a given physical structure (Mönkkönen 1999).
Habitat patch	Surface area of habitat type that differs from its surroundings in nature or appearance (Forman 1995)
Landscape matrix	Background cover type in a landscape, characterized by extensive cover and high connectivity (Forman 1995)
Matrix effect	Effect from the dominating land cover type on the patches of the focal habitat type. Matrix may affect dispersal of individuals (Moilanen & Hanski 1998), the level of available resources (Dunning <i>et al.</i> 1992) or biotic interactions (e.g. influx of competitors or predators from the matrix; Fahrig 2001).
Compensatory mortality	Mortality caused by population harvesting is partially or completely compensated via density-dependent processes; a dead individual is thought "release space" for others. Harvested population decreases less than expected by the number of harvested quota (partial compensation) or does not decrease at all (complete compensation) (Anderson & Burnham 1976).
Additive mortality	Mortality caused by population harvesting simply adds to natural mortality and causes a linear decrease in population size (Anderson & Burnham 1976).
Population demography	Temporal changes in population size, affected by fecundity, mortality, immigration and emigration.

2.2 Meta-analysis (I)

2.2.1 Compiling data

I searched for peer-reviewed, published literature with the Biosis Previews database. We included in our review all studies dealing with forest fragmentation and demographic responses of living birds. I only selected data on species that breed in forest habitats, excluding information on species typical of agricultural or other non-forested habitats. No limits were imposed with respect to year of publication. Artificial nest experiments were excluded from this study because generalisation on the basis of those studies on the effects of fragmentation on survivorship of real bird nests has proven difficult. (e.g. Moore & Robinson 2004, Faaborg 2004, Thompson & Burhans 2004). All the articles selected tested for associations between at least one demographic variable and fragmentation in at least one forest bird species.

It is obvious that my sample is not a random selection of bird species. Naturally, most studies of fragmentation effects are on species that are beforehand thought to be sensitive to fragmentation. However, I do not see species selection as an issue here because our aim is to compare the differences in responses among the fragmentation-sensitive species, not to study the effects of fragmentation on birds in general.

Demographic variables were divided into three groups: 1) fecundity (including pairing success, clutch size and timing) 2) breeding success (nest success, fledgling condition, nest predation and nest parasitism) and 3) survival of adults. Some dispersal studies were also included, even though dispersal is a mechanism rather than a demographic variable. My data included 37 articles and 156 species responses. All articles, however, did not provide information necessary for the calculation of effect size, and so I was not able to use all these data in meta-analysis; the number of species responses suitable for meta-analysis was 80 (in 26 different articles). Some studies did not provide test statistics at all, and in some others, even the direction of fragmentation response was unclear. The lack of statistical details resulted in relatively low sample sizes regarding the testing for some hypotheses outlined. It also seemed that test statistics were missing much more often when results were non-significant, possibly causing publication bias. Thus, I used a more traditional vote-counting method in addition to our meta-analysis. Vote-counting has been criticized for bias because vote-

counting gives equal weight to studies of different sample size (one vote), and small sample sizes are less likely to provide significant results (Gurevitch & Hedges 1999). Meta-analysis and vote-counting can be used jointly to determine the magnitude of an effect (meta-analysis) and test for the generality of a pattern when only a few effect sizes are available for testing (vote-counting). In vote-counting, positive and non-significant fragmentation effects were lumped together, and their frequency was contrasted with the frequency of negative responses with χ^2 -statistics and log-linear modelling.

I defined N to be number of species responses (species \times demographic variable). In other words, if the pairing success, clutch size and nest predation rate of species X were measured in a study, this yielded $n = 3$. All species responses were treated as independent samples.

2.2.2 Estimation of effect sizes

Effect size in a meta-analysis is defined as the level of statistical relationship between two variables of interest (i.e. patch area and demographic parameter for a particular species (Hedges & Olkin 1985). I opted for the Pearson product-moment correlation coefficient, r , as a measure of the fragmentation effect. The Pearson coefficient does not only describe the strength and direction of the relationship between a patch area and a demographic parameter, but can also be used as a measure of the intensity of the fragmentation effect. An effect size with a positive absolute value indicates that a species benefits from fragmentation (Bender *et al.* 1998), and negative effect sizes indicate that a species suffers from fragmentation effects. Correlation coefficients are widely used in a meta-analytic framework, and procedures for the calculation and combination of effect sizes based on r are well-developed (Hedges 1994, Raudenbush 1994). In addition, many demographic studies report r , which makes it a convenient effect size. For studies that did not report r , or that did not provide the data necessary to calculate r , I applied the procedure outlined in (Cooper & Hedges 1994) to estimate r from other test statistics such as Student's t , in conjunction with the treatment means to determine the sign of r (see Connor *et al.* 2000) for a similar approach). Effect sizes were normalised by using the Fisher's transformation of r , Z_r (Sokal & Rohlf 1995).

