Habitat fragmentation and reproductive success: a structural equation modelling approach

Eric Le Tortorec[1]*, Samuli Helle[1], Niina Käyhkö[2], Petri Suorsa[1], Esa Huhta[3] and Harri Hakkarainen[1]

[1]Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland; [2]Geography Division, Department of Geography and Geology, University of Turku, FI-20014 Turku, Finland; and [3]Finnish Forest Research Institute, Rovaniemi Research Unit, FI-96301 Rovaniemi, Finland

Summary

1. There is great interest on the effects of habitat fragmentation, whereby habitat is lost and the spatial configuration of remaining habitat patches is altered, on individual breeding performance. However, we still lack consensus of how this important process affects reproductive success, and whether its effects are mainly due to reduced fecundity or nestling survival.

2. The main reason for this may be the way that habitat fragmentation has been previously modelled. Studies have treated habitat loss and altered spatial configuration as two independent processes instead of as one hierarchical and interdependent process, and therefore have not been able to consider the relative direct and indirect effects of habitat loss and altered spatial configuration.

3. We investigated how habitat (i.e. old forest) fragmentation, caused by intense forest harvesting at the territory and landscape scales, is associated with the number of fledged offspring of an area-sensitive passerine, the Eurasian treecreeper (*Certhia familiaris*). We used structural equation modelling (SEM) to examine the complex hierarchical associations between habitat loss and altered spatial configuration on the number of fledged offspring, by controlling for individual condition and weather conditions during incubation.

4. Against generally held expectations, treecreeper reproductive success did not show a significant association with habitat fragmentation measured at the territory scale. Instead, our analyses suggested that an increasing amount of habitat at the landscape scale caused a significant increase in nest predation rates, leading to reduced reproductive success. This effect operated directly on nest predation rates, instead of acting indirectly through altered spatial configuration.

5. Because habitat amount and configuration are inherently strongly collinear, particularly when multiple scales are considered, our study demonstrates the usefulness of a SEM approach for hierarchical partitioning of habitat amount vs. habitat configuration in landscape ecology that may have bearing on biological conclusions.

Key-words: *Certhia familiaris*, configuration, Eurasian treecreeper, GIS, habitat loss, Landsat TM, SEM

Introduction

Habitat fragmentation is the process by which habitat is lost and the spatial configuration of the remaining habitat patches is altered, leading to reduced mean patch size, increased isolation of habitat patches and increased amount of edge between habitat and non-habitat (Gustafson 1998).

Both habitat loss and altered spatial configuration of habitat patches have been shown to affect a wide range of organisms including mammals (Chiarello 1999), invertebrates (Robertson & Butler 2009) and plants (Valdés & García 2011), although most studies have been conducted with birds (Fahrig 2003). Habitat fragmentation can adversely affect the reproductive success of birds through three main processes (Lampila, Mönkkönen & Desrochers 2005): reducing pairing success (Cooper & Walters 2002), lowering the survival of adults through predation and

*Correspondence author. E-mail: erleto@utu.fi

nestlings through predation and nest parasitism (Hakkarainen *et al.* 2008; Borges & Marini 2010; Poulin & Villard 2011) and reducing the availability of critical resources such as food (Zanette, Doyle & Tremont 2000). Indeed, studies have shown that multiple components of the habitat fragmentation process 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), although the results have been mixed in some species (Cooper, Walters & Ford 2002; Robles *et al.* 2008; Rush & Stutchbury 2008). We thus need more research on what components of reproductive success are most influenced by variation in habitat loss and altered spatial configuration.

We believe that our understanding of the fundamental causal effects of the habitat fragmentation process has been limited by the fact that previous studies have modelled habitat loss and altered spatial configuration as two independent processes, instead of as one hierarchical interdependent process (habitat fragmentation) as recently suggested by Didham, Kapos & Ewers (2012). In addition, previous studies, using univariate statistical methods, have not been able to simultaneously assess the relative strengths of pathways through which habitat loss and altered spatial configuration can affect reproductive success, namely fecundity and nestling survival. Many previous studies have also ignored the dynamic nature of landscapes by using habitat data from only a single year even though multiple years of biological data have been used, and have not generally simultaneously considered several important variables producing variation in reproductive success (e.g. nest predation, weather conditions and body condition of breeding individuals).

It has been recently argued that habitat fragmentation should be considered to be a single hierarchical process, which recognizes the causal dependence of spatial configuration on habitat amount (Didham, Kapos & Ewers 2012). In addition to the direct effects of habitat loss on individuals, it can be considered to have indirect effects acting through altered spatial configuration, for example by decreasing mean patch size and increasing isolation of patches. Many previous studies have treated the effects of habitat loss and altered spatial configuration of the remaining 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 we feel has hampered our understanding of the biological effects of the multiple indirect components of the habitat fragmentation process. One promising but yet underutilized technique to model habitat fragmentation as a single hierarchical interdependent process is structural equation modelling (SEM), which enables researchers to consider multiple univariate associations simultaneously in a hierarchical fashion that, in turn, allows the estimation and comparison of direct and indirect effects (Grace 2006).

Our aim in this paper is to use SEM to partition the relative direct and indirect effects of habitat loss and altered spatial configuration on multiple proximate determinants of reproductive success in the Eurasian treecreeper (*Certhia familiaris* L., 1758, hereafter the treecreeper). The treecreeper is a small area-sensitive passerine (Suorsa *et al.* 2005), which forages for invertebrates on large tree trunks. We used a hierarchical SEM approach, which, despite its advantages, has only been used in relatively few ecological studies to date (e.g. Grace & Guntenspergen 1999; Valdés & García 2011; Studds *et al.* 2012) and, to our knowledge, has not been previously used in studies examining the effects of habitat loss and altered spatial configuration. We classified satellite images for six of the 8 years from which we had data from treecreeper reproductive success, and calculated five metrics explaining the most important facets of variation in habitat amount and altered spatial configuration of habitat at both the territory scale (200 m radius) and the landscape scale (600 m radius) surrounding each treecreeper nest: percentage old forest, mean forest patch size, mean nearest neighbour patch distance, mean forest patch shape index and edge density. To the best of our knowledge, this is the first time that habitat loss and altered spatial configuration effects have been quantified for so many consecutive years. The dynamic nature of landscapes has also often been neglected in ecological studies, with habitat data typically only collected in a single year even when biological data have been collected over multiple years (e.g. Laaksonen, Hakkarainen & Korpimäki 2004; Hinam & Clair 2008; Zitske, Betts & Diamond 2011). This can be problematic, especially in studies that take place in highly dynamic landscapes such as forests subject to harvesting (Schmiegelow & Mönkkönen 2002). In the case of breeding birds, using landscape data from more than 1 year also helps to control for the effect of year-to-year variation in breeding conditions (Dalley, Taylor & Shutler 2009). However, to date, only a few studies have determined habitat structure from more than 1 year (e.g. Mochizuki & Murakami 2011; Muukkonen *et al.* 2012), and they have almost always only used landscape data from 2 years.

