Promoting species protection with predictive modelling: Effects of habitat, predators and climate on the occurrence of the Siberian flying squirrel

Maarit Jokinen[a,*], Ilpo Hanski, Elina Numminen[a], Jari Valkama[b], Vesa Selonen[c]

[a] *University of Helsinki, Finland*
[b] *Finnish Museum of Natural History, Finland*
[c] *University of Turku, Finland*

A B S T R A C T

Species distribution models (SDMs) can be used to predict species occurrence and to seek insight into the factors behind observed spatial patterns in occurrence, and thus can be a valuable tool in species conservation. In this study, we used MaxEnt software to explain the occurrence of a protected forest-dwelling species, the Siberian flying squirrel. We produce occurrence maps covering the main distribution area for the species in the European Union. Using an exceptionally extensive presence-absence dataset collected with a standardized method, we evaluated the relative role of predation pressure, climate, and amount of habitat affecting flying squirrel occurrence. We found that regional variation in mean winter temperature had relatively large predictive power for flying squirrel occurrence. In addition, the regional abundance of flying squirrels was partly explained by differences in predation pressure. The results also support the conclusion that areas with older forests and nearby agricultural areas are optimal for the species. Our study shows that multiple factors affect the species' occurrence in large spatial scales. We also conclude that climate is having a large effect on species occurrence, and thus the changing climate has to be taken into account in conservation planning. Our results help conservation managers in targeting surveys and protection measures on various spatial scales, and decision makers in focusing on the factors that drive the species' occurrence. Our results also indicate that we would need additional tools and measures in the EU for achieving a favourable conservation status of those species that occur in commercial forests.

1. Introduction

Forestry is considered a major driver behind the global loss of forest biodiversity (Lindenmayer and Franklin, 2002). Even countries with large forest reserves and well-developed conservation administration have failed in stopping the decline of forest species (European Commission, 2011, 2015; Rassi et al., 2010; Tonteri et al., 2008). To better target the limited conservation resources (McCarthy et al., 2012) and to better implement the available legislative protection tools, managers need the best information possible on occurrence patterns of vulnerable species.

One conservation tool requiring occurrence information is the *system of strict protection*, where the member states of the European Union have prohibited the deterioration and destruction of so-called *breading sites* and *resting places* for hundreds of protected species (92/43/EEC, Article 12(1) (d)). These sites are defined, among other requirements, by the presence of the species (Anonymous, 2007). The problem is that typically there is information on only a small subset of the sites occupied by any species (Rondinini et al., 2006; Jokinen et al., 2015). Extensive ongoing activities like forestry are especially problematic as persons likely to commit a conservation offence remain unaware of the species existence (Jokinen et al., 2015). One way to increase

information needed in conservation management is to predict where the species should occur and identify the drivers behind observed spatial patterns of occurrence. This can be done with species distribution models (SDMs; Elith and Leathwick, 2009; Guisan et al., 2013), which ideally help in spatial conservation decision making, both on a large scale as well as on the scale of operational land use planning (Moilanen et al., 2011), and to identify likely effective conservation measures by determining the drivers behind population patterns.

In this study, we explain the occurrence of a protected arboreal rodent: the Siberian flying squirrel (*Pteromys volans*, henceforth flying squirrel) on its main distribution area in the EU. The species inhabits boreal and hemiboreal mixed forests of Eurasia (Shar et al., 2008). Within the EU, flying squirrels are found only in Finland − where it is still rather common despite a continuous population decline (Hokkanen et al., 1982; Liukko et al., 2016; Selonen et al., 2010) − and in a small area in Estonia (Timm and Remm, 2011). The primary habitats of the species in Finland are mature forests dominated by the Norway spruce (*Picea abies*) with a mixture of deciduous trees (Hanski, 1998; Reunanen et al., 2002a). Flying squirrels hardly ever move on the ground − however, as the landscape in Finland is forest-dominated, individuals can reach most habitat fragments in the landscape (Selonen and Hanski, 2012). Flying squirrels have relatively large home ranges (size averages

8 ha for females and 60 ha for males; Hanski et al., 2000a) but these typically consist of small-sized core areas where individuals spend most of their time (Hanski, 1998). Adult individuals are site-faithful, and females are territorial towards other females. Site-faithfulness of adults, together with juvenile dispersal behaviour, lead to dynamical changes of occupancy status of suitable sites (Hanski and Selonen, 2009; Brommer et al., 2017).