2.2.3 Statistical analysis

To analyse the relationship between population demography and patch area within a landscape type using individual species estimates, I combined estimates of effect size obtained for individual species using the procedures outlined in Cooper & Hedges (1994), Hedges (1994) and Raudenbush (1994) for random effects models. I fitted random-effects models for all hypothesis tests because it is more appropriate to consider the effect size estimate for each species or fauna to be drawn from an underlying distribution of effect sizes rather than to consider each species to be an estimate of a single common effect size (see Connor *et al.* 2000 for an identical argument).

The random-effects meta-analysis is equivalent to the mixed-effects linear model, with fixed effects as covariates and the random effects being the deviation of the true effect size of a study from the value predicted by the model (Raudenbush 1994). Weighted averages of effect sizes within various categories were obtained by weighting effect sizes by their variances. For random-effects models, this consisted of weighting Z_r values by the reciprocal of the sum of their conditional variance ($1/(n - 3)$), where n is the sample size of the effect size estimate) and the between-study variance (Raudenbush 1994). Random effects variance was estimated using the iterative maximum likelihood procedure presented by (Raudenbush 1994). Given that the effect size estimates were weighted by their variances, model-fitting involved weighted least-squares regression (Cooper & Hedges 1994). All meta-analytic procedures were performed using Metawin software (version 2.1.3.4; Rosenberg *et al.* 2000).

First I wanted to test if the scale of the studies was related to the strength of the responses. All studies were classified into three categories according to scale: 1) Edge studies usually consider individual birds at local scale, and tested if bird demography was associated with the proximity of forest-open habitat edge. 2) Patch scale also considers the responses of individuals, testing the idea that survival, fecundity or nesting success are related to patch size. 3) Landscape level studies typically contrasted two or more landscapes fragmented to a varying degree, and tested for population level effects of fragmentation on demography.

I distinguished between two biogeographic regions, the Nearctic and the Palearctic. From other regions there were not enough studies available, and studies from tropical regions were considered to be possibly very contrasting (see discussion), and they were left out of the analysis. To determine whether species'

life history traits were related to their demographic response, I checked the literature for a number of predictor variables for each species. Nest site was defined into three categories (cavity, open nest in tree or shrub, ground) using information in (Ehrlich *et al.* 1988). When testing if nest site is a significant predictor of demographic response, only the effects related to nest success were included (see Table 1 in Paper I). Migratory status was determined based on (Marshall & Richmond 1992) and (Snow & Perrins 1998). Species were divided into two broad categories, migrants and residents. I included in the migrants category only long-distance (tropical) migrants, which are thought to be time-limited in their breeding, unlike residents and partial or short-distance migrants (Mönkkönen 1992), to test hypotheses derived from species' numerical responses (see above). When testing for differences between biogeographic regions in how migrants vs. residents respond to habitat fragmentation, I was obliged to use vote-counting only because too few effect sizes were available for Nearctic residents ($n = 5$) and for Palaearctic migrants ($n = 4$).

Species were assigned to faunal type (Old World, New World) according to Mayr (1946) to evaluate the historical scenario by (Mönkkönen & Welsh 1994). Finally, for each species habitat, associations were defined to include two broad categories, mature forest specialists vs. forest generalists following (Raivio & Haila 1990) and (Imbeau *et al.* 2003) for Palearctic species, and using information in (Ehrlich *et al.* 1988) and (Imbeau *et al.* 2003) for Nearctic species. Forest specialists are species tightly associated with mature forests, whereas generalists, even though preferring mature forests, make use of a wide variety of succession stages of forests and even non-forested habitats.

The publication bias of the meta-analysis data was tested with both graphical methods (funnel and normal quantile plots) and using the rank correlation test (Kendall's tau) (Rosenberg *et al.* 2000, Sokal & Rohlf 1995).