In estimating the effects of habitat loss and altered spatial configuration on treecreeper reproductive success, we took into account variation in weather conditions by recording the temperature and amount of rain during the breeding season, which are known to affect the reproductive success of birds through their influence on clutch size and nestling growth and survival rates (Rotenberry & Wiens 1991; Dawson, Lawrie & O'Brien 2005; Skagen & Yackel Adams 2012). We also took into account maternal body condition as a surrogate of individual condition, because previous studies have generally overlooked the

degree to which phenotypic differences among individuals might mask the perceived effects of habitat loss and altered spatial configuration (e.g. Hinam & Clair 2008). Therefore, combined with data of laying date, clutch size and nestling survival, the SEM approach used here enabled us to simultaneously evaluate whether habitat loss and altered spatial configuration affect individual reproductive success through fecundity or through nestling survival.

Combining these interdependent, hierarchical effects of habitat fragmentation on multiple proximate determinants of treecreeper reproductive success in our SEM, we hypothesized that habitat loss and altered spatial configuration at the territory scale would reduce reproductive success via smaller clutch size, lower maternal body condition and decrease nestling survival, while habitat loss and altered spatial configuration at the landscape scale would decrease reproductive success via increased nest predation. Based on the strong influence of habitat amount found in previous treecreeper research (Suorsa *et al.* 2003b, 2004, 2005) and on the causal nature of habitat loss within the habitat fragmentation process, we hypothesized that habitat loss would have a stronger total influence on reproductive success in the treecreeper than altered spatial configuration.

Materials and methods

BREEDING DATA

Data on treecreeper breeding attempts were collected during 8 years (1999–2006) from a study site, which covers 1150 km^2 in central Finland (centred on 62°37′N, 26°20′E) (Fig. 1). This area is subjected to intensive commercial forestry with a rotation period of *c.* 80 years. The study area consisted of a total of 241 nest box sites, in each of which two treecreeper-specific nest boxes were placed in order to allow for potential second breeding attempts by the breeding pair. The nest box sites were located both in single discrete forest patches and in continuous forests so that there were more and less fragmented sites. Each nest box site was visited several times between April and July in order to check for first and second breeding attempts. Clutch size and the number of nestlings and fledglings were recorded, and the wing length of nestlings was measured during these visits. Breeding females were trapped with mist nets near nest boxes when nestlings were 5–16 days old, and wing length, tarsus length and weight were measured. A total of 890 separate breeding attempts were included in this study.

HABITAT DATA

Landsat 5 Thematic Mapper satellite images from six different years were downloaded 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 study 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 were
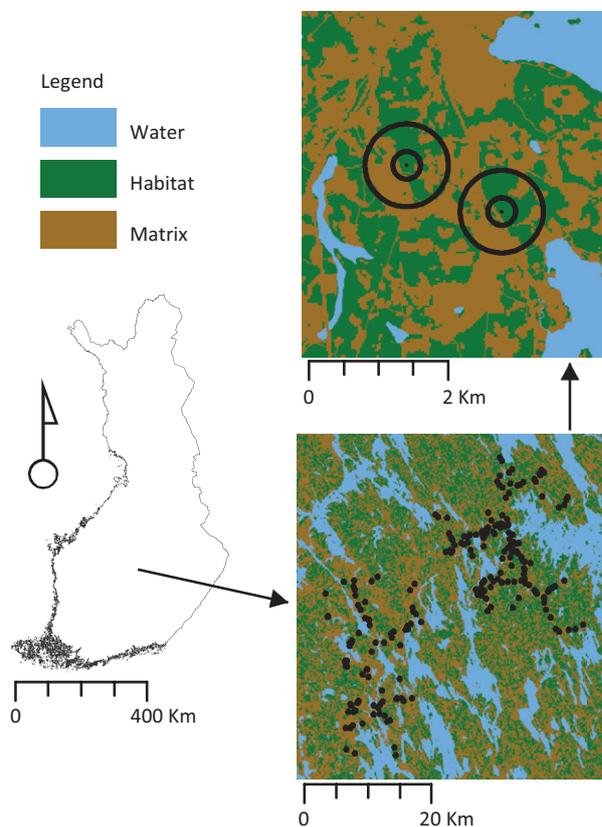
Fig. 1. Map of the study area showing its location within Finland, and the distribution of nest box sites (black dots) within the study area. The smaller circle surrounding the nest box sites represents the territory scale (200 m), while the larger circle represents the landscape scale (600 m).

used as a surrogate. In those nest box sites where harvesting activity was known to have taken place, the image from the next year was used. 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.

Prior to the generation of the habitat data, clouded areas were manually digitized and clipped out of each scene. Due to the fact that from 2006 we had two satellite images taken 16 days apart, the cloudless areas from each image were joined in order to form a cloudless composite image. Due to the clear spectral signals of the anticipated classes (see below), 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).

Each image was classified into two classes: old forest as habitat for treecreepers and matrix as non-habitat. To avoid unnecessary confusion in the classification, water pixels, fields and human-made features were extracted from the satellite images on the basis of the SLICES 2006 (Separated Land Use/Land Cover Information System) GIS data set produced by the National Land Survey of Finland. A rough quantitative comparison of our classified images with those produced by the Finnish Forest Research Institute showed that the old forest

class corresponded to forest over 100 m^3 ha^{-1} 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). The matrix class contained non-suitable habitats for treecreepers, for example young forests, saplings, clear-cuts, water bodies and human-created features such as fields, roads and buildings. Different types of matrix class (e.g. young forests and saplings) were not classified since they could not reliably be separated from each other in the satellite images used here. 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 our classification scheme was also assessed and found to be sufficient for the purpose of this study (Appendix S1, Table S1, Supporting information).

From the classified satellite images, two different sized circular areas surrounding the centre of each nest box site were cut, representing territory and landscape scales (Fig. 1). The radius for the territory scale (200 m) was chosen based on the maximum distance that adult treecreepers extend their feeding trips to during the nesting period (H. Hakkarainen, unpublished data). Furthermore, habitat loss, quantified from satellite images, at the 200-m territory scale has been previously shown to be associated with reduced territory occupancy (Suorsa *et al.* 2005), biased brood sex ratio towards the cheaper sex (Suorsa *et al.* 2003b) and increased physiological stress in nestlings (Suorsa *et al.* 2004) in our study population. Unfortunately, it was not possible to accurately measure the spatial configuration of habitat at finer scales (e.g. 100 m and below) due to the size of the pixels in the original satellite images (30 m × 30 m). The landscape scale (600 m) was included because habitat metrics at the landscape scale are important predictors of nest predation probability in our study system (Huhta *et al.* 2004).