The species is listed in the EU's Habitats Directive Annexes II and IV (a) (92/43/EC), which makes it interesting from the point of effectiveness of conservation policy, but also important for conservation management. Forestry is considered to be the main factor threatening the species (Liukko et al., 2016; Selonen and Mäkeläinen, 2017), but effective implementation of protection has been difficult partly because most of the nest sites of the species remain unknown (Jokinen et al., 2015). The habitat associations of the flying squirrel are well-studied (e.g. Reunanen et al., 2002a, 2004; Santangeli et al., 2013; Koskimäki et al., 2014; Remm et al., 2017), and these studies serve as important background information for our study. However, so far studies have either considered only very limited areas, a limited number of explanatory factors, or not provided their results in a format usable for conservation managers.

For example, Remm et al. (2017) found that the optimal amount of preferred habitat cover for flying squirrels is surprisingly low on a landscape level (10–13% within a 4-km buffer, but see Reunanen et al., 2004). This unexpected result is likely related to the fact that forest edges around agricultural land may provide important resources for the species (Santangeli et al., 2013; Remm et al., 2017; Turkia et al., 2018). On the other hand, agricultural area correlates regionally with climate and soil fertility—both of which may also affect resources available for the species. Deciduous trees, which are especially important source of food and nesting sites, can be more common on edges; flying squirrels eat mainly buds, catkins and leaves of various tree species (Hanski et al., 2000b; Selonen et al., 2016a) and use tree cavities, nest-boxes and dreys as nest sites.

The possible effects of climate and predators on flying squirrel populations remain less studied than habitat associations (but see e.g. Koskimäki et al., 2014). Owls have been reported to cause 70% of mortality in the species (Selonen and Mäkeläinen, 2017). The clear main predator in Finland is the Ural owl (*Strix uralensis*), which has been observed to affect occurrence on a local scale in nest-box use studies (Byholm et al., 2012; Selonen and Mäkeläinen, 2017; Turkia et al., 2018). However, Koskimäki et al. (2014) did not find any indication that vole abundance, an index of owl activity, affects the flying squirrel occupancy of nest-boxes. In comparison, in North America, predation pressure by spotted owls (*Strix occidentalis*) has been documented to be a strong determinant of the Northern flying squirrel (*Glaucomys sabrinus*) population size (Carey et al., 1992; Forsman et al., 1984).

In general, climate affects animals in numerous direct and indirect ways (see e.g. White, 2008; Reside et al., 2010), and is therefore central in most large scale SDMs (see e.g. Thuiller et al., 2004). Winter climate is known to be an important factor in explaining vegetation and animal distributions (see e.g. Kreyling, 2010) and has also been observed to affect reproduction in the flying squirrel (Selonen and Wistbacka, 2016; Selonen et al., 2016). Winter temperatures at higher latitudes are subject to especially rapid climate change (Christensen et al., 2007). In addition to temperature, autumn and winter precipitation are changing in Finland, and might affect, e.g., costs of thermoregulation (Conley and Porter, 1986) or predator behaviour (Terraube et al., 2017).