2.3 Bird census methods

2.3.1 Line transect census (II, IV)

There are various ways to census forest birds. In Papers II and IV, I used data on bird species abundance and distributions collected by the line transect method. In Finland, this census method (Järvinen & Väisänen 1976, Järvinen & Väisänen 1983) is perhaps the most commonly used, especially when the goal is to estimate

bird fauna in large land areas. In this census method, a census line (usually 3–10 km) is walked during early morning and all observed birds are noted, the majority of the observations often being acoustic. Observations are divided into a main band 50 m wide and a supplementary band (the rest of the observations). From the relation of these, a correction coefficient for the species detectability is estimated. The coefficient is the higher the harder the species is to detect, i.e. the bigger proportion of the observations comes from the main band. The results are still further corrected with noise coefficient, because when densities are high, distant birdsongs are less audible. Over the decades, there has been some discussion about the method's reliability. (e.g. Hildén & Järvinen 1989, Helle & Pulliainen 1983) It is apparent that it is neither suitable for species with a tendency to form colonies nor species occurring in very low numbers, but it is a useful tool in the investigation of numerical relationships between reasonably common birds. Densities obtained using the line-transect method (or any other single census method) are perhaps the best-regarded semi-quantitative indices of density, rather than “real” densities. In smaller data sets (c. dozens of kilometers of census line), density estimates of e.g. birds of prey tend to be unreliable. Furthermore, care must be taken when placing the line transects into the landscape so that the birds observed really represent the average of the area of interest.

I used line-transect counts conducted in spruce-dominated old-growth or mature forests on both sides of the border between Finland and Russia at ca. 64–65° N during June 2002, for a total transect length of ca. 700 km. This effort involved censuses in 44 separate old-growth forest reserves in Kainuu, Finland, and 37 transects of a total length of ca. 200 km in Viena, Russia. The transects were placed in forest reserves on the Finnish side and in similar (both protected and non-protected) forest areas on the Russian side. On the Finnish side of the border, the reserves were mostly surrounded by a matrix of younger and managed forests, whereas on the Russian side, fairly continuous old-growth forest dominated the landscape. I also used older transect-count data from the same area, collected in the 1940s and between 1983–2003, resulting in 16 years of data from Finland, and 5 years of data from Russia. These data were collected in a less systematic way than the 2002 data but were interpreted similarly. Censuses used in Papers II and IV were placed mainly into Norway spruce-dominated forests, and peatlands were avoided. Therefore, our results do not reveal anything about the general bird fauna in those areas, only about the part that lives in spruce-

dominated forests. A rule of thumb is usually given whereby 1km census line per 1km² is enough to give reliable density estimates.

2.3.2 Bird census analyses (II, IV)

Several alternative theoretical frameworks exist with regard to understanding species distribution in patchy and fragmented landscapes. The random sampling hypothesis can be considered a reasonable null model, against which the biologically more interesting explanation for the distribution of organisms in a patchy landscape can be compared.

If assemblages in the patches of protected areas comply with the random sampling hypothesis, the densities of individual species would not vary with area or isolation (Brotons *et al.* 2003), and species richness should merely vary with the total number of individuals residing on a patch (Connor & McCoy 1979). Accordingly, larger areas foster more species but only because of a larger pool of individuals, and patch isolation should not have any effect on species richness.

If bird assemblages in Finnish forest reserves are merely random samples from the very same regional pool of individuals and species as those on the Russian side of the border, they should foster approximately the same number of species. To test this, I calculated the expected species number for Finnish areas using species-abundance distribution in the Russian data by the rarefaction method outlined in (Krebs 1999). For each Finnish forest reserve, I calculated the difference between the observed and expected species richness separately for all forest bird species and for species associated with old forests (22 species). The classification of species into old-forest associated species follows (Väisänen *et al.* 1998). Further, for each Finnish forest reserve, I calculated the total density of pairs per km² and tested the data to determine if these data differ from the average density in Russia. Densities of all forest species and old-forest species between Russia and Finland were compared using the 1-sample *t*-test.

Likewise, under the random sampling hypothesis the structure of bird assemblages in the Finnish forest reserves should not systematically differ from the structure of the Russian bird assemblages. To test this hypothesis, I calculated the Bray-Curtis similarity index between the bird assemblages in the Finnish forest reserves and combined the Russian data using species density (pairs/km²) data. If a Finnish reserve fosters a bird assemblage with the same species-abundance distribution as in the Russian data, the similarity equals to unity. With no shared species the index yields zero.

In Paper II, I submitted the total bird density in the Finnish forest reserves, the deviations in species richness from the expected, and the similarity of bird assemblages to the Univariate Generalised Linear Model (GLM) with forest area (km²) and distance (in km) from the Finnish-Russian border as covariates to test for patch-size and isolation effects. Forest area and distance do not correlate significantly. I also entered latitude (degrees N) into the models to correct for latitudinal variation in densities and species richness. Outlier areas were removed before final analyses using standardised residuals; $|Z_r| > 1.96$ coding as outlier.