For each nest box site for each year, the following habitat metrics were calculated for both the territory and landscape scales using FRAGSTATS 3.4 (McGarigal *et al.* 2002): percentage old forest, mean forest patch size, mean nearest neighbour patch distance, mean forest patch shape index and edge density (Table 1). Shape index, a measure of shape complexity, was calculated by dividing the perimeter of a patch by its area and adjusting it to compensate for the decrease in perimeter/area ratio caused by increasing patch size. Edge density was calculated by summing the total amount of edge between habitat and matrix within each circular area and dividing it by the area of the circular area, which did not include potential clouded areas. Proportional habitat metrics were used in order to ensure that metrics between cloud-free and cloud-covered nest box sites could be compared to each other. Only those nest box sites that had a total cloud cover that was under 10% at the 200-m scale and under 30% at the 600-m scale were included in the analyses, dropping 32 breeding attempts from the analyses. Of the remaining 890 breeding

Table 1. Means (SD) of measured treecreeper and habitat variables averaged per year

	1999	2000	2001	2002	2003	2004	2005	2006
n	65	156	124	93	145	148	77	82
Laying date (1st nests)	25·63 (5·62)	26·85 (5·15)	29·64 (8·38)	29·24 (7·74)	28·08 (5·74)	27·47 (5·39)	35·15 (6·66)	31·52 (3·83)
Laying date (2nd nests)	66·00 (5·97)	69·24 (4·16)	66·27 (6·18)	68·51 (5·27)	68·56 (6·52)	69·27 (5·52)	67·94 (6·18)	–
Clutch size	5·66 (0·75)	5·47 (0·93)	5·30 (1·29)	5·28 (1·19)	5·22 (1·28)	5·45 (0·95)	5·06 (1·57)	5·47 (0·75)
Maternal body condition	8·82 (0·69)	8·49 (0·53)	8·44 (0·62)	8·67 (0·55)	8·52 (0·47)	8·41 (0·53)	8·24 (0·52)	8·55 (0·59)
Nest predation%	10·3	5·6	18·2	9·7	6·1	15·8	6·6	10·3%
Nestling survival	0·74 (0·36)	0·71 (0·38)	0·54 (0·45)	0·65 (0·41)	0·74 (0·38)	0·66 (0·41)	0·64 (0·42)	0·58 (0·45)
Number of fledglings	4·21 (2·08)	3·87 (2·20)	3·29 (2·59)	3·90 (2·22)	4·09 (2·17)	4·14 (2·29)	4·42 (2·18)	3·49 (2·32)
% mature forest 200 m	56·50 (18·59)	56·38 (18·34)	54·63 (18·11)	52·33 (18·41)	54·16 (19·18)	52·48 (19·15)	50·44 (19·56)	43·57 (19·51)
Mean patch size 200 m	2·82 (2·37)	2·83 (2·38)	2·79 (2·35)	2·50 (2·12)	2·70 (2·39)	2·62 (2·38)	2·61 (2·45)	1·95 (1·71)
Shape index 200 m	1·48 (0·23)	1·47 (0·23)	1·47 (0·25)	1·46 (0·23)	1·48 (0·25)	1·48 (0·25)	1·49 (0·29)	1·42 (0·26)
Mean nearest neighbour 200 m	32·91 (20·33)	33·09 (20·33)	35·45 (22·96)	38·89 (25·40)	33·72 (22·93)	34·65 (23·97)	36·76 (25·72)	44·94 (28·11)
Edge density 200 m	140·96 (44·42)	139·88 (44·29)	135·16 (42·06)	137·12 (41·85)	139·59 (43·66)	140·58 (43·53)	139·03 (43·13)	130·89 (40·57)
% mature forest 600 m	47·97 (15·357)	47·87 (15·20)	46·27 (13·99)	45·25 (14·09)	47·37 (14·74)	46·56 (14·92)	43·19 (14·56)	37·56 (13·60)
Mean patch size 600 m	5·50 (5·21)	5·52 (5·24)	4·99 (3·91)	4·59 (3·75)	5·46 (5·62)	5·29 (5·61)	4·17 (3·61)	3·18 (3·14)
Shape index 600 m	1·59 (0·22)	1·59 (0·21)	1·58 (0·16)	1·56 (0·18)	1·59 (0·21)	1·58 (0·21)	1·54 (0·18)	1·49 (0·16)
Mean nearest neighbour 600 m	41·09 (12·87)	41·18 (13·05)	42·17 (14·17)	40·78 (10·93)	40·68 (12·93)	41·16 (13·16)	42·66 (13·07)	46·18 (12·51)
Edge density 600 m	116·09 (22·91)	115·70 (22·85)	113·07 (21·43)	115·96 (19·88)	117·30 (21·81)	117·72 (22·07)	117·55 (22·99)	113·10 (22·45)

attempts, 837 were fully cloud-free at the territory and landscape scales.

Between 1999 and 2006, a total of 85 nest box sites out of 241 (35%) had been lost due to forest harvesting. Also, the amount of old forest per nest box site had decreased on average 23% at the territory scale and 22% at the landscape scale. This corresponded with an increase in patch density and mean nearest neighbour distance between patches (Table 1), and underpins the importance of quantifying habitat structure for more than 1 year when multiple years are studied.

WEATHER DATA

Daily weather data were collected since temperature and precipitation during nesting can affect nestling survival (Skagen & Yackel Adams 2012). All weather variables were obtained from the meteorological station situated at Jyväskylä airport, located about 30 km south-west from the centre of our study area. Weather variables were calculated for each individual breeding attempt separately, starting at the laying date and ending at 32 days after egg laying, which was the average length of time between egg hatching and fledging in the study population. The following weather variables were calculated: thermal sum (sum of average daily temperatures exceeding +5 °C), minimum temperature, maximum temperature, average daily rain and maximum daily rain.

STATISTICAL ANALYSES

The association between habitat fragmentation and the reproductive success of treecreepers was analysed by using structural equation modelling (SEM) (Jöreskog 1973). SEM is a multivariate statistical approach, which enables 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).

We used confirmatory factor analysis in MPLUS 7.0 (Muthén and Muthén 1998–2012) to create latent factors representing the factors 'rain' and 'temperature' during the breeding period. The model where the factor 'temperature' was measured by thermal sum and minimum and maximum temperatures, and the factor 'rain' by average daily rain and maximum rain showed inadequate fit to the data (results not shown). Therefore, we modified the model based on modification indices, which estimate the increase in model fit when a parameter is freely estimated (Grace 2006), by adding a cross-loading of maximum temperature on the factor 'rain'. After this, the factor loadings, which describe the correlations of measured indicators with latent factors, of the weather variables on the latent factors rain and temperature were all clearly significant [temperature: thermal sum estimate (95% CI) 0·985 (0·992, 0·977), minimum temperature 0·943 (0·956, 0·929), maximum temperature 0·796 (0·855,

0·738), rain: mean rain 0·903 (0·936, 0·870), maximum rain 0·949 (0·978, 0·921), maximum temperature −0·304 (−0·234, −0·373)] and the model showed good fit to the data (results not shown).

