REPRODUCTIVE SUCCESS RESPONSES TO HABITAT FRAGMENTATION IN EURASIAN TREECREEPERS

by

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For Anniina and Kristian

TABLE OF CONTENTS

LIST OF ORIGINAL ARTICLES

This thesis consists of the following publications and manuscripts, which will be referred to in the text by their Roman numerals.

I. Le Tortorec, E., Helle, S., Suorsa, P., Hakkarainen, H. (2012) Parental and genetic factors not nesting forest patch size affect physiological traits of offspring in an area-sensitive passerine: an experimental study. *IBIS* **154(2)**:345-353

II. Le Tortorec, E., Helle, S., Suorsa, P., Sirkiä, P., Huhta, E., Nivala, V., Hakkarainen, H. (2012) Feather growth bars as a biomarker of habitat fragmentation in the Eurasian treecreeper. *Ecological Indicators* **15(1)**:72-75

III. Le Tortorec, E., Helle, S., Käyhkö, N., Suorsa, P., Huhta, E., Hakkarainen, H. Habitat fragmentation and reproductive success: a structural equation modeling approach. *Journal of Animal Ecology* DOI: 10.1111/1365-2656.12075

IV. Le Tortorec, E., Helle, S., Käyhkö, N., Suorsa, P., Huhta, E., Hakkarainen, H. Multiscale spatio-temporal modelling reveals detrimental influences of habitat loss on treecreeper reproductive success. *Manuscript*

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1   INTRODUCTION

The concept of habitat has been defined as the species-specific resources and conditions that bring about occupancy in that area (Hall et al. 1997). Therefore a reduction in the area of habitat and the breaking apart of habitat into spatially isolated fragments will have negative consequences on species dependent on that habitat type. Accordingly, the process of habitat fragmentation, whereby habitat is lost and the spatial configuration of remaining habitat patches is altered (Fahrig 2003), is of special concern to biologists (Fazey et al. 2005), as it poses an important threat to global biodiversity among almost all the taxonomic groups studied (Foley et al. 2005). Hansen et al. (2010) showed that between 2000 and 2005 3.1% of global forest cover was lost, owing mainly to human activity and fires, representing an annual loss of 0.6%, with the largest amount of loss occurring in the boreal biome. Overall, the loss of habitat due to forestry and agriculture has been identified by the International Union for Conservation of Nature Species Survival Commission (Baillie et al. 2004) as the most pervasive threat to bird species worldwide.

The effects of habitat fragmentation on individuals, populations and communities has received a vast amount of attention (Andrén 1994, Fahrig 2003, Turner 2005). Habitat fragmentation has been shown to affect a wide range of organisms including vertebrates (Chiarello 1999), invertebrates (Robertson & Butler 2009) and plants (Valdés & Garcia 2011), although most studies have been conducted with birds (Fahrig 2003). However, there is increasing recognition that the conceptual foundations of habitat fragmentation research are lagging behind empirical and theoretical advances in habitat fragmentation research (Didham et al. 2012). In addition, this field suffers due the confusing use of terms related to loss of habitat and altered spatial configuration of habitat patches (Fahrig 2003), which has lead to unproductive debates (Lindenmayer & Fischer 2007). Taken together, these problems have meant that our understanding of the fundamental effects of habitat fragmentation on individuals, populations and communities remains lacking.

The aim of this thesis was to study how the fragmentation of old forests affect life history parameters of the Eurasian Treecreeper (*Certhia familiaris* hereafter

treecreeper). Biological data was collected from individuals since understanding the effects of habitat fragmentation on individuals provides a functional means to understanding the effects of this important process on populations (Bowers & Dooley 1999). A nest-box approach was used in order to allow for the collection of a large amount of comparable nesting data from a study site that contained a mix of both fragmented and unfragmented landscapes. The four articles included in this thesis inspect the effects of habitat fragmentation on nestling growth, adult condition and reproductive success.

In article (**I**) I used a cross-fostering experimental approach to determine the effect of habitat amount on offspring phenotype while controlling for genetic background and parental effects. In article (**II**) I analysed the widths of feather growth bars, which indicate individual nutritional status, to study if feather growth bar width was associated with habitat fragmentation in adult treecreepers. In article (**III**) I used a structural equation modelling approach to realistically model the process of habitat fragmentation as a hierarchical process, and analysed how habitat fragmentation influences reproductive success. Finally, in article (**IV**) I studied how landscape change, measured as the linear trend in habitat amount for each nest box site separately, influenced territory-based reproductive success. In conjunction with the biological questions that I investigated in this thesis, I also explored different uses of remote sensing data in studying the effects of habitat fragmentation. This ranged from a single year of habitat data in article (**I**) to using an almost yearly set of habitat data in article (**III**), and producing a spatio-temporal dataset of habitat change data in article (**IV**).

All articles were analysed and written by myself. Harri Hakkarainen provided help in planning the studies and editing the manuscripts. Samuli Helle and Niina Käyhkö were involved in planning the studies, performing statistical and GIS analyses and editing the manuscripts. Petri Suorsa and other co-authors were involved in data collection, performing GIS analyses or commenting on the manuscripts.

2   BACKGROUND

2.1   Development of habitat fragmentation research

The concept of habitat fragmentation is generally considered to have arisen from island biogeography theory (IBT) introduced in the monograph of MacArthur & Wilson (1967). In the theory of MacArthur and Wilson the biological diversity of islands increases with increasing island size, decreasing distance between islands and increasing compactness of islands via colonisation and extinction. This theory was taken further in the theory of metapopulation dynamics (Levins 1969, Hanski 1998), which considers networks of individual populations (metapopulations) spread out over habitat patches. In this theory the persistence of individual populations depends on dispersal and colonisation between patches, which are influenced by patch area and isolation.

A legacy still remaining from the IBT approach is the binary nature of the landscape – islands are separated from each other by a sea of inhospitable matrix. This distinction between strict habitat and matrix was retained when terrestrial ecosystems were taken into account. Now patches of habitat were considered as islands, and matrix (non-habitat) was the sea separating habitat patches from each other. There has been growing recognition that this view of the matrix as being hostile or uniform in nature is not realistic (McIntyre & Barrett 1992, Ricketts 2001, Brotons et al. 2003, Watson et al. 2005, Fischer & Lindenmayer 2007, Laurance 2008, Prevedello & Vieira 2010). However, the binary view of habitat fragmentation has persisted, most likely due to the relative ease with which habitat metrics describing habitat fragmentation can be calculated and interpreted.

The IBT approach to studying the habitat fragmentation was superseded by the discipline of landscape ecology in the 1980's (Haila 2002). Landscape ecology has its roots in the writings of the biogeographer Carl Troll (Troll 1950), who combined and refined earlier ideas from geography and ecosystem science to forge the concept of landscape ecology (Wiens et al. 2007). Landscape ecology initially focused mainly on geography and related fields, while ecological theory and studies still assumed spatial homogeneity in landscapes. However, in the 1960's and 1970's influences

from the field of ecology became more apparent (Wiens et al. 2007). In contrast with IBT, which only considered the size and isolation of patches, landscape ecology considered variables related to the spatial arrangement of patches. Indeed, one of the fundamental principles underlying landscape ecology is the recognition of the link between spatial pattern and ecological process (Gustafson 1998). Currently landscape ecology can be broadly split into two main branches: one concentrating on the spatial planning and management of landscapes and the other on the effects of spatial patterns and heterogeneity on ecosystem and population ecology (Hobbs & Wu 2007), of which this thesis focuses on the latter.

2.2   *The process of habitat fragmentation*

Landscapes are naturally dynamic due to storms, fires and other natural events, but anthropogenic causes of landscape change are increasing at an unprecedented rate. In the model of Forman (1995) five processes act together to cause the fragmentation of habitats (Fig. 1). The most common way by which landscapes begin to change is through *perforation*, whereby holes appear in a uniform area of habitat. An alternative process that starts landscape transformation is *dissection*, where a uniform area is subdivided into smaller areas by long equal-width lines such as roads. After the initiation of landscape transformation, *fragmentation* begins to break up the habitat into smaller patches separated from each other, and *shrinkage* decreases the size of the remaining patches. Finally, *attrition* causes the disappearance of patches to result in a modified landscape. A similar, although not necessarily competing, model is the variegation model of McIntyre & Barrett (1992) where a landscape is degraded from being intact to variegated, then fragmented, and finally relictual, where only small heavily modified patches of the original habitat are left.
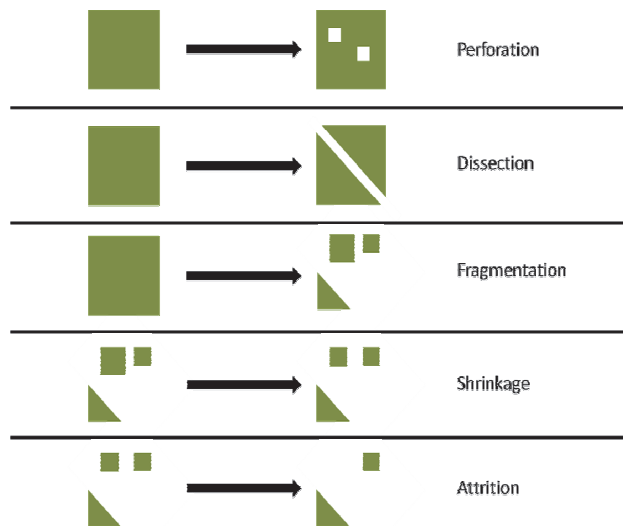
Figure 1. Five processes that act together to cause the loss and fragmentation of habitats. Modified from Forman (1995).