In Paper IV, I also used data from the early 1940s, taken from (Lehtonen 1946). Note that these data originate from both sides of the present Finnish-Russian border. Unfortunately, Lehtonen (1946) did not provide exact transect lengths for each country, although he stated that “the lengths of the census lines are almost similar on both sides of the border”. The method used by Lehtonen (1946) differed slightly from Järvinen and Väisänen (1976): he applied a 60-m wide main belt and ignored birds >200 m away. For this reason, I used only the main belt data from Lehtonen’s data. Furthermore, Järvinen and Väisänen (1978) concluded that the bird numbers reported by Lehtonen (1946) may have been low because his data-collection season extended into early July (when birds sing less actively), and the fact that during the census work he wrote detailed descriptions of forest structure. I tested the similarity in the numbers of survey-belt observations between Kainuu and Viena for 2002; for other years, I was unable to control for the annual (random) variation in bird populations and testing was therefore not conducted. Differences in densities were tested using chi-square tests, with transect length to calculate expected values.

2.3.3 Wildlife triangle censuses and estimation of grouse hunting bags (III)

I used wildlife triangle census data from Kainuu province (appr. 65°N, 28°E), North-eastern Finland, from 1989 to 2004. Wildlife triangle census routes are 12 km long, and each side of the triangle is 4 km (for details, see Pellikka *et al.* 2007, Helle *et al.* 1996). Censuses are conducted in August, mainly by local hunters. The main belt is 60 m in breadth, covered by a three-person chain. Density estimates are calculated by multiplying the main belt area with the number of grouse observed adjusted for total forest area. This is a fairly accurate method as the census efficiency is high (80% on average; Brittas 1990)

All observed grouse individuals were aged as juveniles or adults and counted. Census routes are assumed to be situated randomly in the landscape. The province of Kainuu was chosen as a study area due to the best coverage of wildlife triangle censuses in Finland. Forest land covers about 75% of the area, peat-lands 15%, and lakes 10%. Practically all old-growth forests are confined to the nature conservation areas, which form c. 3% of the land area. The province borders the practically continuous ‘green belt’ of old-growth forests on the Russian side of the border.

Information on the grouse hunting bag was obtained from the Finnish Game and Fisheries Research Institute. These estimates are based on nation-wide questionnaires sent out to 5000 (c. 2% of all hunters in Finland) hunters annually.

2.3.4 Modelling grouse dynamics (III)

I shall describe the grouse population dynamics with:

$$X(t+1) = a_0 + a_1X(t) + a_2X(t-1) - hB(t) - cW(t) + \varepsilon,$$

where X is grouse population density (individuals km^{-2}), a_0 , a_1 (lag one) and a_2 (lag 2) are model parameters related to grouse numbers, while B is the annual grouse bag (killed grouse km^{-2} in the Kainuu province); W is an index of the severity of the winter (Baltic Sea Ice coverage); normalised to mean zero and unit variance, and ε is an error (or noise) term. The Baltic Sea ice coverage (see http://www.itameriportaali.fi/en/tietoa/jaa/jaatalvi/en_GB/jaatalvi/) varies notably between the years and is generally a good surrogate of winter severity in the surrounding areas. It also correlates strongly with NAO (Koslowski and Loewe 1994), therefore I assume it to describe winter conditions also in our study area but possibly with better accuracy than NAO or Arctic oscillation. The severity of winter has various effects on grouse species as summarised by Lindén (2002). The effects of winter weather are not necessarily straightforward on grouse, as the mild winters may actually make the life of grouse more difficult. This is e.g. because the formation of ice on trees increases when the temperature often crosses the 0°C line. Also the typical habit of forest grouse, using a snow roost during the night, is not possible if the snow layer is very thin, hard and icy. Lindén (1982) found out that capercaillie survival was higher in Southern Finland in short and mild winters, whereas in Northern Finland survival was higher in long, cold and snowy winters. Winter conditions clearly have a significant effect on the life of grouse spp., but exact responses are obviously difficult to predict.

Adding such a climatic variable into our models was to control for a potential source of variation in grouse populations, and to get a comparison with the hunting effect from a variable presumed to have an effect on the survival and fecundity of grouse.

The species-specific grouse population data differentiate the adult and young birds, but the hunting bag data do not. Therefore, my model changes in annual total grouse density under harvest. The equation (1) is referred to as the full model, and the Akaike Information Criterion (corrected for small samples), AIC_C and δAIC_C (difference between AIC models) is used to check out whether a reduced model [stripping off in turn h , W and lag 2 terms in equation (1)] gives a better fit (Burnham and Anderson 2002, Johnson and Omland 2004). For biological reasons I retained the constant, a_0 , and the first order lag term, a_1 . Hence, various parameter inclusions give us eight different models (Table 1).