Latent factors describing habitat loss and altered spatial configuration were not created since each of the habitat metrics could be considered to directly represent different aspects of the habitat fragmentation process (Fahrig 2003): loss of habitat (% old forest), decreased patch size (mean patch size), increased isolation of patches (mean nearest neighbour distance), increased shape complexity (shape index) and increased edge amount (edge density). Habitat fragmentation was modelled using the proposed hierarchical conceptual model by Didham, Kapos & Ewers (2012), but modified slightly since there was no information available on matrix quality (Fig. 2). Since habitat metrics were calculated at two different scales, the errors of the same metrics (e.g. amount of old forest at 200 and 600 m) were allowed to correlate. This model architecture manages the statistical implications of the hierarchical structure in the data (see for example Harrison *et al.* 2006).

The SEM, constructed in MPLUS, included several response variables, all of which were calculated for each individual breeding attempt: laying date, clutch size, maternal body condition, whether the nest was predated or not, proportion of nestlings that survived and number of fledged offspring (Table 1). Laying date was calculated on the basis of a linear regression of nestling wing length on nestling age and recorded so that 1 was the first day of April. Maternal body condition was estimated by using body mass and tarsus length to calculate the scaled mass index (SMI), a more reliable body condition index compared to traditional residual body mass (Peig & Green 2010). Nest predation included predation by all potential nest predators (see Discussion).

Based on expected pathways, the *a priori* SEM was built so that habitat loss and altered spatial configuration at the territory scale predicted maternal body condition, laying date, clutch size and nestling survival, because this is the scale at which feeding trips take place during the breeding season. Habitat loss and altered spatial configuration at the landscape scale predicted nestling survival via nest predation. Latent factors representing rain and temperature were assumed to influence both maternal body condition and nestling survival, and to correlate with laying date because these factors were calculated based on laying date. Clutch size and the survival of nestlings in turn were taken to explain the number of fledged offspring (Fig. 2).

The fit of the SEM to the data was tested using several different methods. First, the absolute fit of the model to the observed data was tested with a chi-squared test, and by checking the value of the standardized root mean square residual (SRMR), where a value of 0·08 or less indicates good fit. The root mean square error of approximation (RMSEA), which takes model parsimony into consideration, and where a value of 0·06 or below indicates good fit, was also checked. In addition, the comparative fit index (CFI), which compares model fit to a nested baseline model, and the Tucker–Lewis index (TFI), which is similar to the CFI but takes model parsimony into account, were checked. In both of these indices, a value of 0·95 or larger indicates good model fit (Brown 2006). Based on modification indices, the *a priori* SEM was slightly modified to obtain better fit by allowing the errors of mean nearest neighbour distance and shape index, and mean nearest neighbour distance and edge density to correlate.
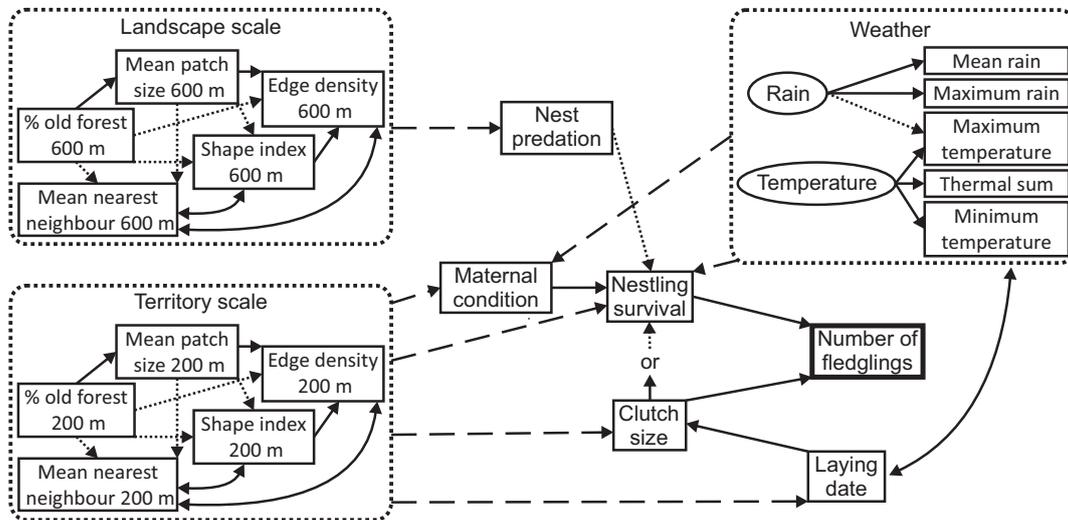
Fig. 2. Graphical representation of a structural equation model describing the expected associations between habitat fragmentation and the reproductive success of treecreepers. Single-headed arrows represent expected causal paths, while double-headed arrows represent unspecified associations. Hypothesized positive paths are marked with solid lines, while hypothesized negative paths are marked with densely dashed lines. Boxes represent individual measured variables, while solid circles represent unmeasured latent factors. For the sake of clarity, the diagram has been simplified so the sparsely arrows originating from the dashed rectangles represent each individual path from the habitat metrics and weather latent factors to the response variables. Due to this, hypothesized positive and negative arrows from habitat metrics and weather latent factors are not shown. Also, the error of each habitat metric at the territory (200-m) scale is assumed to be correlated with that of its counterpart at the landscape (600-m) scale, but these are omitted for simplicity.

Prior to analysis, all variables were standardized (mean = 0, SD = 1) by year and breeding attempt (first or second) to control for annual trends and breeding attempt-related variation. Nest box site identity was used as a clustering variable in order to control for the fact that sites were occupied multiple times during the study period. Missing data were handled using full information maximum-likelihood (FIML) estimation that assumes data are missing at random (Enders & Bandalos 2001). Due to the fact that we had non-normally distributed response variables, we used a robust maximum-likelihood (MLR) estimator that provides standard errors that are not sensitive to non-normal data (Muthén and Muthén 1998–2012). The data were also tested for potential spatial autocorrelation without finding any (Appendix S2).