The process by which landscapes are modified is known as habitat fragmentation, which includes both loss of habitat and altered spatial configuration of habitat patches. However, there has been much debate about the use of terms related to loss of habitat and altered spatial configuration of remaining habitat patches (Fahrig 2003, Lindenmayer & Fischer 2007). Habitat loss refers to a change in *composition* – i.e. decreased habitat amount. On the other hand, altered spatial *configuration* of the habitat patches result in reduced mean patch size, increased isolation of habitat patches and increased amount of edge between habitat and non-habitat (Gustafson 1998). Habitat loss and the altered spatial configuration of remaining habitat patches have traditionally been considered to be strictly independent, and various statistical methods have been used to try and separate the independent effects of reduced habitat amount and the altered spatial configuration of patches. However, these two processes have recently been suggested to be part of a single hierarchical process with the direction of causality operating from habitat loss to altered spatial configuration of habitat patches (Didham et al. 2012).

2.2.1   Forestry as a cause of habitat fragmentation in Finland

Although over 85% of the surface area of Finland is classified as forestry land by the forest industry, only about 65% of the total surface area is covered by actual forests (Finnish Forest Research Institute 2011). Of the land covered by forests only 10% is strictly protected, the great majority of protected areas being located in Northern Finland (Finnish Forest research Institute 2011). This means that the vast majority of Finnish forests subjected to intensive commercial forestry. Forests are generally cut when they reach certain criteria regarding average diameter and basal diameter – roughly 60-110 years in the study site of this thesis, depending on the soil type and dominant tree species in question (Metsätalouden kehittämiskeskus Tapio 2007). Forest cutting is generally accomplished with clear-cutting almost all of the trees regardless of age and size, and small stands of live and dead trees are left for biodiversity purposes. The soil of the cut stands is then generally scarred to aid the early growth of trees and monocultures of evenly aged seedlings, the majority of which are Norway Spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*), are planted.

Although clear-cutting is meant to mimic natural dynamics of forests caused by, for example, forest fires and storms, commercial forestry has profoundly altered the composition and spatial configuration of forests in Finland. Firstly, the age structure of forests has shifted towards a distribution dominated by forests under 50 years of age. Indeed, the amount of forests under 40 years between 1951 and 2010 has more than doubled, while the amount of forests over 100 years has decreased by a third (Finnish Forest Research Institute 2011). Clear-cutting has also lead to homogeneous tracts of old forests being split into small isolated units, (Esseen et al. 1997). In addition, sharp linear borders between forested and open areas have increased, in contrast with the convoluted, gradual transitions between habitat types caused by forests fires (Hansson 1992).

In general, the loss and fragmentation of forests by commercial forestry has lead to the decrease of old-growth forest and edge-avoiding bird species, with a concurrent increase in bird species that prefer edges and early successional forest stages (Schmiegelow & Mönkkönen 2002). Among the declining species certain traits, such

as large area requirements, preference for old forests, dependency on decaying wood for foraging and cavity nesting are prevalent (Imbeau et al. 2001). Indeed, these are all attributes that have declined in forests subjected to intensive commercial forestry.

2.3   Studying the effects of habitat fragmentation

2.3.1   How can habitat fragmentation be measured?

Fahrig (2003) outlines four broad processes that are included in the concept of habitat fragmentation: loss of habitat, increased isolation of patches, increased number of patches and reduced mean patch size. Similarly, Didham et al. (2012) suggest that habitat fragmentation comprise of the following processes: loss of habitat, increased isolation of patches, decreased mean patch size, increase patch shape complexity, increased amount of edge with non-habitat and modified matrix quality. Habitat metrics (Table 1) describing these processes can be calculated from binary datasets of habitat and non-habitat using free programs such as Fragstats (McGarigal et al. 2002). The amount of habitat, the number and mean size of patches and the total amount of edge between habitat and non-habitat within a landscape can all be easily be quantified with simple habitat metrics. The isolation of patches can be quantified by calculating the mean distance between neighbouring patches. Patch shape complexity can be determined with a number of habitat metrics that calculate perimeter-area ratios, with a possible correction for the phenomenon of decreasing ratio values with increasing patch size (McGarigal et al. 2002).

It is important to note that all of the habitat metrics outlined above are correlated with each other, some very strongly so (Turner 2005, Smith et al. 2009), which can make the simultaneous interpretation of their effects challenging. In addition to the traditional landscape habitat metrics outlined above, various metrics that are able to handle for example, landscape gradients (McGarigal et al. 2009) and spatio-temporal landscape data (Parrott et al. 2008) have been proposed but so far these have not gained general use in the field of landscape ecology most likely due to the relative ease of calculation and interpretation of traditional habitat metrics.

	Attribute	Measured by	Article	Significance	Examples of use
Lanscape *composition*	Habitat amount	Absolute cover	**I, II**	Amount of habitat can be considered to be the most important metric - if there is no habitat there will no species that utilise that habitat.	Laaksonen et al. 2004, Zitske et al. 2011
		Percent cover	**III, IV**		
Landscape *configuration*	Patch size	Mean patch size	**II, III**	Measures the mean size of patches. Smaller patches are more affected by edge effects and have altered microclimates.	Didham et al. 1998, Muukkonen et al. 2012
	Number of patches	Number of patches	**II**	Describes the number of disjunct habitat patches. A larger number of patches leads to reduced connectivity in the landscape	Hinam & St. Clair 2008, Cunninham & Johnson 2011
	Isolation	Mean nearest neighbour distance	**II, III**	Measures how isolated patches are from each other. Increased isolation of patches leads to reduced connectivity, which can impact dispersal, foraging and pairing success	Nour et al. 1997, Richard & Armstrong 2010
	Edge amount	Absolute amount of edge	**II**	Increased amount of edge between habitat and matrix can increase entry of predators but can also increase food availability.	Suorsa et al. 2005, Thompson et al. 2008
		Edge density	**III**		
	Patch shape	Shape index	**III**	Describes how complex patches are in terms of shape. A higher number means a more complex shape (i.e. larger diameter in relation to surface area).	Buechner 1989, Spanhove et al. 2009

Table 1. Summary of habitat metrics generally used in landscape ecological studies, and their use in the articles included in this thesis.

2.3.2 The hierarchical nature of habitat fragmentation

It has been recently argued that habitat loss and altered spatial configuration of habitat patches cannot be considered to have truly independent effects, as suggested by many (e.g. Fahrig 2003). Instead, these two processes can be considered to be a single hierarchical process with the direction of causality clearly operating from habitat loss to altered spatial configuration of habitat patches, and not the other way around (Didham et al. 2012). This approach has the benefits of being able to take the correlated nature of habitat metrics into consideration, and enabling the simultaneous estimation of both direct and indirect effects. For example, in addition to the direct effect of reduced habitat amount habitat loss can be considered to have indirect effects acting through altered spatial configuration of habitat patches by decreasing mean patch size and increasing isolation of patches (Fig. 2).
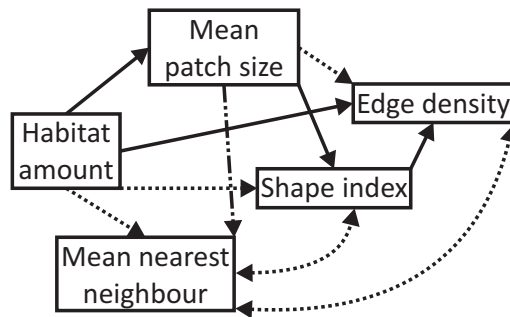
Figure 2. Diagram of hierarchical habitat model (modified from Didham et al. 2012) used in article (**III**), showing the associations between habitat metrics. Solid arrows refer to positive associations and dashed lines refer to negative associations. The direction of the association between mean patch size and mean nearest neighbour distance depended on spatial scale – it was negative at the territory scale but positive at the landscape scale. Double-headed arrows refer to non-causal correlations between habitat metrics.