For each model (i goes from 1 to 8) we also calculated the Akaike weight

$$w = \frac{\exp[-0.5 \times \delta AIC_C(i)]}{\sum [\exp(-0.5 \times AIC_C)]}$$

to see how likely each model is. With eight models the expectation is 1/8, or 0.125.

I derived a few life history characters using the August census data for grouse and annual bag for the harvest: (1) a measure of reproductive success is simply $Juveniles(t)/Adults(t)$, (2) survival rate is $Adults(t+1)/[Total(t) - Harvest(t)]$, and (3) harvest mortality is $Harvest(t)/Total(t)$. The estimates were derived from the best fitting model with $\delta AIC_C = 0$. Note that the survival rate estimate also includes 1st-winter survival, which may be lower than in older age classes.

Furthermore, I estimated how well the current harvesting pattern fits the given harvesting recommendations (small population should be harvested less than large; a decreasing one less than an increasing one) (Linden 1991, Lande *et al.* 1997) by regressing the harvest mortality at time t against the size of the population ($X(t)$) and against the change in population size from year $t - 1$ to t . We also estimated the recovering ability of grouse populations by plotting the population change from t to $t + 1$ against the harvest rate at t .

3 Results

3.1 Sensitivity to habitat fragmentation (I)

I discovered that the species most sensitive to fragmentation were ground- or open-nesters nesting in shrubs or trees. This points towards the important role of increased (nest) predation in fragmentation effects, as birds nesting in cavities are generally better protected from nest predators. Residents were equally sensitive to fragmentation in the Nearctic and Palearctic regions, but Nearctic migrants were more sensitive than Palearctic migrants. This result stems from the differing distribution history of birds with different migration strategies. Generally speaking, long-distance migrants of the forest habitats in the different continents are quite distantly related, whereas residents and short-distance migrants are fairly closely related and continents share many species (Mönkkönen 1992). Old World species in general were less sensitive than New World species, which was predicted based on the history of forest fragmentation on these two continents (see Introduction, 1.3).

Pairing success was the variable most negatively associated with fragmentation. This suggests that disturbed dispersal is significantly involved in negative fragmentation effects as it is apparently the most important mechanism that could affect pairing success. Respectively, fledgling number or condition, timing of nesting, and clutch size were not associated with sensitivity to fragmentation, suggesting that negative fragmentation effects on birds do not generally result from diminished food resources with an increasing level of fragmentation.

3.2 Species richness, population density and community assemblage in the Finnish forest compared with the Russian continuous forest (II)

Species richness in the Finnish forest reserves was on average 3.0 forest species fewer than expected under the random sampling hypothesis. The deviation from the expected species richness was not related to forest area of the reserve or its latitude, but the distance from the Russian forests had a significant effect, so that each 100 km increment in distance increased the deviance from the expected by three species.

Old-forest species richness in the Finnish forest reserves was on average 1.2 species lower than expected under the random sampling hypothesis. This difference was not related to the distance from the Russian forests, but was associated with the latitude and forest area of the reserve. Large reserves lacked more old-forest species than small reserves, so that each 100 km² increment in forest area inflated the deviance by approximately two species. Reserves further north showed larger deviations from the expected than more southerly located forest reserves.

The average density of all forest birds in the Finnish forest reserves (average 125 pairs/km²) was almost 40% higher than in Russia (average 90 pairs/km²). The density did not vary with the distance from Russia, forest area or latitude. Likewise, the density of old-forest birds was higher in the Finnish forest reserves (average 7.4 pairs/km²) than in the Russian forests (6.0 pairs/km²). Neither latitude nor forest area had an effect on the density of old-forest birds, but their density decreased with the distance from the Russian forests, with each 100 km increment in distance being associated with 2 pairs/km² (27%) reduction in density.

The average similarity of the structure of bird assemblages in the Finnish forest reserves was 71%, suggesting that seventy-one out of one hundred individuals belong to the same species in the Finnish and the Russian forests. Similarity increased with the forest area of the reserves and decreased with the distance from the Russian border. Areas larger than 10 km² and situated less than 70 km away from the Russian forests had a similarity larger than the average 71%.