Results

The final, accepted SEM model (Fig. 2) fit the data used in this study well. Although the chi-squared test indicated a significant deviation between the model and the data ($\chi^2 = 365\cdot0$, $n = 890$, d.f. = 141, $P < 0\cdot0001$), this was likely due to its high statistical power to detect even small deviations owing to our large sample size (Grace 2006). The root mean square error of approximation (95% CI), which adjusts somewhat for sample size, for the model was 0·044 (0·04, 0·05), the comparative fit index was 0·97, the Tucker–Lewis index was 0·95, and the standardized root mean square residual was 0·05, all of which indicate adequate fit to the data (Brown 2006).

The results from the model showed that habitat loss and altered spatial configuration at the territory scale were not associated with traits related to reproductive success in the treecreeper (Table 2). Habitat variables at the

territory scale were not significantly associated with laying date, clutch size or maternal body condition, and consequently did not influence fledging number. The only habitat variable that had a significant association with the number of fledged offspring was the amount of habitat at the landscape scale (Table 2). Increasing amount of old forest at the landscape scale was directly associated with increased nest predation, which in turn strongly reduced nestling survival and, as a consequence, decreased the number of fledged offspring to almost zero.

All associations between the habitat metrics were significant (Table 3), and all correlated errors specified between habitat metrics were significant, apart from that between mean nearest neighbour distance at the territory (200-m) and landscape (600-m) scales (Table S2). This suggests that the part of the SEM describing habitat fragmentation at the two scales was properly modelled. Individual paths between habitat metrics are not, however, interpreted in more detail here since it is beyond the scope of this article. None of the correlations between errors were very strong, making the coefficients for directed paths readily interpretable and comparable.

Discussion

Our results suggest that habitat fragmentation at both the territory and landscape scales did not have the expected negative association with reproductive success in the Eurasian treecreeper. None of the territory scale habitat variables, or those associated with weather or maternal body condition, were associated with laying date, clutch size, nestling survival or the number of fledged offspring.

Table 2. Results of a structural equation model examining how habitat fragmentation at the territory and landscape scales is associated with laying date, clutch size, maternal body condition, nest predation, nestling survival and number of fledglings in the treecreeper. To aid the comparison of different habitat variables, the estimates have been standardized so that they show how many standard deviations a dependent variable will change in response to a one standard deviation change in an independent variable. Statistically significant associations, where the 95% confidence intervals do not overlap with zero, are marked with boldface. Direct effects refer to the direct effect of one variable on another. Indirect effects refer to the mathematical product of all of the possible paths from one variable to another via intermediate variables. Total effects refer to the sum of the direct and indirect paths

	Total effect Estimate (±CI)	Direct effect Estimate (±CI)	Indirect effect Estimate (±CI)
Laying date (n = 690)			
% mature forest 200 m	0·027 (−0·004,0·058)	0·027 (−0·020,0·075)	−0·001 (−0·040,0·039)
Mean patch size 200 m	0·012 (−0·039,0·063)	0·003 (−0·094,0·099)	0·009 (−0·091,0·110)
Shape index 200 m	0·014 (−0·046,0·073)	0·016 (−0·073,0·104)	−0·002 (−0·048,0·044)
Mean nearest neighbour 200 m	0·013 (−0·047,0·073)	0·013 (−0·047,0·073)	
Edge density 200 m	−0·003 (−0·059,0·054)	−0·003 (−0·059,0·054)	
Clutch size (n = 695)			
% mature forest 200 m	0·035 (−0·053,0·123)	0·029 (−0·088,0·147)	0·006 (−0·067,0·078)
Mean patch size 200 m	0·036 (−0·045,0·117)	−0·074 (−0·240,0·093)	0·109 (−0·058,0·276)
Shape index 200 m	0·025 (−0·054,0·103)	0·077 (−0·049,0·203)	−0·052 (−0·159,0·054)
Mean nearest neighbour 200 m	−0·063 (−0·168,0·041)	−0·064 (−0·169,0·041)	0·000 (−0·002,0·002)
Edge density 200 m	−0·064 (−0·195,0·066)	−0·064 (−0·195,0·066)	0·000 (−0·001,0·001)
Laying date	0·012 (−0·108,0·132)	0·012 (−0·108,0·132)	
Maternal body condition (n = 668)			
% mature forest 200 m	0·002 (−0·090,0·093)	−0·040 (−0·184,0·103)	0·042 (−0·065,0·149)
Mean patch size 200 m	0·037 (−0·091,0·166)	0·128 (−0·095,0·351)	−0·090 (−0·260,0·079)
Shape index 200 m	0·013 (−0·095,0·121)	−0·049 (−0·199,0·101)	0·062 (−0·037,0·162)
Mean nearest neighbour 200 m	0·054 (−0·052,0·159)	0·054 (−0·052,0·159)	
Edge density 200 m	0·076 (−0·043,0·196)	0·076 (−0·043,0·196)	
Temperature	0·029 (−0·08,0·138)	0·029 (−0·08,0·138)	
Rain	−0·037 (−0·123,0·050)	−0·037 (−0·123,0·050)	
Nest predation (n = 760)			
% mature forest 600 m	**0·094 (0·015,0·173)**	0·093 (−0·064,0·250)	0·001 (−0·168,0·169)
Mean patch size 600 m	0·039 (−0·106,0·184)	0·029 (−0·219,0·277)	0·010 (−0·145,0·165)
Shape index 600 m	−0·021 (−0·133,0·090)	−0·009 (−0·148,0·131)	−0·013 (−0·074,0·049)
Mean nearest neighbour 600 m	0·026 (−0·051,0·103)	0·026 (−0·051,0·103)	
Edge density 600 m	−0·018 (−0·103,0·067)	−0·018 (−0·103,0·067)	
Nestling survival (n = 654)			
% mature forest 200 m	0·038 (−0·007,0·083)	0·015 (−0·052,0·082)	0·023 (−0·033,0·078)
Mean patch size 200 m	0·022 (−0·037,0·080)	−0·010 (−0·137,0·116)	0·032 (−0·075,0·140)
Shape index 200 m	−0·015 (−0·073,0·043)	0·005 (−0·082,0·092)	−0·020 (−0·081,0·041)
Mean nearest neighbour 200 m	−0·058 (−0·132,0·017)	−0·053 (−0·127,0·020)	−0·004 (−0·012,0·003)
Edge density 200 m	−0·031 (−0·107,0·046)	−0·025 (−0·100,0·050)	−0·005 (−0·014,0·004)
% mature forest 600 m	**−0·072 (−0·133, −0·011)**		**−0·072 (−0·133, −0·011)**
Mean patch size 600 m	−0·030 (−0·141,0·081)		−0·030 (−0·141,0·081)
Shape index 600 m	0·016 (−0·069,0·102)		0·016 (−0·069,0·102)
Mean nearest neighbour 600 m	−0·020 (−0·079,0·039)		−0·020 (−0·079,0·039)
Edge density 600 m	0·014 (−0·051,0·079)		0·014 (−0·051,0·079)
Temperature	0·034 (−0·025,0·093)	0·035 (−0·024,0·094)	−0·001 (−0·006,0·004)
Rain	0·014 (−0·039,0·066)	0·012 (−0·041,0·066)	0·001 (−0·003,0·005)
Laying date	0·000 (−0·004,0·005)	0·000 (−0·004,0·005)	
Maternal body condition	−0·039 (−0·095,0·017)	−0·039 (−0·095,0·017)	
Clutch size	0·037 (−0·032,0·106)	0·037 (−0·032,0·106)	
Nest predation	**−0·767 (−0·819, −0·716)**	**−0·767 (−0·819, −0·716)**	
Number of fledglings (n = 834)			
% mature forest 200 m	0·042 (−0·001,0·085)		0·042 (−0·001,0·085)
Mean patch size 200 m	0·027 (−0·028,0·082)		0·027 (−0·028,0·082)
Shape index 200 m	−0·010 (−0·066,0·047)		−0·010 (−0·066,0·047)
Mean nearest neighbour 200 m	−0·066 (−0·141,0·008)		−0·066 (−0·141,0·008)
Edge density 200 m	−0·041 (−0·117,0·035)		−0·041 (−0·117,0·035)
% mature forest 600 m	**−0·068 (−0·126, −0·011)**		**−0·068 (−0·126, −0·011)**
Mean patch size 600 m	−0·028 (−0·134,0·077)		−0·028 (−0·134,0·077)
Shape index 600 m	0·016 (−0·065,0·096)		0·016 (−0·065,0·096)
Mean nearest neighbour 600 m	−0·019 (−0·075,0·037)		−0·019 (−0·075,0·037)
Edge density 600 m	0·013 (−0·049,0·074)		0·013 (−0·049,0·074)