Previous studies have generally treated the effects of reduced habitat amount and changes in the spatial configuration of habitat patches as independent processes acting at the same hierarchical level, and have used various statistical techniques to tease apart their relative influences such as residual regression (e.g. Cooper & Walters 2002), model selection (e.g. Olson et al. 2004) and variance partitioning (e.g. Betts et al. 2006), all of which are flawed to some degree (Smith et al. 2009). These approaches have meant that the hierarchical nature of habitat fragmentation has not yet been taken into account, which has hampered the understanding of the biological effects of habitat fragmentation. Indeed, it has been suggested that the strong effect of habitat loss, relative to altered spatial configuration of habitat patches, on species richness (Fahrig 2003) may well be due to a bias originating from the statistical separation of habitat loss and altered spatial configuration (Didham et al. 2012).

2.3.3 Scale-dependency of habitat fragmentation effects

The concept of scale is of vital importance in the field of landscape ecology, where it can refer to both spatial and temporal scale. More specifically, in landscape ecology spatial scale is generally considered to be the product of the spatial resolution (grain), which refers how fine details are examined, and spatial extent of the area to

be considered (Linke et al. 2007). In a fully homogeneous landscape, which is either fully uniform or perfectly random, spatial scale would not matter (Wu 2007). However, real landscapes are heterogeneous, and their properties depend on the spatial scale at which it is studied. As a carry-over from the IBT roots of landscape ecology early habitat fragmentation studies did not focus on spatial scale, instead essentially concentrating exclusively on the scale of individual patches (e.g. Forman et al. 1976, Robbins et al. 1989). However, it is becoming increasingly obvious that habitat fragmentation is a landscape-scale process that cannot be studied by inspecting individual patches alone (Stephens et al. 2003, Turner 2005, Fleishman & Mac Nally 2007).

There is evidence that the relevant spatial scale to study species responses to habitat fragmentation depends on the species in question. For example, Lee et al. (2002) and Desrochers et al. (2010) found differing responses in presence and abundance of different bird species in Canada to habitat amount depending on the spatial scale studied. In addition, Huhta et al. (2004), Driscoll et al. (2005), Graf et al. (2005) and Suorsa et al. (2005) all found differing responses of different life history traits within individual bird species to habitat fragmentation at varying scales. Although different species respond differently to habitat fragmentation at varying scales, some general trends have been found. Nest site selection, food abundance and microclimate effects are generally affected by local scale habitat structure, and predation and competition are affected by neighbourhood/landscape scale structure (Desrochers et al. 2010). In addition, Chalfoun et al. (2002) found in a meta-analysis of habitat fragmentation effects on nest predation that nest predation effects appeared to be more prevalent in studies conducted at the landscape scale.

2.3.4   Remote sensing data in habitat fragmentation research

The enormous increase in the number of landscape ecology articles (Turner 2005) can be at least partially attributed to the current availability of remote sensing products such as aerial images and satellite images. Remote sensing has enabled the collection of land surface data from large areas, and from areas not otherwise accessible (Lillesand et al. 2008). In a review of 438 landscape ecology articles

published between 2004 and 2008 Newton et al. (2009) found that 46% had used aerial images and 42% had used images acquired by Landsat satellites to quantify landscape structure.

The use of satellite images in ecological research has been steadily increasing since the early 1970's when NASA launched the first Landsat satellite, the first civilian satellite capable of capturing terrestrial data. From the beginning of the program Landsat satellites have carried multi-band sensors capable of capturing data from both visible and near infrared wavelengths. These wavelengths have made possible the separation of different vegetation classes (Lillesand et al. 2008).

The capturing of reflectance data from multiple wavelengths has also enabled the calculation of simple vegetation indices such as the normalised difference vegetation index (NDVI) used in numerous studies (e.g. Lyon et al. 1998, Hayes & Sader 2001, St-Louis et al. 2009, Swatantran et al. 2012).

However, perhaps the greatest strength of multi-band remote sensed data products is the possibility to classify them into biologically meaningful classes, which has enabled the prediction of distributions of both individual species and species assemblages from large areas (Kerr & Ostrovsky 2003). The use of classified satellite images to quantify habitat structure has become an integral part of studies inspecting the effects of habitat fragmentation (e.g. Burke & Nol 1998, Kurki et al. 2000, Suorsa et al. 2005, Hinam & St. Clair 2008), with data acquired from Landsat satellites playing a pivotal role (Cohen & Goward 2004).

However, despite the large amount of remote sensing products currently available to researchers multiple years of remote sensing data have been used surprisingly infrequently. This has meant that the dynamic nature of landscapes has often been neglected since many ecological studies where multiple years of biological data have been collected have included landscape data from only one year (e.g. Laaksonen et al. 2004, Hinam & St. Clair 2008, Zitske et al. 2011). This can be problematic especially in studies, which take place in dynamic landscapes, such as forests subject to harvesting

(Schmiegelow & Mönkkönen 2002). Using landscape data from more than one year also helps to control for the effect of year-to-year variation in breeding conditions (Dalley et al. 2009). However, to date only a few studies have determined habitat structure from more than one year (e.g. Mochizuki & Murakami 2011, Muukkonen et al. 2012).

2.3.5 Detecting changes in landscapes

Although habitat data from multiple years can be analysed as individual snapshots in time (Fig. 3a), such datasets offer a possibility to perform change detection of landscapes. In practice, change detection involves the identification of changes in landscape structure between two or more time periods. Depending on the remote sensing product used change detection can be performed at finer scales (e.g. changes in habitat amount for individual species) or coarser scales (e.g. regions or even biomes). The importance of quantifying dynamics in landscape structure to account for natural fluctuations in species abundance, and to determine possible trends in presence and abundance has been highlighted by many (e.g. Maron et al. 2005, Lindenmayer & Cunningham 2011, Lindenmayer et al. 2011). Quantifying change has become a practically feasible option as free access to global and regional spatial data sets has substantially increased (e.g. Vogelmann et al. 2009, Griffiths et al. 2012, Sexton et al. 2013). More specifically, change detection has been facilitated by satellite-based remote sensing programs such as Landsat, Satellite Pour l'Observation de la Terre (SPOT) and Advanced Very High Resolution Radiometer (AVHRR) (Lu et al. 2004). Indeed, recent years have witnessed a growing number of studies quantifying land cover changes in various ecosystems (e.g. Sader et al. 2001, Röder et al. 2008, Fraser et al. 2011).

Although change data can be generated using a large variety of different techniques (Lu et al. 2004) these can be split into two main categories: bi-temporal (Fig. 3b) and multi-year approaches (Fig. 3c). The most common method of change detection is by analysing differences in landscape structure between two adjacent years (bi-temporal) (Lu et al. 2004) using sensor-calibrated indices (e.g. normalised difference vegetation index) or classified images. Although these bi-temporal approaches are relatively easy to use since they only need two years of habitat data, they are rather

limited since they cannot quantify rates and dynamics of change (Gillanders et al. 2008), and can be sensitive to seasonal effects unless images are acquired at the same time period in both years (Lambin 1996). In addition, bi-temporal approaches require the user to determine a threshold, which separates real changes from those arising from causes such as misalignment of images (Lu et al. 2004). On the other hand, trajectory-based change detection methods based on multi-year remote sensing data are considered a much more effective method of quantifying landscape change for pre-defined areas and time periods (Coppin et al. 2004, Kennedy et al. 2007). In trajectory-based methods multiple years of habitat data are overlaid, and trajectories describing change are calculated for each pixel or region. Trajectories can be either classified into different classes (e.g. stable, loss of habitat then regeneration of habitat, loss of habitat then stable) (e.g. Käyhkö & Skånes 2008) or linear or non-linear mathematical curves describing habitat amount can be calculated (e.g. Griffiths et al. 2012). In both cases long-term trends in habitat amount can be quantified, and potential dynamics in habitat amount between the beginning and end of the time period in question can be detected.
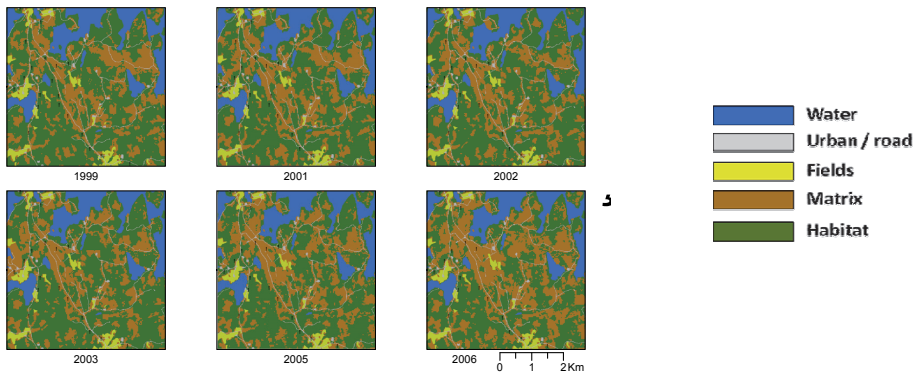
a) Series of snapshots
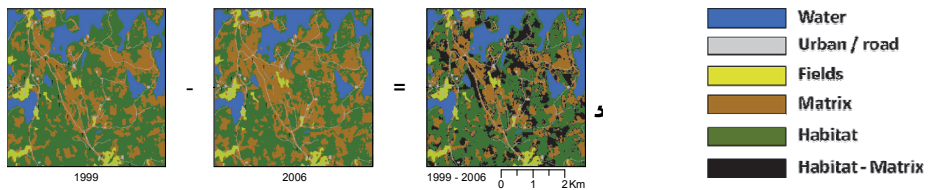
b) Image differencing
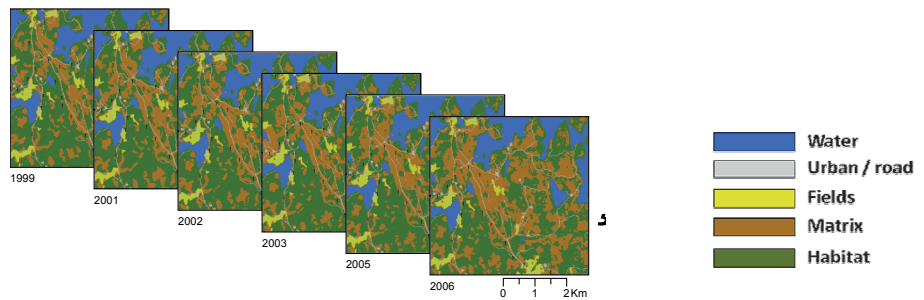
c) Spatio-temporal trajectory