3.3 Effects of harvesting on grouse populations in Kainuu (III)

The main result was that all forest grouse spp. populations were significantly affected by the harvesting, as indicated by the inclusion of the harvest term in the best models. This supports our preliminary idea that hunting may be able to hide the effects of landscape composition on grouse populations. The winter severity index, which was taken as a comparative value for harvest mortality, was included in the models only for the willow grouse.

Furthermore, the harvesting of the Kainuu grouse population did not seem to follow the given guidelines, and the current harvesting strategy is apparently suboptimal: the proportion of birds shot was not dependent on population size. Further, declining populations tended to have been harvested more than

increasing ones, which could have a destabilising effect on grouse population dynamics (Kaitala 1996). A change in harvesting strategies could result simultaneously in an increased hunting bag and smaller risk of population decline.

3.4 Chiffchaff distribution patterns (IV)

In 2002 censuses, 51 chiffchaff territories were discovered (=singing males, equivalent of c. 0.6 pairs/km²) in Viena (Russia) and none on the Finnish side in Kainuu. None of the well-known old-forest specialist bird species showed a striking distribution pattern. Furthermore, the densities of potential competitors (or apparent competitors, see (Bonsall & Hassell 1997) did not show a clear difference in density between the Finnish and the Russian side of the border. In the willow warbler, however, there was considerable temporal variation in densities, which could hide the density difference between the areas. My main conclusion here is that fragmentation can create unexpectedly striking changes in communities, if all underlying processes are not fully understood.

Furthermore, I wanted to test whether there have been changes in chiffchaff migration directions over the years. Both Swedish and Finnish ringing recovery data show the same trend: the average autumn migration has changed from south-east to south-west, which is likely to be associated with changes in the composition of the chiffchaff populations. The nominate subspecies *P.c. collybita* has spread to Southern Sweden, and based on our results, south-westerly migrating chiffchaffs have apparently spread also to Finland during the last few decades. This is important to note, because chiffchaff was classified as vulnerable on the Finnish Red List of 2000 but was moved to the group of least concern in the 2010 evaluation, due to an apparent increase in its population size. This, however, might be misleading, as the increase may be the result of the increase in the numbers of the nominate *collybita* (or *collybita/abietinus* intergrades), and *P.c. abietinus* might still qualify for threatened status.

4 Conclusions and directions for further studies

The example of the chiffchaff (IV) shows that there can be considerable temporal and spatial variation in forest bird populations, even within a short time interval and within small distances. Even though I was not able to prove the exact reasons behind the observed pattern of relatively high population density in unfragmented Russian forests and the complete lack of chiffchaffs in Finland, this case shows that a change in a single factor (an increase in forest fragmentation in this case) can create unexpectedly dramatic population responses, if there are other factors affecting the population. I suggest that the addition of one more negative element, habitat fragmentation, to the population growth rate of the chiffchaffs at the northern edge of its global distribution has pushed it to local extinction in NE Finland.

There is hardly any detailed knowledge of the factors affecting animal populations; therefore, there is always a chance that even a very moderate alteration of habitats can result in considerable population responses. The fundamental effect in the destruction or alteration of the animals' habitat is the declining population size, even if we would assume only the habitat loss effect to take place. Declining population sizes lead to an elevated extinction risk, particularly among species with poor dispersal ability inhabiting isolated sites, where local extinction events are not readily reversed by colonisation. However, declining populations often take considerable time to go locally extinct, the result being so called extinction debt (e.g. Hanski & Ovaskainen 2002, Cousins & Vanhoenacker 2011, Kuussaari *et al.* 2009). In single species, extinction debt can be defined as the number or proportion of populations expected to eventually become extinct after habitat change (Kuussaari *et al.* 2009). This phenomenon makes it difficult to predict species responses, as new equilibrium may take decades or centuries to develop (Helm *et al.* 2006), although in experimental studies in short-lived soil organisms the extinction debt was paid in 6-12 months (Gonzalez & Chaneton 2002, Gonzalez 2000). In natural systems, even their time lag is probably longer, due to a slower response from other species in the community. However, the majority of the empirical evidence related to extinction debt relates to vascular plants, as reliable long-term datasets are easier to gain than from animal populations. In any case, the main danger of the extinction debt is that it may lead us to make too optimistic estimates of the species' conservation

status. If there are several factors simultaneously affecting the population negatively, extinction debt can be rapidly realised, as apparently has been the case with the chiffchaff.