Our goals in this study are to 1) produce spatial information with MaxEnt software (Phillips et al., 2006) that helps to target limited monitoring and survey resources efficiently for the flying squirrel; and 2) evaluate the relative role of different factors (predator pressure, climate, and area of habitat) behind flying squirrel occurrences. This information is used for discussing how to develop more effective conservation strategies for the species.
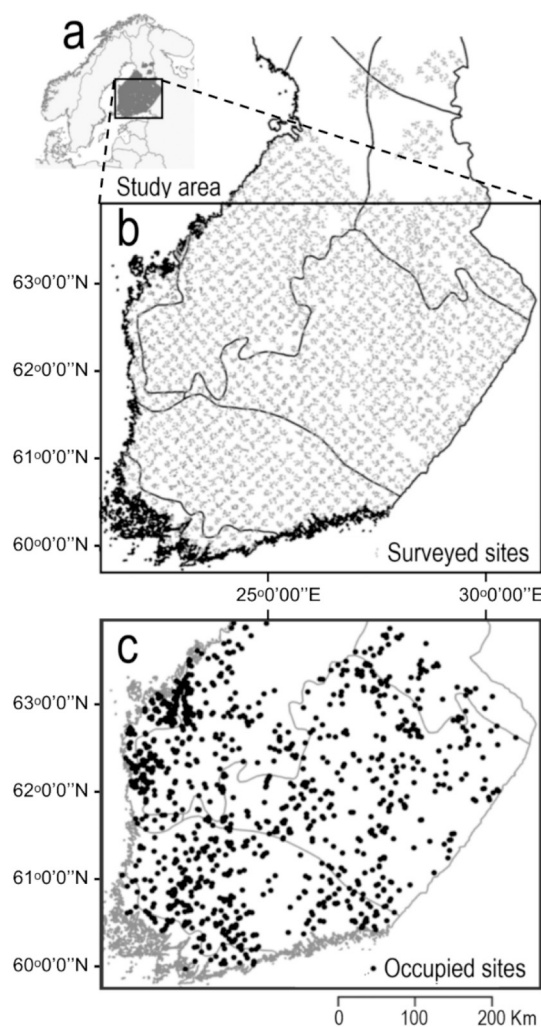

Fig. 1. A) The location of Finland and the study area, B) surveyed sites in the study area (n = 9256), C) occupied sites in the study area (n = 1020). Six vegetation zones (delimited by lines) overlap the study area.

2. Material and methods

2.1. Study area and presence-absence data for the flying squirrel

The study area included southern and central Finland between 59.96°N, 21.20°E and 64.13°N, 31.50°E, covering land area of 188,866 km² (Fig. 1a, b). The distribution area of the species continued to the north, but the surveillance data does not cover the northern parts, where occurrence data is very sparse.

An extensive systematic survey for the species was performed within the study area during springs and early summers of 2003–2005 (see Hanski, 2006 or Santangeli et al., 2013). The survey sampling was performed as follows: 1) the total area was divided into 10 km × 10 km squares, 2) every second square was selected to surveyed, 3) 10 survey sites were placed randomly on each of these selected squares. Surveyed sites were located on mineral soil and were at least 1 km apart. The size of sites, 300 m × 300 m (9 ha), was selected to match the average female home range (8.3 ha, Hanski et al., 2000b).

Presence or absence of the species was defined according to the presence of faecal droppings. This is the standard method in flying squirrel surveys, as pellets, that have accumulated in individuals' core areas during winter, are easily detectable and identifiable during spring and early summer (e.g. Reunanen et al., 2002a; Reunanen et al., 2002b; Hanski, 2006; Santangeli et al., 2013).

2.2. Predator data: the Ural owl

We could not estimate the predation pressure directly, so we built a MaxEnt model for nesting Ural owls. In the model, we used the sites where nestlings were ringed in 2005 (n = 959), information provided by the Finnish Museum of Natural History (Saurola, 2008; Valkama et al., 2011). The data is originally from professional and amateur ornithologists who provided nest-boxes for the species and ringed the nestlings they found in them or in natural nest sites (Meller et al., 2017).

The predation pressure was calculated as a sum of raw output values of the Ural owl model (Supplement 1) within a 5-km radius. It thus indicates the relative numbers of nests and owls in this area, and should therefore represent the relative predation pressure on the landscape scale. The estimate can be affected by both nest-box locations and ringer activity, but it should be noted that it seems that a large part of the Ural owl population does nest in these boxes (Valkama et al., 2011). However, the correlation between our estimate and the true predation pressure caused by Ural owls has not been validated.