Figure 3. Comparison of three different ways of analysing habitat data from multiple years. In (a) habitat characteristics from each year can be calculated and their effects analysed, but the habitat characteristics of different years have no effect on each other. In (b) differences between the initial and final stages of the landscape are quantified, and class transitions can be identified (e.g. conversion from habitat to matrix). However, if the time period is long short-term changes in the landscape can be missed. In (c) data from each year is used to construct spatio-temporal trajectories of change. Trajectories can be linear or non-linear curves, as in article (**IV**), or split into classes such as "stable", "increasing", "decreasing" or "increasing then decreasing".

2.4   *Effects of habitat fragmentation on birds*

In addition to immigration and emigration, the persistence of a species in a landscape is strongly affected by the balance of births and deaths (Pulliam 1988), which are determined by reproductive success and survival. Reproductive success and survival are determined by a number of different factors such as selection of breeding habitat, parental investment and predation of both adults and young. Therefore, processes, such as habitat fragmentation, that affect the above-mentioned traits can have profound implications on the persistence of species in a certain landscape. Indeed, previous studies have shown that habitat fragmentation can negatively affect birds through three main processes: reducing pairing success by disrupting the functional connectivity of the landscape, lowering the survival of adults through predation and nestlings through predation and nest parasitism, and reducing the availability of critical resources such as food (Lampila et al. 2005).

Cooper & Walters 2002 experimentally showed that female Brown Treecreepers (*Climacteris picumnus*) do not disperse into individual forest fragments, which leads

to the high proportion of unpaired males in fragmented habitats. Hakkarainen et al. (2008) found that in Tengmalm's owls (*Aegolius funereus*) the survival of resident males decreased with decreasing cover of old growth forests within territories. Similarly Borges & Marini (2010) showed in a study of 19 bird species nesting in central Brazil that fragmented landscapes were associated with increased nest predation rates. Also, Poulin & Villard (2011) found that in Brown Creepers (*Certhia americana*) nestling survival was decreased due to nest predation in nests closer to forest edges than in nests in forest interiors. Burke & Nol (1998) found that total invertebrate biomass in large forest patches was more than 10 times higher, and more than twice as high in randomly placed quadrats, than in small forest patches. Similarly, Zanette et al. (2000) found that in small forest patches invertebrate biomass was about half of that in large patches, and incubating female Eastern Yellow Robins (*Eopsaltria australis*) and nestlings received less food than those in large patches.

Taken together, the results of previous studies show that habitat fragmentation can reduce reproductive success by reducing the number of fledged offspring in a number of bird species (e.g. Luck 2003, Huhta et al. 2004, Fedy & Martin 2011). However, it is important to note that the results have been mixed in some species (Cooper et al. 2002, Pasinelli et al. 2008, Robles et al. 2008, Rush & Stutchbury 2008), which is why more research on what components of reproductive success are most influenced by habitat fragmentation is still needed.

3   METHODS

3.1   *Study species*

The treecreeper (Fig. 4)is a small arboreal passerine that is specialized in foraging on tree-trunks for arthropods (Suhonen & Kuitunen 1991). Treecreepers are area-sensitive and breed preferentially in old growth forests (Suorsa et al. 2005). Indeed, treecreeper breeding densities have been shown to be three times higher in old-growth forests than in managed ones (Haila et al. 1989, Virkkala et al. 1994). The size of the territory during the breeding season is about 12 ha (P. Suorsa unpublished data), which is large for a small passerine. Males defend a breeding territory reaching at least 70 m from the nest (Cramp & Perrins 1993), while feeding trips within the home range can extend three times this distance (H. Hakkarainen unpubl. data). Treecreepers construct natural nests under a flap of loose bark or in crevices in tree trunks (Cramp & Perrins 1993), but also readily accept specially designed nest boxes. Taken together with its even distribution in Finland, this makes the treecreeper a very useful study species in the context of studying habitat fragmentation.

**Figure 4.** The Eurasian treecreeper (*Certhia familiaris*).

The treecreeper has been studied extensively in the context of habitat fragmentation. Kuitunen & Helle (1988) found that the distance of treecreeper nests

to forest edges was not associated with egg laying data, clutch size or the size of breeding adults. However, more nests were destroyed within 20m of forest edges than nests located in interior forests, and nest box occupancy was higher in large (>50ha) forest patches than in small ones (<20ha). Similarly Kuitunen & Mäkinen (1993) experimentally showed that treecreepers preferentially breed in forest interiors. Suorsa et al. (2003a) found that in treecreepers male offspring are more costly to produce in terms of larger body size and increased nestling mortality, and that the proportion of male nestlings was lower in nest box sites with high edge and old forest patch density. Suorsa et al. (2003b) showed that physiological stress, measured as plasma corticosterone concentration in nestlings, was negatively associated with breeding forest patch size. This meant that nestlings reared in large forest patches were in better conditions, since increased corticosterone levels were shown to be associated with decreased body condition and survival in nestlings. Suorsa et al. (2004) showed, by experimentally manipulating brood size, that the heterophil-lymphocyte (H/L) ratio, which measures physiological stress, was higher in small nesting forest patches than in large ones in both enlarged and unmanipulated broods.

Huhta et al. (2004) found that nest predation explained the most variation in the number of successful nests and fledged offspring, and that nest predation was positively associated with amount of habitat fragmentation at the landscape scale (500m from the nest box). Suorsa et al. (2005) showed that the occupancy of territories decreased with loss of old forest at the territory (200m from the nest box) and territory core (30m from the nest box) scales. Finally, Jäntti et al. (2007) found that distance at which male treecreepers begin to alarm in response to predators increased with decreasing forest patch size, while in females the association was the opposite. In summary, the results of previous studies have shown that habitat fragmentation negatively influences treecreepers in many ways. However, a direct link between habitat fragmentation and reproductive success has been lacking, and the effects of habitat fragmentation on adult treecreepers have not been studied.

3.2   *Study area and Treecreeper data collection*

Data on treecreeper breeding events was collected between 1999 and 2006 mainly by Petri Suorsa from the University of Turku, as part of a projected funded by the Academy of Finland. All data was collected from a study site in Central Finland (centred on 62°37'N, 26°20'E) (Fig. 5). The study site originally consisted of 45 nest pairs placed in individual forest patches surrounding Konnevesi Research Station. In autumn 1998 the study site was extended to consist of 240 nest box pairs in an area covering 1150 km^2. Based on aerial images taken of the study area the nest box sites were placed so that they were located both in single discrete forest patches and in continuous forests. This ensured that there was a gradient of relatively intact and heavily fragmented nest box sites. Two treecreeper-specific nest boxes were placed in each site in order to allow for potential second breeding attempts by the breeding pair.
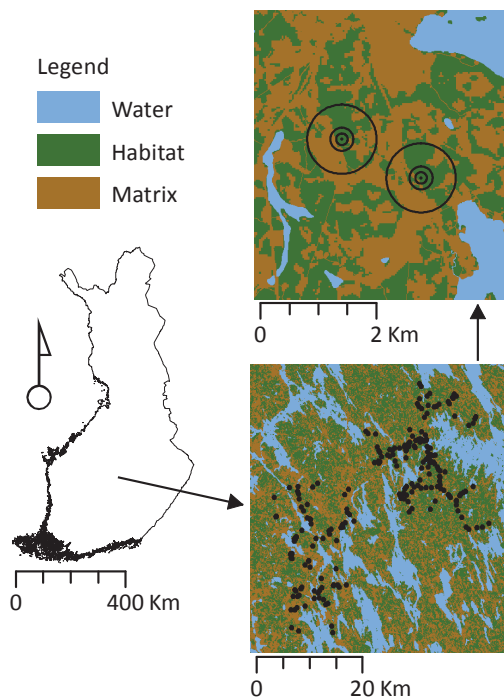
Figure 5. Map showing location of the study site in Finland, the locations of nest box sites within the study area in 1999 and two example nest box sites with circles representing the three different scales used in analyses.