Table 2. (continued)

	Total effect Estimate (±CI)	Direct effect Estimate (±CI)	Indirect effect Estimate (±CI)
Temperature	0·032 (−0·024,0·088)		0·032 (−0·024,0·088)
Rain	0·013 (−0·037,0·063)		0·013 (−0·037,0·063)
Laying date	0·003 (−0·024,0·029)		0·003 (−0·024,0·029)
Maternal body condition	−0·037 (−0·090,0·016)		−0·037 (−0·090,0·016)
Clutch size	**0·220 (0·155,0·285)**	**0·185 (0·153,0·217)**	0·035 (−0·030,0·100)
Nest predation	**−0·726 (−0·781, −0·671)**		**−0·726 (−0·781, −0·671)**
Nestling survival	**0·947 (0·932,0·962)**	**0·947 (0·932,0·962)**	

Table 3. Associations between habitat metrics used in a structural equation model examining how habitat fragmentation at the territory and landscape scales is associated with reproductive success in the treecreeper. Statistically significant associations, where the 95% confidence intervals do not overlap with zero, are marked with boldface. Please refer to Table 2 and Fig. 2 for an explanation of the interpretation of the estimates

	Total effect Estimate (±CI)	Direct effect Estimate (±CI)	Indirect effect Estimate (±CI)
Edge density 200 m			
% old forest 200 m	0·003 (−0·132,0·138)	**0·486 (0·358,0·614)**	**−0·483 (−0·549, −0·418**
Mean patch size 200 m	**−0·462 (−0·579, −0·344)**	**−1·092 (−1·230, −0·955)**	**0·631 (0·457,0·804)**
Shape index 200 m	**0·815 (0·691,0·938)**	**0·815 (0·691,0·938)**	
Mean nearest neighbour 200 m			
% old forest 200 m	**−0·505 (−0·585, −0·425)**	**−0·302 (−0·413, −0·191)**	**−0·203 (−0·285, −0·121)**
Mean patch size 200 m	**−0·315 (−0·435, −0·195)**	**−0·315 (−0·435, −0·195)**	
Shape index 200 m			
% old forest 200 m	**0·270 (0·159,0·382)**	**−0·228 (−0·321, −0·135)**	**0·499 (0·413,0·584)**
Mean patch size 200 m	**0·774 (0·663,0·885)**	**0·774 (0·663,0·885)**	
Mean patch size 200 m			
% old forest 200 m	**0·644 (0·595,0·693)**	**0·644 (0·595,0·693)**	
Edge density 600 m			
% old forest 600 m	**0·310 (0·181,0·439)**	**0·835 (0·720,0·949)**	**−0·525 (−0·628, −0·422)**
Mean patch size 600 m	**−0·555 (−0·676, −0·434)**	**−1·151 (−1·317, −0·985)**	**0·596 (0·449,0·743)**
Shape index 600 m	**0·722 (0·598,0·845)**	**0·722 (0·598,0·845)**	
Mean nearest neighbour 600 m			
% old forest 600 m	**−0·442 (−0·561, −0·323)**	**−0·650 (−0·784, −0·517)**	**0·208 (0·118,0·298)**
Mean patch size 600 m	**0·275 (0·159,0·392)**	**0·275 (0·159,0·392)**	
Shape index 600 m			
% old forest 600 m	**0·480 (0·400,0·560)**	**−0·145 (−0·265, −0·026)**	**0·625 (0·546,0·703)**
Mean patch size 600 m	**0·826 (0·729,0·923)**	**0·826 (0·729,0·923)**	
Mean patch size 600 m			
% old forest 600 m	**0·757 (0·722,0·791)**	**0·757 (0·722,0·791)**	

However, we found that increased habitat amount at the landscape scale increased the probability of nest predation and that habitat amount acted directly on nest predation probability instead of indirectly through altered spatial configuration of habitat patches. This increase in nest predation probability in turn dramatically decreased nestling survival and led to almost zero fledged offspring, which suggests that habitat loss affects the reproductive success of treecreepers mainly through nestling survival.

To the best of our knowledge, this study is the first to use a SEM approach to model habitat fragmentation as a hierarchical process, the first to quantify habitat structure at an almost yearly frequency, and among the few that

have taken relevant biotic and abiotic covariates producing phenotypic responses into account. However, our results, suggesting no negative effects of habitat loss and altered spatial configuration, appear to contrast with the current knowledge from the fragmentation literature (e.g. Hinsley, Rothery & Bellamy 1999; Kurki *et al.* 2000; Laaksonen, Hakkarainen & Korpimäki 2004) and of the treecreeper (Huhta *et al.* 2003, 2004). The main reason for this discrepancy may be that the treecreeper is stringent in its nest site selection by actively avoiding unsuitable nesting sites (Suorsa *et al.* 2005). The fact that mean clutch size and its variation are small and unfavourable potential nesting sites are not occupied may have impaired our ability to detect

any severe direct cost such as reduced reproductive success. In contrast, more fine-tuned physiological responses of nestlings (Suorsa *et al.* 2003a, 2004) have been shown to be influenced by habitat characteristics at the territory scale. The finding that habitat loss and altered spatial configuration at the territory scale were not associated with laying date or clutch size seems to suggest that females were able to gain sufficient energy resources for egg production in all nest box sites. However, it is important to note that there is no information available on the pre-breeding season space use of treecreeper, which means that habitat metrics measured around nest box sites might not reflect the characteristics of areas that female treecreepers were feeding in before the breeding season. In addition, we were not able to measure habitat characteristics at the territory core scale (Suorsa *et al.* 2005), which may have limited our ability to study the effects of habitat loss and altered spatial configuration at the scale that is most used during the breeding period.