2.3. MaxEnt software

The MaxEnt software package is a presence-background modelling tool that employs the maximum entropy algorithm for modelling species distributions and estimating parsimonious effects of various landscape features on the occurrence (Phillips et al., 2006) (Elith et al., 2011). The inference is based on contrasting the landscape features in the locations of observed occurrence to random background points from the entire landscape, and thus the selection of the background points influences the results. The requirement is that the background points have yielded a presence observation a priori. As the study locations of the large-scale data were selected based on this exact criterion, we chose them as the background locations. This excluded all the sites that were not surveyed, and thus also all sites that had < 9 ha forest land—the average was 48 ha (85%) in an area of 750 m × 750 m (see Supplement 2, Table 2). For the owl model, the background was selected to correspond to grid cells that were 250 m × 250 m and consisted at least 50% forest.

MaxEnt model performance can be evaluated using Area Under the Curve (AUC) statistics of the receiver operating characteristic (ROC) plot. The ROC plot is generated by plotting the predicted false positive rate of against the true positive rate (Phillips and Dudík, 2008), for a random set of test data points. We used 20% of the data for this. The AUC of the ROC plot corresponds to the probability that an observed presence is correctly differentiated from a random background point (Phillips et al., 2006).

The relative importance of explanatory variables can be estimated with Jackknife tests or by comparing variables' permutation importance. To determine permutation importance, for each environmental variable in turn, the values of that variable are randomly permuted across presence and background samples. The model is revaluated on the permuted data, and the resulting drop in training AUC is fetched. Jackknife tests (Phillips et al., 2006) perform pairwise comparisons of the models fitted with and without a variable allowing to assess how much the predictive power of a model increases when a variable is included in it.

Having presence-absence data available, we transformed MaxEnt's raw output into estimates of occupancy probability (Guillera-Arroita et al., 2014), taking into account the different grid cell size used in the presence-absence study and for the landscape features (see Appendices in Guillera-Arroita et al., 2014).

2.4. Environmental data and raster modifications

To calculate forest variables, we used National Multisource National Forest Inventory data (MS-NFI) from 2005 provided by Natural

Resource Institute Finland. MS-NFI employs satellite images and field measurements for producing forest estimates in the form of rasters with different variables (Tomppo et al., 2008). For the 2005 data, the MS-NFI raster grid cells are 25 m × 25 m. We used the data for the total growing stock volume, volume of pine, stand age and site fertility index (rank of 1, high to 8, low fertility). The fertility index is based on ranks using habitat type as a proxy for fertility: 1. Herb-rich sites, 2. Herb-rich heath forests, 3. Mesic, 4. Subxeric forests, 5. Xeric forests, 6. Barren forests, 7. Rocky and sandy soils, and 8. Summit and fjeld forest (Tomppo et al., 2008). We updated this data for 2016 by decreasing the age of cells that had been cut according to Hansen et al. (2013; https://earthenginepartners.appspot.com/science-2013-global-forest) and increasing the age of other cells by 11 years.

Climate information was obtained from the Finnish Meteorological Institute (FMI) on a 10 × 10 km raster grid. For the selection of climate variables, we compared model performance with various variable combinations (Supplement 2). Due to strong correlations between certain variables (e.g. winter, spring and autumn temperatures) it was not reasonable to use all climate variables in the same model (Supplement 2). The selected variables for the final models were winter temperature: average temperature of December, January and February of 10 winters (the first winter being the winter of 1995–1996; the last the winter, 2004–2005); and autumn precipitation: average for September, October and November of 10 autumns (1995–2004).