Each nest box site was visited several times between April and July in order to check for first and second breeding attempts. If signs of nesting activity were present then the nest box site in question was visited more often in order to reliably record breeding parameters. Clutch size and the number of nestlings and fledglings were recorded. The number of fledged offspring was determined by subtracting the number deceased offspring from the number of nestlings. Each nest was also recorded as being predated or not by observing the state of the nest. During these visits the wing, tarsus retrix and beak length, as well as weight, of nestlings was measured. In addition, the amount of subcutaneous fat in the abdomen and tracheal pit (Kaiser 1993) and the overall condition of pectoral muscles (modified from Gosler 1991) were recorded. Nestlings could not be sexed since determining sex at this stage requires molecular methods. Breeding females and males were trapped with mist nets near nest boxes when nestlings were 5-16 days old. Adult birds were then sexed and aged (age of two calendar years or older) based on plumage characteristics, and the same measurements as recorded from nestlings were also taken. Data from a total of 1105 separate breeding attempts, including 524 breeding adults and 4405 nestlings, were collected.

3.2.1   Cross-fostering experimental design

Although experimental approaches are needed to reliably separate cause and effect between habitat fragmentation and ecological processes, studies investigating the consequences of habitat fragmentation on individuals and populations have mainly been correlative in nature. This has mainly been due to the practical difficulties in conducting landscape-level experiments (McGarigal & Cushman 2002). In article (**I**) I analysed the results of a cross-fostering experiment (Fig. 6) designed to separate genetic and environmental effects of offspring condition. In the cross-fostering experiment pairs of nests (duplicates) were formed between simultaneously hatched nests, with one nest being located within a small forest patch and the other within a large patch. Half of the nestlings from small nesting forest patches were then swapped with nestlings from large patches. The chicks that were not swapped served as controls. I used general linear mixed models (Littell *et al.* 2006) to perform a full-sib analysis in order to determine the relative contributions of nesting patch

size, genetic background and parental effects on offspring traits. Despites its limitations in regards to overestimating genetic effects, full-sib analysis has been successfully used in a number of studies to separate environmental, genetic and genotype-by-environment effects on morphological traits (Merilä & Sheldon 2001).
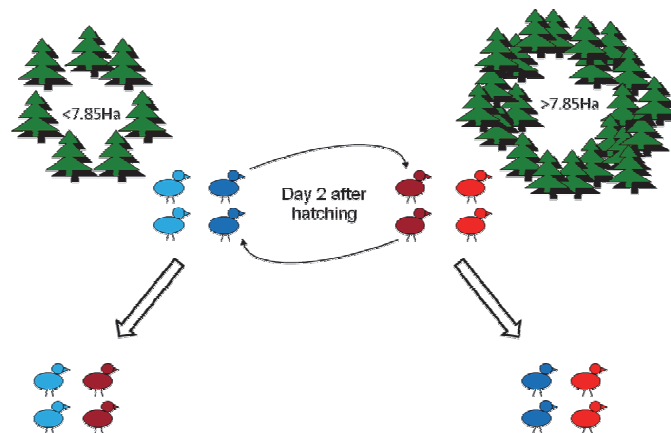
Figure 6. Schematic representation of cross-fostering experiment. Blue and red nestlings represent separate nests belonging to a single duplicate, within which nestlings were swapped.

3.3   Habitat data collection

Three different sources of habitat data were used in this study: National Land Survey (NLS) (**I**), National Forest Inventory (NFI) (**II**) and satellite images that I classified myself (**III**) and (**IV**). In articles (**III**) and (**IV**) I used satellite images that I had classified myself since the temporal frequency at which images were available from NLS and NFI were not sufficient, and because reliable change detection could not be performed using the NLS and NFI data.

3.3.1   Land Cover and Forest Classification data

Habitat data from the Land Cover and Forest Classification (LCFC) data, containing information about land use and forest classification in Finland, was used in article (**I**). The LCFC, produced by the National Land Survey of Finland, was based on Landsat images taken between 1995 and 1997. The pixel size of 30m present in the original satellite images was resampled to a size of 25m. Forests were classified with a k-nearest neighbour method using data from National Forest Inventory field plots.

Based on the total volume of forest per hectare forests were classified into volume classes with intervals of 50m^3/ha. Clear cuts were classified as containing less than 4 m^3/ha, and saplings as containing between 4 and 12 m^3/ha. After classifying by wood volume forests were classified according to the dominant tree species and soil type (Vuorela 1997). Since the satellite images used in the LCFC had been taken up to four years before the beginning of treecreeper data collection the habitat data was updated by digitising clear cuts based on up-to-date aerial images.

3.3.2   National Forest Inventory data

Because the LCFC was discontinued after 1997 data from multi-source National Forest Inventory (NFI) was used for article (**II**). NFI is a nation-wide survey of forest structure based on satellite-based remote sensing combined with data from field plots, conducted every five years by the Finnish Forest Research Institute. In multi-source NFI datasets Landsat images, as well as other high-resolution satellite data, are classified into different forest categories by using field measurements, satellite images and digital maps. Pixels from the original satellite images were resampled to a pixel size of 25m, and geometric rectification and illumination correction was carried out. A digital mask was used to select only forested areas and mires for the classification. A non-parametric k- nearest neighbour classification was performed, resulting in 16-20 forest layers containing information about e.g. wood volume (in 50 m^3/ha intervals), tree height and tree age (Tomppo et al. 2008). Habitat data from NFI 9 and 10, representing forest structure from 2002 and 2005, respectively, was used in article (**II**).

3.3.3   Interpretation and classification of satellite images

Since, the temporal frequency at which NFI data products are produced was not sufficient for tracking forest dynamics at a yearly frequency, I classified Landsat 5 satellite images of the study site myself for articles (**III**) and (**IV**). Landsat 5, launched in 1984 and operational until 2011, carried two sensors: Thematic Mapper (TM), data from which was used in this thesis, and Multispectral Scanner System. TM images have a spatial resolution of 30m and have an image size of 185km by 172km. TM images consist of seven separate bands ranging from the visible bands to thermal

infrared (0.45 - 12.5 μm wavelength) (U.S. Geological Survey, 2012). This enables the reliable classification of different vegetation classes at a moderate spatial resolution.

I downloaded six Landsat 5 Thematic Mapper images from the United States Geological Survey Global Visualization Viewer service (http://glovis.usgs.gov). These images were acquired on the following dates: 31.7.1999, 27.6.2001, 6.6.2002, 19.8.2003, 2.9.2005, 17.6.2006 and 3.7.2006. . All of the images used in this thesis had a total cloud cover of 10% or less. As the images from summer 2000 and 2004 were too cloudy for use in this study, data from the previous year was used as a surrogate. The averaging of pixel values between consecutive years was avoided since forest harvesting is typically abrupt and results in dramatic changes in satellite image values.

Each image was classified into two classes: old forest as habitat for treecreepers and matrix as non-habitat (Fig. 5). In order to avoid unnecessary confusion in the classification, water pixels, fields and human-made features were extracted from the satellite images prior to classification. A rough quantitative comparison of the classified images with those from NFI 10 showed that the old forest class corresponded to forest over 100m^3/ha of wood, which indicates forest age of over 50 years (Tomppo et al. 1999) and is very close to the mean forest age around the nest boxes (52 years, Suorsa et al. 2003b). However, it is important to note that it was not possible to separate forest patches on the basis of age or trunk density. The matrix class contained non-suitable habitats for treecreepers e.g. young forests, saplings, clear cuts, water bodies and human-created features such as fields, roads and buildings, which could not be separately classified since they could not reliably be separated from each other in the satellite images used here.

Prior to the generation of the habitat data, clouded areas were manually digitised and clipped out of each scene. In 2006 two images taken 16 days apart were joined in order to form a cloudless composite image. Due to the clear spectral signals of the anticipated classes, no further atmospheric correction of the images was considered necessary. Furthermore, the geometric accuracy of the downloaded images was considered sufficient for direct comparison since all images had been precision and

terrain corrected using ground control points and a digital elevation map (United States Geological Survey Level 1T processing).