The discrepancy between our results and previous ones may also arise from the way in which the habitat fragmentation process has been statistically modelled. The SEM approach used here enabled us to model habitat fragmentation as a hierarchical interdependent process, whereby habitat loss leads to altered configuration of habitat patches (Didham, Kapos & Ewers 2012). In contrast, previous studies have not addressed the hierarchical nature of habitat fragmentation. Assuming that habitat loss and altered spatial configuration take place at the same hierarchical level has resulted in estimation problems due to high collinearity (Smith *et al.* 2009). Several statistical techniques have also been used to try to partition the effects of habitat loss from those of altered habitat configuration. However, all of these statistical techniques are known to be flawed, some of them seriously so (Koper, Schmiegelow & Merrill 2007; Smith *et al.* 2009), supporting the SEM approach used in the present study.

Our results showed that an increasing amount of old forest at the landscape scale was associated with increased nest predation rate, an important variable influencing reproductive success in birds (Zanette & Jenkins 2000; Huhta *et al.* 2004), which reduced nestling survival and consequently reproductive success. Although the direction of this association was counter to what has generally been found, our study is not the first to find a positive association between habitat amount and nest predation (Chapa-Vargas & Robinson 2007; Cox, Thompson & Faaborg 2012). In our study area, treecreepers' nests are mainly depredated by red squirrels (*Sciurus vulgaris* L., 1758), great spotted woodpeckers (*Dendrocopos major* L., 1758), and in scant vole years by least weasels (*Mustela nivalis* L., 1766) and stoats (*Mustela erminea* L., 1758) (Huhta *et al.* 2004). Both red squirrels and great spotted woodpeckers thrive in old forests and are known to suffer due to loss of forests (Koprowski 2005; Mazgajski & Rejt 2006), which could explain the elevated nest predation risk of treecreeper nests surrounded by large extents of old forest at the landscape

scale. We were not able to classify matrix habitat into saplings, young forests and fields (see methods) and could not confirm the results of Huhta *et al.* (2004) where nest predation risk was found to increase with increasing extent of cultivated fields and saplings.

In conclusion, our study suggests that habitat loss and altered spatial configuration did not have the expected negative association with the reproductive success of the Eurasian treecreeper. Instead, increasing amounts of habitat (i.e. old forest) at the landscape scale increased the risk of nest predation and thus greatly reduced the reproductive success of treecreepers. None of the habitat metrics at the territory scale were associated with reproductive success or associated variables, highlighting the importance of landscape-level habitat fragmentation in this study population. Moreover, our study demonstrates the advantages of a SEM approach as a tool to model complex hierarchical ecological associations, making it possible to find indirect associations that commonly used univariate statistical approaches would not be able to detect. Using SEM thus offers a potentially more realistic way to model the process of habitat fragmentation than what has previously been possible.

Acknowledgements

References

Betts, M.G., Forbes, G.J., Diamond, A.W. & Taylor, P.D. (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. *Ecological Applications*, **16**, 1076–1089.

Borges, F. & Marini, M. (2010) Birds nesting survival in disturbed and protected Neotropical savannas. *Biodiversity and Conservation*, **19**, 223–236.

Brown, T.A. (2006) *Confirmatory Factor Analysis for Applied Research*. The Guilford Press, New York.

Chapa-Vargas, L. & Robinson, S.K. (2007) Nesting success of Acadian flycatchers (*Empidonax virescens*) in floodplain forest corridors. *The Auk*, **124**, 1267–1280.

Chiarello, A.G. (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation*, **89**, 71–82.

Cooper, C.B. & Walters, J.R. (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, **16**, 471–478.

Cooper, C.B., Walters, J.R. & Ford, H. (2002) Effects of remnant size and connectivity on the response of Brown Treecreepers to habitat fragmentation. *Emu*, **102**, 249–256.

Cox, W., Thompson, F. & Faaborg, J. (2012) Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape Ecology*, **27**, 659–669.

Dalley, K.L., Taylor, P.D. & Shutler, D. (2009) Success of migratory songbirds breeding in harvested boreal forests of Northwestern Newfoundland. *The Condor*, **111**, 314–325.

Dawson, R., Lawrie, C. & O'Brien, E. (2005) The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*, **144**, 499–507.

Didham, R.K., Kapos, V. & Ewers, R.M. (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*, **121**, 161–170.

Enders, C.K. & Bandalos, D.L. (2001) The relative performance of full information maximum likelihood estimation for missing data in structural equation models. *Structural Equation Modeling: A Multidisciplinary Journal*, **8**, 430–457.

ERDAS (2010) ERDAS Field Guide.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fedy, B. & Martin, K. (2011) The influence of fine-scale habitat features on regional variation in population performance of Alpine White-Tailed Ptarmigan. *The Condor*, **113**, 306–315.

Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.

Grace, J.B. & Guntenspergen, G.R. (1999) The effects of landscape position on plant species density: evidence of past environmental effects in a coastal wetland. *Ecoscience*, **6**, 381–391.

Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems*, **1**, 143–156.

Hakkarainen, H., Korpimäki, E., Laaksonen, T., Nikula, A. & Suorsa, P. (2008) Survival of male Tengmalm's owls increases with cover of old forest in the territory. *Oecologia*, **155**, 479–486.

Harrison, S., Safford, H.D., Grace, J.B., Viers, J.H. & Davies, K.F. (2006) Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs*, **76**, 41–56.

Hinam, H.L. & Clair C.C. (2008) High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern Saw-whet Owls. *Biological Conservation*, **141**, 524–535.

Hinsley, S.A., Rothery, P. & Bellamy, P.E. (1999) Influence of woodland area on breeding success in great Tits *Parus major* and Blue Tits *Parus caeruleus*. *Journal of Avian Biology*, **30**, 271–281.

Huhta, E., Jäntti, A., Suorsa, P., Aho, T., Kuitunen, M., Nikula, A. & Hakkarainen, H. (2003) Habitat-related nest predation effect on the breeding success of the Eurasian Treecreeper. *Ecoscience*, **10**, 283–288.