Water area was calculated from CORINE land cover map data (resolution 20 m × 20 m). The landscape level area of waterbodies was included in the model because large water areas affect microclimate and may also function as dispersal barriers. For agricultural land/forest edges, we used polygonal data for agricultural lands produced by the National Land Survey of Finland (NLS). The area of forest edge habitats was calculated from 25 m × 25 m forestland raster by defining an 'edge' as an area ≤50 m from an agricultural land polygon.

MaxEnt picks values of environmental variables from the raster cell at the coordinates of observations. Thus, it was not possible to calculate the environmental variables for the exact survey plots. First, we reduced the resolution of original rasters to a cell size of 250 m × 250 m and then calculated environmental variables for each raster cell for an area of 750 m × 750 m. This way we could take into account the ways a survey plot can be situated within the raster grid and the uncertainty of the exact coordinates of the observation on surveillance plots (see Fig. 2a).

2.5. Flying squirrel model

The flying squirrel model was built with the presence data; presence-absence data was used to calculate occurrence probability estimates from the raw-output of MaxEnt. The tested variables for the flying squirrel model were selected according to several previous studies reporting factors affecting the occurrence of flying squirrels (e.g. Byholm et al., 2012 (the Ural owl); Santangeli et al., 2013 (amount of habitat, agricultural areas, soil fertility); Remm et al., 2017 (spatial scale of the variables); Turkia et al., 2018 (the Ural owl); Selonen and Hanski, 2012 (habitat); Selonen and Wistbacka, 2016; Selonen et al., 2016 (weather); Hoset et al., 2017). In addition, we considered potentially relevant observations regarding other species (Conley and Porter, 1986; Terraube et al., 2017 (autumn precipitation) and the most interesting climate variables from the perspective of climate change and speculation of their potential effects as well as consistent spatial patterns in them (winter temperature, winter and autumn precipitation). We also compared models with different variables.

For the final model, we used the following variables and scales: 1) Area of habitat (within 750 m × 750 m) in 2005 (for the model) and in 2016 (for the projection), 2) Mean soil fertility (750 m × 750 m), 3) Area of edges (750 m × 750 m), 4) Predation pressure calculated from the results of the Ural owl model (5 km radius), 5) Water area (5 km radius) 6) 10 years mean for precipitation during autumn
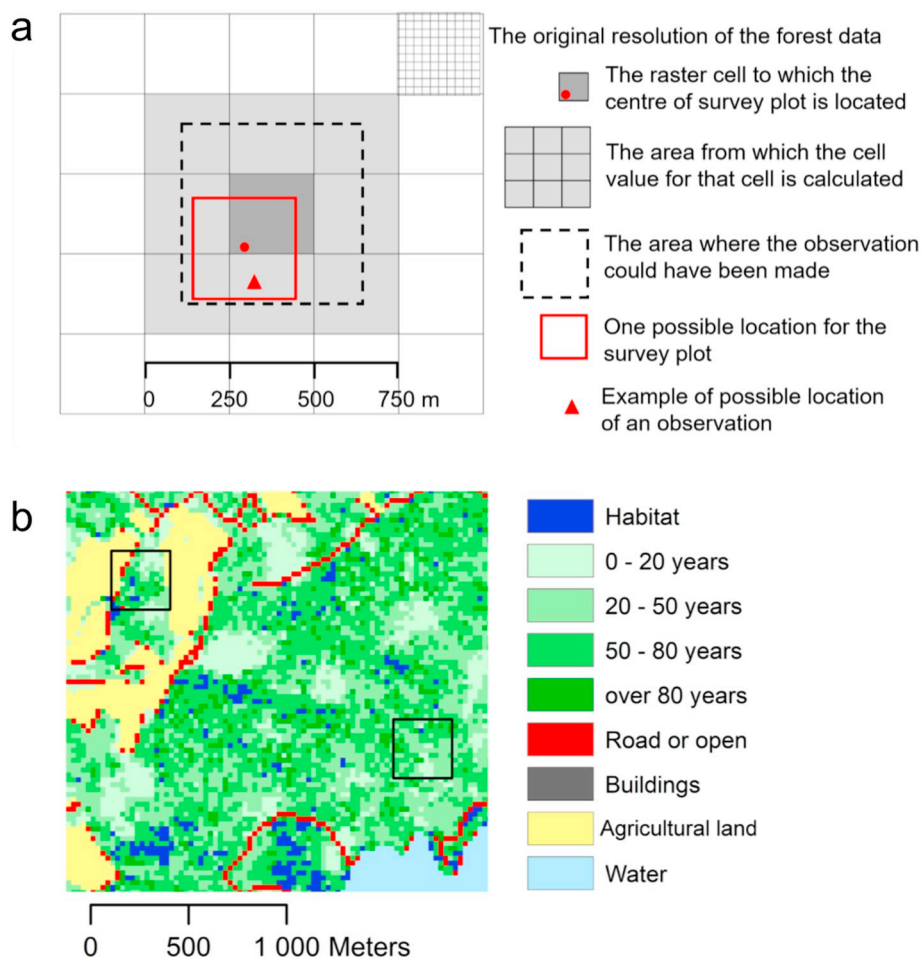
Fig. 2. A) Example of a survey plot on the modified environmental raster layer. B) Two 300 m × 300 m survey plots presented on the raster showing a distribution of 25 m × 25 m habitat cells (blue), the age of other forest cells, agricultural lands, waters and roads. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(September–November 1995–2004; 10 km × 10 km), 7) 10 years mean for winter temperature (December–February 1994–2005; 10 km × 10 km). The latter two describe the average regional variation in climate variables within our study area. Remm et al. (2017) found that the optimal scale for different habitat variables for site occupancy is between 250 and 500 m, and for local density, between 1 km and > 4 km (Remm et al., 2017). Spatial scales used for the habitat, edge and fertility thus reflect optimal scales for habitat variables (Remm et al., 2017). The larger scale for water area (5 km radius) was set to reflect the fact that large water bodies are dispersal barriers for the species, but they also affect the microclimate. Climate variables were at the minimum spatial scale available (10 km × 10 km) The correlations between explanatory variables can be seen in Supplement 2, Table 2.