Classification was based on supervised classification using the maximum likelihood rule using ERDAS Imagine 11.0 (ERDAS 2010). In supervised classification the computer automatically assigns each pixel in the satellite image into a user-defined class using information from training areas, which are areas judged to be representative of a certain class, and delineated by the user. Training areas were identified based on visual identification using different band combinations (bands 1,2,3 and 1,4,7) for ease of identification. The spectral separation of the two classes was good, with each separate classification having a transformed divergence value of 2000, indicating that the classes can be spectrally separated from each other (Jensen 2005). The accuracy of the classification scheme was also assessed, and found to be sufficient for the purpose of this study (see appendix in article **III**).

3.3.4 Generation of nest box site-specific habitat data

In this thesis the definition of habitat was set according to the requirements of the treecreeper. A cut-off value of 100 m3/ha, which corresponds to a mean forest age of over 50 years in the study area (Suorsa et al. 2003b), was used to distinguish old forest (habitat) from matrix. This definition of habitat has previously been shown to influence physiological stress and sex ratio of nestlings as well as predation rates in Treecreepers in the same study population (Suorsa et al. 2003a, Suorsa et al. 2003b, Suorsa et al. 2005).

Habitat metrics describing habitat fragmentation were calculated from three different scales (Fig. 5). In article (**I**) the size of the nesting forest patch within 200m from the nest box pair, representing the territory scale, was used to explain habitat amount. In article (**II**) habitat fragmentation metrics (Table 1) were calculated at the landscape (500m) scale, which should correspond better to the area that treecreepers utilise after their breeding season than the territory scale (Suorsa et al. 2005). In article (**III**) two different sized circular areas surrounding the centre of each nest box site were cut, representing territory (200m) and landscape (600m) scales,

and habitat metrics describing habitat fragmentation were calculated (Table 1). In article (**IV**) the change in habitat amount was calculated at the territory core (100m) and landscape (600m) scales. Although it would have been interesting to specifically measure altered spatial configuration of habitat patches within 100m from the nest box pair, the size of the pixels in the original satellite images (30m) was too large to accomplish this reliably in article (**III**).

In articles (**I**) and (**II**) absolute habitat metrics (e.g. amount of habitat) were calculated, while in articles **III** and **IV** only proportional habitat metrics (e.g. percent cover of habitat) were calculated. Proportional habitat metrics were calculated in order to ensure that metrics between cloud- free and cloud- covered nest box sites could be compared to each other.

3.3.5   Measuring habitat change

In article (**IV**) habitat change was measured from spatio-temporal trajectories of habitat amount for each unmoved nest box from which at least two years of habitat data was available from. Change trajectories of habitat amount were calculated since habitat amount has previously been shown to be associated with territory occupancy (Suorsa et al. 2005), nest predation (Huhta et al. 2004) and nestling body condition (Suorsa et al. 2003b) in treecreepers. The 200 nest box sites included in this study had an average (sd) of 5.1 (1.5) years of habitat data, with 11 (5.5%) sites having only two years. Change trajectories were calculated from a database containing habitat amount during individual years for each separate nest box site using random regression modelling (see below). The result was an estimate of the slope of change for each nest box site, which described the direction and magnitude of the linear change in habitat amount. Many of the nest box sites used in article (**IV**) had non-linear trends in habitat amount, with loss and apparent regeneration of old forest. However, the period of eight years during which data was collected was so short that forests were not expected to experience significant rates of regeneration. Instead, potential increases in habitat amount were expected to be the product of classification error. Therefore, only linear change trajectories were calculated as opposed to calculating non-linear curves.

3.4   Special statistical methods

3.4.1   Structural equation modeling

In articles (**III**) and (**IV**) I used a structural equation modeling (SEM) (Jöreskog 1973) approach to study the influences of habitat fragmentation and land cover changes on the reproductive success of treecreepers. SEM is a multivariate statistical approach that enables the hierarchical modelling of complex ecological processes, where multiple interacting processes take place simultaneously (Grace 2006). In other words, SEM can handle both direct (e.g. loss of habitat affects number of fledged offspring) and indirect effects (e.g. loss of habitat leads to increased edge density, which affects number of fledged offspring).

SEM also has the added benefit of being able to incorporate unobserved latent factors whose implied values can be estimated from multiple observed indicators that are correlated because they are assumed to be caused by the latent factor(s). Such latent factors serve to reduce the bias in parameters by averaging over errors, providing estimates with greater reliability (Grace 2006). In the context of research on habitat fragmentation, SEM also has the advantage of offering a way to simultaneously evaluate the paths through which habitat fragmentation affects species. For example, SEM can be used to evaluate whether habitat fragmentation affects reproductive success through fecundity or nestling survival.

3.4.2   Random regression modelling

In article (**IV**) random regression models were used to calculate the linear trend in habitat amount at two different spatial scales for each individual nest box site. Random regression models enable the calculation of regression coefficients for individual subjects or clusters and can be considered to be independent from each other (Littell et al. 2006). Random slopes were calculated separately for both spatial scales by using random regression models of habitat amount versus year. Nest box site identity was used as a subject-effect, which enabled the calculation of random slopes and intercepts for each individual nest box site. This meant that linear change trajectories could be calculated for 200 nest box sites in one statistical test. From the random regression models, best linear unbiased predictors (BLUPs), which represent

the deviation of change in habitat amount of a nest box site from the population mean (i.e. fixed slope), were extracted (Littell et al. 2006). I then used these estimates to represent the changes in habitat amount at the territory core and landscape scales in subsequent analyses.

4   MAIN RESULTS AND DISCUSSION

4.1   *Environmental, genetic and parental components of offspring traits*

Genetic and parental components of offspring traits have not previously been taken into account in studies inspecting the effects of habitat fragmentation on individuals, even though they are important components producing phenotypic variation between individuals (Falconer & MacKay 1996, Kruuk & Hadfield 2007). In article (**I**) I analysed the results from a cross-fostering experiment. I found that genetic background and parental effects explained most of the variation in physiological traits of offspring, while the size of the nesting patch had a negligible effect. Genetic background explained the majority of variation in morphological size, body condition and physiological stress, which is in agreement with the results of previous studies (Merilä et al. 2001, Campo & Davila 2002, Bize & Roulin 2009), while parental effects explained the majority of variation in the condition of pectoral muscles and inflammation status. Although the lack of an effect of habitat amount seems to be at odds with the results of Suorsa et al. (2004) who found a clear effect of nesting forest patch size on physiological stress in treecreeper nestlings, the difference might have been due to differences in weather conditions between the two years.

Studies conducted during only one breeding season may miss potential temporal variation in the environment (Harrison & Bruna 1999), such as year-to-year differences in climate conditions. This was highlighted in the results of article (I) where no effect of nesting forest patch size was found on physiological traits of nestlings. However, since the data for article (**I**) was collected from only one breeding season I was not able to rule out the possibility that beneficial weather-related conditions during 2002 might have lead to high food supply for treecreeper nestlings, masking the effect of nesting forest patch size. A comparison of the weather-related conditions between 2002 and 2001, when the data for Suorsa et al. (2004) were collected, showed that the breeding season of 2002 was clearly warmer with less rainy days than in 2001. In addition, potential mild winter weather conditions during the previous winter might have positively influenced the condition of breeding treecreepers (Virkkala 2004) in 2002, which could have masked the effect of nesting forest patch size.

4.2   Influence of habitat fragmentation on adults

Although the effects of habitat fragmentation on treecreepers have been extensively studied in nestlings (Suorsa et al. 2003a, 2003b, 2004, Huhta et al. 2004) no studies have been conducted concerning the responses of adult traits. In article (**II**) I studied how habitat fragmentation is associated with the widths of feather growth bars, which reflect the nutritional condition of the bird when the feathers were grown. When all individuals were inspected I found that habitat fragmentation was not associated with nutritional condition. However, when age classes were analysed separately I found that in young adult treecreepers the number of individual patches and the amount of edge within 500m of the nest box site was weakly negatively associated with nutritional status. Only one other study has inspected the effects of habitat fragmentation on feather growth bars. Stratford & Stouffer (2001) found that birds in small forest fragments were in poorer nutritional condition than those in large forest patches. However, a comprehensive set of habitat metrics was not included, and the sex and age of individuals was not considered.

Large forest patches should contain more food due to an increased number of tree trunks on which treecreepers can feed on (Kuitunen 1989). In addition, decreased patch size has been shown to be associated with reduced food supply in birds (Burke & Nol 1998, Zanette et al. 2000), and, treecreepers have been shown to locally deplete food abundance during the breeding season (Jäntti et al. 2001), suggesting that food supply may be a limiting factor. The lack of a clear influence of habitat fragmentation on the nutritional condition of treecreepers appears to be at odds with the points outlined above. However, since all of the treecreepers used in this study were breeding individuals it is possible that they simply shifted the effects of reduced food supply on their offspring, thus hiding any direct influence on adult condition. In addition, the apparently slightly stronger influence of habitat fragmentation on younger adults could be explained by older individuals being more experienced, and thus being able to forage more efficiently than younger ones. The negative association between the amount of edge and nutritional condition in young adults was in line with several previous studies that have found negative effects of edges on birds (e.g. Batáry & Báldi 2004, Banks-Leite et al. 2010, Poulin & Villard

2011). This seems to go against the results of (Helle & Muona 1985) who found that forest edges in Finland contain higher numbers of invertebrates than forest interiors, although it is important to keep in mind that the association found in article (**II**) was weak at best.