No single factor seems to satisfactorily explain the continuous decline of the forest grouse spp. in Finland, either. The effects of the harvesting documented in this study (III) combined with the consequences of the massive changes in landscape structure due to forestry and the climate change are the most obvious cause for the steady decline in grouse populations. My results suggested significant hunting effects on all grouse species, but the magnitude varied almost ten-fold, being the highest for the black grouse and the lowest for the hazel grouse. Likewise, the effect of environmental changes on grouse is not necessarily equal on all grouse species, as they, especially the black grouse, may to some extent even benefit from moderate land transformation (Storaas & Wegge 1987, Swenson & Angelstam 1993). Of the four studied grouse species, the willow grouse as a northerly distributed species is thought to be the most susceptible to climate change according to (Huntley *et al.* 2007). Indeed, the distribution area of the willow grouse has also severely decreased (by approximately 30%) during the past few decades, but the distributions of the other grouse species has been more unwavering (Valkama *et al.* 2011). Therefore, the relative importance of the three factors (hunting, landscape change and climate change) to grouse populations is not easily deduced, and it may also vary locally and among grouse species.

From the management perspective, harvest mortality is of course easier to control than landscape-level environmental factors, even though it has its own challenges, too. The harvesting of grouse populations in Kainuu did not seem to have followed the given guidelines, and therefore, the current harvesting strategy is apparently suboptimal. Relative harvest mortality was not dependent on population size, and declining populations tended to have been harvested more than increasing populations, which potentially has a destabilising effect on grouse population dynamics. Better management may result in a larger hunting bag and a reduced likelihood for population declines (Lande *et al.* 1997). A major issue has been the very short time gap between late-summer brood censuses, which the hunting quota is based on, and the start of the hunting season. During the last few years, in Finland there has been an effort to incorporate also the same year's results of the brood censuses into the decision-making of the same years hunting quota. This is essential if the aim is to be able to control the quota in relation to the current stage of the population fluctuation and to the density.

There has also been some discussion about the relative effects of habitat loss and hunting, e.g. (Fahrig 1997, Fahrig. 2003, Stratford & Robinson 2005, Piessens *et al.* 2005). Population harvesting evidently creates an important additional threat to biodiversity and may exacerbate the negative effects from fragmentation and climate change on populations. From the management perspective, harvesting adds an element of unpredictability to species responses to habitat alterations, complicating any management planning. This calls for integrated planning where harvesting and land management decisions are made simultaneously.

The key message of Paper II is that in order to fully understand changes in distributions and densities of species, we cannot only study species occurrence and abundance in their habitats, but a wider landscapes context must be considered. The matrix and the habitat types surrounding the preferred habitat patches can also have a significant effect on populations (Sisk *et al.* 1997, Prugh *et al.* 2008, Watling *et al.* 2010). The matrix may enhance or disturb dispersal, provide alternative or supplemental resources, and act as a source of competitors and predators (Dunning *et al.* 1992, Moilanen & Hanski 1998, Fahrig 2001). Therefore, nature conservation focusing solely on protected areas network and neglecting the areas surrounding the protected areas is doomed to be misleading.

While formal protected areas have an important role, both scientists and land-managers widely recognise the need for conservation beyond the boundaries of protected areas. Nearly 90% of the land across the globe lies outside of formal protected areas (WRI 2003), and many protected areas are located on lands set aside for reasons other than biodiversity conservation, such as aesthetics or low economic values (Pressey & Tully 1994, Virkkala 1996, Balmford & Whitten 2003). Therefore, land-use and land-management decisions in landscapes outside of protected areas are vitally important. A key question is whether the landscape as a whole, including both protected areas and areas devoted to commodity production outside of protected areas, sustains the persistence of elements of biodiversity on the landscape. My results suggest that improving matrix quality may lead to considerable conservation benefits, but only if a sufficient amount of the forest area is protected. In boreal forest landscapes, a managed forest matrix provides habitats and resources even for many old-forest associated species. One might assume that the benefits of improving the matrix quality may even be larger in other systems where relative matrix quality is lower.

In highly modified ecosystems, such as south temperate and many tropical forest areas, human land use results in more or less permanent conversion of forests for agricultural production or urban sprawl, whereas in forest ecosystems managed for timber production, human activities merely change the quality of the habitats rather than their overall availability. Forestry practices, for example, in Fennoscandia and Canada result in dynamic landscapes that remain primarily forested and undergo spatial and temporal changes in composition and age structure. In contrast, forest conversion typical of many south temperate and tropical regions results in near static landscape configurations of habitat vs. non-habitat (Schmiegelow & Mönkkönen 2002). Therefore, it seems reasonable to expect that biotic and abiotic responses to these human disturbances might differ among forest systems with varying landscape contexts. As a consequence, “fragmentation” as a concept may have a different meaning depending on the main type of human land use, adding further difficulty to defining it (Lindenmayer & Fischer 2007). Moreover, matrix effects from the habitats surrounding the remaining patches of natural habitats, such as old forests, may be quantitatively and qualitatively different among forest biomes. These repercussions need to be kept in mind when putting the results of my Paper I into a wider perspective.