Huhta, E., Aho, T., Jäntti, A., Suorsa, P., Kuitunen, M., Nikula, A. & Hakkarainen, H. (2004) Forest fragmentation increases nest predation in the Eurasian Treecreeper. *Conservation Biology*, **18**, 148–155.

Jensen, J.R. (2005) *Introductory Digital Image Processing: A Remote Sensing Perspective*. Prentice Hall, Upper Saddle River, NJ.

Jóreskog, K.G. (1973) A general method for estimating a linear structural equation system. *Structural Equation Models in the Social Sciences* (eds A.S. Goldberger & O.D. Duncan), pp. 85–112. Academic Press, New York.

Koper, N., Schmiegelow, F.K.A. & Merrill, E. (2007) Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. *Landscape Ecology*, **22**, 811–820.

Koprowski, J.L. (2005) The response of tree squirrels to fragmentation: a review and synthesis. *Animal Conservation*, **8**, 369–376.

Kurki, S., Nikula, A., Helle, P. & Linden, H. (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology*, **81**, 1985–1997.

Laaksonen, T., Hakkarainen, H. & Korpimäki, E. (2004) Lifetime reproduction of a forest-dwelling owl increases with age and area of forests. *Proceedings of the Royal Society B: Biological Sciences*, **271**, S461–S464.

Lampila, P., Mönkkönen, M. & Desrochers, A. (2005) Demographic responses by birds to forest fragmentation. *Conservation Biology*, **19**, 1537–1546.

Luck, G.W. (2003) Differences in the reproductive success and survival of the Rufous Treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. *Biological Conservation*, **109**, 1–14.

Mazgajski, T.D. & Rejt, L. (2006) The effect of forest patch size on the breeding biology of the great spotted woodpecker *Dendrocopos major*. *Annales Zoologici Fennici*, **43**, 211–220.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS v3: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst. Available at: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Mochizuki, S. & Murakami, T. (2011) Change in habitat selection by Japanese macaques (*Macaca fuscata*) and habitat fragmentation analysis using temporal remotely sensed data in Niigata Prefecture, Japan. *International Journal of Applied Earth Observation and Geoinformation*, **13**, 562–571.

Muthén, L.K. & Muthén, B.O. (1998–2010) *Mplus User's Guide*. Muthén & Muthén, Los Angeles, CA.

Muukkonen, P., Angervuori, A., Virtanen, T., Kuparinen, A. & Merilä, J. (2012) Loss and fragmentation of Siberian jay (*Perisoreus infaustus*) habitats. *Boreal Environmental Research*, **17**, 59–71.

Olson, G.S., Glenn, E.M., Anthony, R.G., Forsman, E.D., Reid, J.A., Loschl, P.J. & Ripple, W.J. (2004) Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *Journal of Wildlife Management*, **68**, 1039–1053.

Peig, J. & Green, A.J. (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology*, **24**, 1323–1332.

Poulin, J. & Villard, M. (2011) Edge effect and matrix influence on the nest survival of an old forest specialist, the Brown Creeper (*Certhia americana*). *Landscape Ecology*, **26**, 911–922.

Robertson, D.N. & Butler, M.J. (2009) Variable reproductive success in fragmented populations. *Journal of Experimental Marine Biology and Ecology*, **377**, 84–92.

Robles, H., Ciudad, C., Vera, R., Olea, P.P. & Matthysen, E. (2008) Demographic responses of middle spotted woodpeckers (*Dendrocopos medius*) to habitat fragmentation. *The Auk*, **125**, 131–139.

Rotenberry, J.T. & Wiens, J.A. (1991) Weather and reproductive variation in Shrubsteppe Sparrows: a Hierarchical Analysis. *Ecology*, **72**, 1325–1335.

Rush, S.A. & Stutchbury, B.J.M. (2008) Survival of Fledgling Hooded Warblers (*Wilsonia citrina*) in small and large forest fragments. *The Auk*, **125**, 183–191.

Schmiegelow, F.K.A. & Mönkkönen, M. (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications*, **12**, 375–389.

Skagen, S.K. & Yackel Adams, A.A. (2012) Weather effects on avian breeding performance and implications of climate change. *Ecological Applications*, **22**, 1131–1145.

Smith, A., Koper, N., Francis, C. & Fahrig, L. (2009) Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. *Landscape Ecology*, **24**, 1271–1285.

Studds, C.E., DeLuca, W.V., Baker, M.E., King, R.S. & Marra, P.P. (2012) Land cover and rainfall interact to shape waterbird community composition. *PLoS ONE*, **7**, e35969.

Suorsa, P., Helle, H., Huhta, E., Jäntti, A., Nikula, A. & Hakkarainen, H. (2003a) Forest fragmentation is associated with primary brood sex ratio in the Treecreeper (*Certhia familiaris*). *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2215–2222.

Suorsa, P., Huhta, E., Nikula, A., Nikinmaa, M., Jäntti, A., Helle, H. & Hakkarainen, H. (2003b) Forest management is associated with physiological stress in an old-growth forest passerine. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 963–969.

Suorsa, P., Helle, H., Koivunen, V., Huhta, E., Nikula, A. & Hakkarainen, H. (2004) Effects of forest patch size on physiological stress and immunocompetence in an area-sensitive passerine, the Eurasian Treecreeper (*Certhia familiaris*): an experiment. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 435–440.

Suorsa, P., Huhta, E., Jäntti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V. & Hakkarainen, H. (2005) Thresholds in selection of breeding habitat by the Eurasian Treecreeper (*Certhia familiaris*). *Biological Conservation*, **121**, 443–452.

Tomppo, E., Henttonen, H., Korhonen, K., Aarnio, A., Ahola, A., Ihalainen, A., Heikkinen, J. & Tuomainen, T. (1999) Forest resources and their development in central Finland, 1967–1996. *Metsätieteen aikakausilehti Foli Forestalia*, **2B**, 309–388.

Valdés, A. & García, D. (2011) Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb. *Journal of Applied Ecology*, **48**, 1422–1431.

Zanette, L., Doyle, P. & Tremont, S.M. (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology*, **81**, 1654–1666.

Zanette, L. & Jenkins, B. (2000) Nesting success and nest predators in forest fragments: a study using real and artificial nests. *The Auk*, **117**, 445–454.

Zitske, B.P., Betts, M.G. & Diamond, A.W. (2011) Negative effects of habitat loss on survival of migrant warblers in a forest mosaic. *Conservation Biology*, **25**, 993–1001.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Accuracy assessment of classification.

Appendix S2. Spatial autocorrelation.

Table S1. Error matrix resulting from a random sample of classified pixels.

Table S2. Results from structural equation model showing correlations of errors between habitat metrics used in a structural equation model examining how habitat fragmentation at the territory and landscape scales is associated with reproductive success.