4.3 Influence of habitat fragmentation and change on reproductive success

In article (**III**) I studied the influence of habitat fragmentation on reproductive success. I used a SEM approach to model the hierarchical nature of habitat fragmentation, and to model causal effects between important variables determining reproductive success, such as clutch size, maternal condition, nest predation and nestling survival. The only habitat metric that had a significant association with reproductive success was the amount of old forest at the landscape level. The amount of old forest at the landscape scale had a strong association with reproductive success since it was associated with an elevated probability of nest predation. This dramatically decreased nestling survival since of the 98 predated nests 90 produced no fledged offspring. As would be expected, clutch size and nestling survival were strongly positively associated with the number of fledged offspring, while nest predation probability had a strong negative association. In addition, I found strong associations between habitat metrics (Fig. 2) within the process of fragmentation, as has been suggested by Didham et al. (2012).

Interestingly, in article (**III**) I found that at the landscape scale loss of habitat was associated with decreased nest predation and increased fledgling success. This is contradictory to the results of Huhta et al. (2004) where loss of habitat at the landscape scale was found to be associated with increased nest predation. I suggest that the differences in results between my research and those of Huhta et al. (2004) are mainly due to the location differences – the data for Huhta et al. (2004) was collected from a field-dominated area of the study site. This could have increased the number of mustelid predators, which are not affected by the loss of old forest habitat. It is also important to note that the definition of habitat in this study was based on a rough estimate of forest age, and included both old forests over 100 years and middle-aged forests between 50 and 100 years. In addition, I was not able

to classify forests by attributes such as trunk density and thinning status, which has been shown to impact the nesting success of another old-forest specialist, the Siberian tit (*Poecile cinctus*) (Virkkala 1990). This means that there could have been differences in habitat quality irrespective of habitat fragmentation between nest box sites. However, this is not the first time that habitat fragmentation has been found to positively influence reproductive success (Chapa-Vargas & Robinson 2007, Cox et al. 2012). I suggest that this result is due to the two main nest predators of treecreepers, red squirrels (*Sciurus vulgaris*) and great spotted woodpeckers (*Dendrocopos major*) (Huhta et al. 2004), suffering due to loss of forests (Virkkala et al. 1994, Koprowski 2005, Mazgajski & Rejt 2006).

In article (**IV**) I studied the influence of change in habitat amount on reproductive parameters summed per nest box site. Firstly, I found that there was a general decreasing trend in habitat amount with a clear decrease after 2003 (Fig. 7). On average nest box sites lost 1.6% habitat cover per year at the territory core scale, and 1% at the landscape scale. In addition, nest box sites significantly differed from each other in terms of the rate of change in habitat amount. I found that the change in habitat amount, as well as initial habitat amount, at the territory core and landscape scales were associated with treecreeper reproductive parameters. At the territory core scale a decreasing trend in habitat amount, as well as less initial habitat, were associated with decreased numbers of nesting events, laid eggs and fledged offspring in nest box sites.
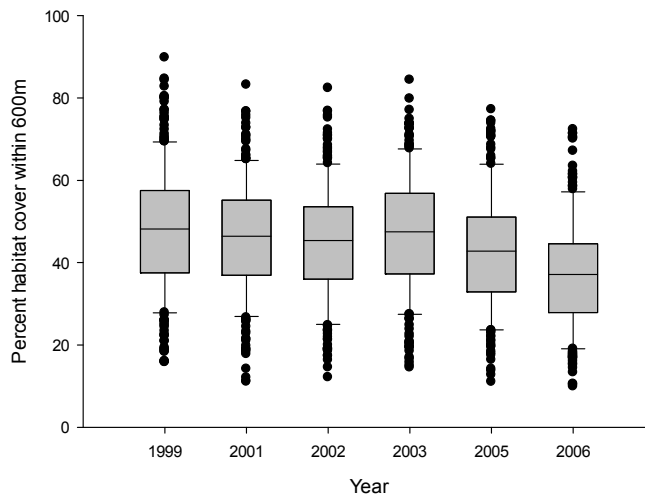
Figure 7. Box plot show percent cover of habitat (old forest) measured at the landscape scale (600m from nest box) for each year separately. The tops and bottoms of the grey boxes represent the 75th and 25th percentiles, respectively, while the lines in the middle of the grey boxes represent the median. The error bars above and below the grey boxes represent the 90th and 10th percentiles, and the individual points represent values beyond these percentiles.

At the landscape scale the slope of change in habitat amount and initial habitat amount showed a significant interaction, which needs to be taken into account when interpreting the influence these terms. When initial habitat amount was equal to the population average a decreasing trend in habitat amount decreased the number of fledged offspring, and increased the number of predation events. In contrast, when the slope of change in habitat amount was equal to the population average a smaller amount of initial habitat was associated with a decreased number of fledged offspring, and an increased number of predation events. However, the interaction between the slope of change in habitat amount and initial habitat amount was such that an increasing amount of initial habitat lessened the influence of change in habitat amount on the number of fledged offspring and predation events. As expected, an increased number of nesting events resulted in an increased number of eggs laid, predation events and fledged offspring. In addition, an increased number of eggs laid increased the number of fledged offspring, while an increased number of predation events had a negative effect.

In both articles (**III**) and (**IV**) I found that habitat loss strongly influenced the reproductive success of treecreepers. However, in article (**III**) only habitat loss at the landscape scale had an influence on reproductive success, while in article (**IV**) changes in habitat amount at both the territory core and landscape scales were important. The most likely explanation for this is the difference in spatial scales – article (**III**) measured habitat fragmentation 200m from the nest box pair while article (**IV**) used a smaller radius of 100m. Characteristics very near the nest box have previously been shown to be important for nest site selection in treecreepers (Suorsa et al. 2005), and feeding trips have been shown to extend to a maximum of 200m from the nest box site (H. Hakkarainen unpublished data). Therefore, there is reason to believe that habitat fragmentation measured close to the nest box pair has a strong influence on reproductive success. Due to the relatively large size of the pixels in the satellite images (30m) habitat metrics describing the spatial configuration of old forest patches could not be reliably quantified at a radius of 100m. Therefore it was not possible to include the territory core scale in article (**III**). An alternative explanation for the lack of an association at the territory scale in article (**III**) could be due to the fact that I only included nest box sites in which nesting events took place. In contrast, in article (**IV**) I included both occupied and unoccupied nest box sites, and found that those nest box sites that had lost the most habitat had fewer nesting events. Therefore, nest box sites that had lost so much habitat that an influence on reproductive success could be seen were simply not occupied, and therefore no direct influence was apparent.

4.4   Methodological issues

4.4.1   Classification accuracy of habitat data

An important point to note is that the classification scheme used in articles (**III**) and (**IV**) considered the study area as a binary landscape of habitat and non-habitat. This classification scheme was relatively simplistic compared to the methods used in the NLS (Vuorela 1997), which has been used in previous treecreeper studies (Suorsa et al. 2003a, 2003b, 2005, Huhta et al. 2004) and habitat datasets of other studies (e.g. Hakkarainen et al. 2003, Laaksonen et al. 2004, Muukkonen et al. 2012). Although it is well accepted that a binary landscape is not a realistic representation of true

landscapes (Fischer & Lindenmayer 2007), this simplification of the landscape was required for the calculation of habitat metrics describing the spatial configuration of habitat patches.

In addition, the simple two-class classification also enabled me to quantify landscape structure with relatively little error for almost all of the years from which treecreeper data was available from. Both Newton et al. (2009) and Lechner et al. (2012) outline the importance of assessing classification error, which is not generally carried out in landscape ecological studies. Therefore in article (**III**) I performed a classification accuracy assessment (Lillesand et al. 2008), which showed that 81.1% of the sampled pixels from the classified satellite image had the same class as the corresponding pixels in the classified aerial images. The kappa coefficient of 0.58 showed that the classification performed 58% better than a random classification scheme. This equates to a moderate strength of agreement, close to the limit of 0.6, which would indicate substantial agreement (Landis & Koch 1977).