My results in Paper I indicated that historical factors affect bird species susceptibility to fragmentation effects as evidenced by the difference between the responses of Nearctic vs. Palaearctic birds. However, the database was too scanty to contrast north (boreal) vs. south temperate forests, even though landscape context and land use history typically differ in these two regions. A comparison among forest biomes (boreal vs. south temperate vs. tropical) in terms of fragmentation effects remains a challenge for future studies.

During the preparation of Paper I, there were very few studies of fragmentation effects on tropical forest bird species measuring some demographic variable(s), and it was not possible to include the few existing studies into a meta-analysis. Since 2005, a handful of studies have been published to fill the knowledge gap (e.g. Ruiz-Gutiérrez *et al.* 2008, Young *et al.* 2008). Moore *et al.* 2008 found out that the dispersal capability of forest birds in Panamanian lacustrine archipelago varies considerably: even as short distances as c. 100m between the fragments can be considerable barriers for some species. Ruiz-Gutiérrez *et al.* (2008) found evidence that the survival of the white-ruffed manakin (*Corapipo altera*) is reduced due to fragmentation. This can be especially detrimental to species that have low fecundity and a naturally long

lifespan. Despite these new results, there is insufficient evidence to draw more far-reaching conclusions.

It is likely that the patterns in the Tropics are potentially very contrasting to temperate regions in terms of fragmentation effects on the population demography of birds. For example, the clutch size is not a relevant variable to study the effects of fragmentation in the tropical context, as in many tropical birds the clutch size is almost invariably two, not really depending on any environmental variable. The life history parameters in tropical birds are often contrasting to those of temperate birds. In tropical species, low fecundity is typically associated with a long life span, but the opposite tends to prevail among temperate species. Therefore, decisions and investments related to reproduction are more important and perhaps also more susceptible to fragmentation in temperate bird species, whereas in the Tropics survival-related factors may be more critical.

Harrison & Bruna (1999) stated that “while the few available large-scale empirical studies of fragmentation all tend to show that it has major effects, these documented effects tend to be relatively simple ones such as the degradation of habitat quality within fragments.” Fragmentation literature is seriously biased towards south temperate forest ecosystems (e.g. Paper I), and a full understanding of the effects of fragmentation in all main ecosystems still remains to be completed. In part, this thesis provides some answers to the appeal quoted above.

To sum up, from the conservation biology perspective, my results suggest that in natural systems there is always a multitude of factors influencing population distribution and abundance. This complexity makes it difficult to discern and predict the consequences of human activities, and any additional human activity, such as habitat fragmentation or harvesting, can cause seemingly unexpected population consequences. My results also suggest that considering protected areas in isolation of the matrix is not sufficient to understanding species distribution and abundance within the conservation network. All management practices in commercial forests affect the landscape where protected areas are embedded, but simultaneously, conservation actions also influence the management planning. Therefore, an integrated approach is needed to sustain forest biodiversity. An integrated approach is particularly relevant in European landscapes that have a long history of human influence and a variety of protected areas. Finally, I showed that there are marked differences in responses to fragmentation among regions and among ecologically different species, which are partly associated with

the evolutionary history of the biota in different regions. Therefore, patterns and processes in one region may not be transferrable to other regions. Moreover, disentangling the fragmentation effects on bird species requires careful consideration when selecting for research a combination of life-history variables that can distinguish among the underlying demographic mechanisms, because the mechanisms and the variables susceptible to these mechanisms may vary among regions.

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- I Lampila P, Mönkkönen M & Desrochers A (2005) Demographic responses by birds to forest fragmentation. *Conservation Biology* 19: 1537–1546.
- II Lampila P, Mönkkönen M & Rajasärkkä A (2011) Bird communities in old forest fragments are more dense but less diverse than in continuous forest. Manuscript.
- III Lampila P, Ranta E, Mönkkönen M, Lindén H & Helle P (2010) Grouse dynamics and harvesting in Kainuu, NE Finland. *Oikos* 120: 1057–1064.
- IV Lampila P, Mönkkönen M & Rajasärkkä A (2009) Ability of forest reserves to maintain original fauna – why the Chiffchaff (*Phylloscopus collybita abietinus*) has disappeared from eastern central Finland? *Ornis Fennica* 86: 71–80.

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