The simple classification scheme was especially important in article (**IV**) in which I calculated change trajectories from an almost yearly set of classified satellite images. Although misclassification of pixels does not necessarily have a great impact on habitat metrics calculated from a single classified remote sensing image (Wickham et al 1997), the effect of classification error on change metrics can be severe (Burnicki 2012). For example, Brown et al. (2000) showed that errors in habitat metrics caused larger differences in change metrics than would be expected to arise from errors in habitat metrics alone, which was also found by Burnicki (2012) in a simulated study. Also, Linke et al. (2009) found that spatial misalignment of habitat states lead to changes in the direction and strength of various change metrics. Indeed, the slight rise in habitat amount between 2002 and 2003 was almost certainly caused by classification error in 2003. This supports the use of the change trajectories, since merely comparing habitat amount between pairs of years would have shown an increase in habitat amount, which could not have taken place in such a short period of time.

4.4.2 Separation of direct and indirect effects of habitat fragmentation

The SEM approach used in articles (**III**) and (**IV**) enabled the estimation of both direct and indirect effects of habitat fragmentation on treecreeper reproductive parameters. Indirect effects are calculated as the mathematical product of all of the possible paths from one variable to another via intermediate variables (Grace 2006). For example in article (**IV**) I found that change in habitat amount did not directly influence the number of eggs laid. However, the change in habitat amount had an indirect effect by positively influencing the number of nesting events, which in turn increased the number of eggs laid. Similarly, in article (**III**) I found that both the direct and indirect effects of the amount of habitat at the landscape scale were not associated with the probability of nest predation. However, the total effect of habitat amount, which is the sum of direct and indirect effects, was significant. In both of these cases important associations between habitat fragmentation and the reproductive success of treecreepers would have been missed if traditional univariate statistical methods had been used.

However, perhaps the greatest benefit of SEM in this thesis was its ability to model habitat fragmentation as a single hierarchical process in article (**III**) (Fig. 2). In general I found that the associations between habitat metrics were comparable in terms of relative strength and direction between the territory and landscape scales. The clearest exception to this was the association between the mean size of patches and the isolation of patches. At the territory scale an increase in average patch size was association with a decrease in the isolation of patches, while at the landscape scale there was a positive association. Interestingly, I found that the direct and indirect effects between some variables acted in opposing directions. For example, the amount of habitat at the territory scale had a positive direct effect on the amount of edge, but the indirect effect was negative. The negative indirect effect arose as a consequence of increased habitat amount decreasing the amount of edge by decreasing average shape complexity, and by increasing the mean size of patches. At the territory scale the positive direct effect and negative indirect effect cancelled each other out so that the total effect was not statistically significant, while at the landscape scale the direct effect was so strong that the total effect remained positive

despite the negative indirect effect. If the associations between habitat metrics had been analysed with traditional univariate statistical methods the association between habitat amount and edge amount would have been negative, which would only reflect one side of the situation.

4.5   Applications

In general, the results from this thesis support the importance of the composition (namely the amount of habitat) over the spatial configuration of landscapes. The importance of habitat amount was found even though the relations between habitat metrics were modelled realistically as a hierarchical process. The artificial separation of habitat loss and altered spatial configuration of habitat patches using statistical methods has previously been suggested to be a reason that habitat amount has been found to have a much stronger influence on ecological processes than spatial configuration (Didham et al. 2012). Therefore, these results support the importance of concentrating on protecting large intact areas of habitat, which is also supported by the ability of increased habitat amount to buffer against the negative effects of decreasing trends in habitat amount found in article (**IV**). The negative, albeit weak, influence of increased edge amount on the nutritional condition of adults also suggests that the negative effects of edges created by commercial forestry might outweigh potential increases in food abundance found in edge habitats (Helle & Muona 1985).

The collection and classification of satellite images taken of the study area four years after the end of the collection of biological data shows the power of remote sensing products to quantify landscape composition and configuration retrospectively. The multiple years of habitat data created for this thesis also enabled reliable change detection to be conducted for individual nest box sites. The results from article (**IV**) show that with freely available satellite images it is feasible to incorporate change detection into studies examining the effects of habitat fragmentation on species. However, it is important to note that in order to carry out reliable change detection classes need to be easily separable from each other, which speaks in favour of using relatively simple classification schemes for change detection. Incorporating a

temporal component into studies examining the effects of habitat fragmentation can enable the identification of cumulative effects on, for example, reproductive success too subtle to be visible using single years of data.

The results of this thesis also underline the importance of incorporating more than one year of habitat data in studies examining the effects of habitat fragmentation, especially in experimental studies. In article (**I**) the lack of an effect of habitat amount on offspring traits could well have been due to beneficial weather conditions during the breeding season. In contrast, the data for articles (**II-IV**) was collected over multiple years, which controlled for potential differences in year-to-year conditions.

5   CONCLUSIONS

Overall, the results of my thesis show that the loss and altered spatial configuration of old forests has a general negative influence on the reproductive success of treecreepers. Although I did not find a clear negative association between habitat fragmentation and nestling condition (**I**) or fledging success (**III**), article (**II**) showed a weak negative influence of habitat fragmentation on young adults and article (**IV**) showed that a decreasing trend in habitat amount was associated with decreased nest site occupancy, clutch size and fledging success. Together with the results of previous studies conducted in the same study system, these results show that habitat fragmentation can have negative influences on many life history traits of treecreepers, but that these effects are often scale-dependent (Table 2).

Treecreeper attribute	Scale		
	Territory core (100m)	Territory (200m)	Landscape (500m-600m)
Nest site occupancy	Lowered	Lowered	No association
Laying date		No association	
Clutch size	Lowered	No association	
Nest predation			Lowered or increased, depending on landscape context
Nesting success	Lowered		Increased
Body condition of adults		No association	
Nutritional condition of adults			No influence on old adults, weak influence on young adults
Sex ratio within broods		Female-biased	Female-biased
Immunocompetence of nestlings		No association	
Physiological stress of nestlings	Increased, but dependent on year-to-year differences		Increased
Inflammation status of nestlings		No association	
Nestling size and body condition		No association	
Nestling survival			Increased

Table 2. Summary table of the effects of increased habitat fragmentation at three different spatial scales on treecreeper attributes. Results have been summarised from analyses conducted between 1988 and 2012.

I suggest that habitat fragmentation mainly affects treecreepers at the breeding habitat selection stage – those territories with the most habitat fragmentation were not occupied. Therefore occupied territories were of sufficiently high quality that the effects of habitat fragmentation were not readily detectable as reduced reproductive success in article (**III**). Another important avenue through which habitat fragmentation can influence treecreepers is by affecting predation rates since predation events generally resulted in the complete destruction of the nest in question. In article (**III**) I found that an increased amount of habitat actually increased the probability of nest predation, which is most likely due to forest-dwelling nest predators of treecreepers also suffering due to the loss and fragmentation of old forests. This result especially highlighted the importance of considering varying spatial scales when studying the effects of habitat fragmentation on species.

Habitat fragmentation did not appear to have a strong influence on the body condition or nutritional condition of adult treecreepers. However, since all captured adult treecreepers were breeding individuals it is possible that they shifted potential food shortages to their offspring. Indeed, the influences of habitat fragmentation on nestling treecreepers appear to be wide and varied, ranging from altering the sex ratio of broods to increasing physiological stress in nestlings, but also increasing nestling survival (Table 2). The influences of habitat fragmentation on nestlings can have long-lasting impacts later in life since early growth conditions have been shown to have long-lasting consequences on subsequent life-history traits (Lindström 1999, Monaghan 2008), which can impact population growth rate (Pelletier et al. 2007).

In general, the results of my thesis suggest that loss of habitat, especially near the centre of the territory, has a stronger influence on treecreepers than processes related to altered spatial configuration of habitat patches. Habitat loss at the territory core scale decreased the number of nesting events, eggs laid and fledged offspring. Although the results of article (**II**) suggest that altered spatial configuration has a stronger role than loss of habitat on adult treecreepers, the association was weak at best. The importance of habitat loss was apparent even when I took the

causal relations between habitat metrics describing habitat fragmentation into account in article (**III**). As such my results are in agreement with those of Suorsa et al. (2005) and Huhta et al. (2004) that show that habitat loss has a strong association with both breeding habitat selection and reproductive success in treecreepers.

In brief, the results of this thesis support findings from previous studies showing generally negative effects of habitat fragmentation on reproductive success in birds, but have also highlighted the how these effects can change depending on the spatial scale in question. However, the negative effects of habitat fragmentation may not be readily visible if habitat fragmentation has a strong influence on nest site selection, and may sometimes only be detectable if long-term datasets are used. This thesis has employed three novel techniques for the studying of the effects of habitat fragmentation on animals –the use of multiple years of habitat data, change analysis and structural equation modeling. The results of this thesis have highlighted the importance of assessing the effects of habitat fragmentation over time periods longer than one year and at various spatial scales, and demonstrated the usefulness of incorporating change detection to detect cumulative effects of habitat fragmentation. In addition, the results presented here have shown that care needs to be taken in order to detect potential indirect effects of habitat fragmentation on species. All of these aspects need to be taken into account in order to fully understand the consequences of this important threat to global biodiversity.

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Eric Le Tortorec

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