Flying squirrels use many kinds of forest (Selonen and Mäkeläinen, 2017; Remm et al., 2017; Turkia et al., 2018); thus, all non-habitat/ habitat classifications are somewhat misleading. The definition we used for habitat dictated that a forest had to be over 80 years of age and that it could not have more than a 66% volume of pine. This classification highlights the potentially higher quality of older mixed forest but allows variation in tree species composition within forests.

Spatial clustering of survey locations or occurrence can cause model over-fitting. In our case, spatial clustering of survey locations is not an issue (see Fig. 1b). We therefore made models first by using all survey locations. However, since previous studies show that there is a strong spatial autocorrelation in flying squirrel occupancy (Remm et al., 2017), we tested if spatial rarefying of the observations would change

the model outputs. According to Remm et al. (2017), spatial auto-correlation of neighbouring sites should be halved at a distance of 11.3 km. Based on this result, we rarefied the data so that the minimum distance between observations was 10 km. We further tested whether adding the information on the nearest occurrence observation would change the model outcome.

2.6. Regional models

We performed the MaxEnt analysis, for the whole study area and also separately for three regions to highlight possible regional differences in factors affecting flying squirrel distribution. The division into regions was based on vegetation zones and geography in Finland (Fig. 3). For descriptive statistics of variables in different regions, see Supplement 2, Table 1. The three regions were:

Southwest: Hemiboreal zone, Southwestern Finland and Southern Ostrobothnia

Forests (61% within a 5-km radius) and agricultural lands (22% within a 5-km radius) dominate the landscapes. Because of the lower latitudes and nearness of the coast of the Baltic sea, winters are relatively mild. Deciduous trees can be dominant in the Hemiboreal zone (southwestern coast). The western coast is less fertile than the middle and eastern parts. The southern coast is rainy during autumn and winter.
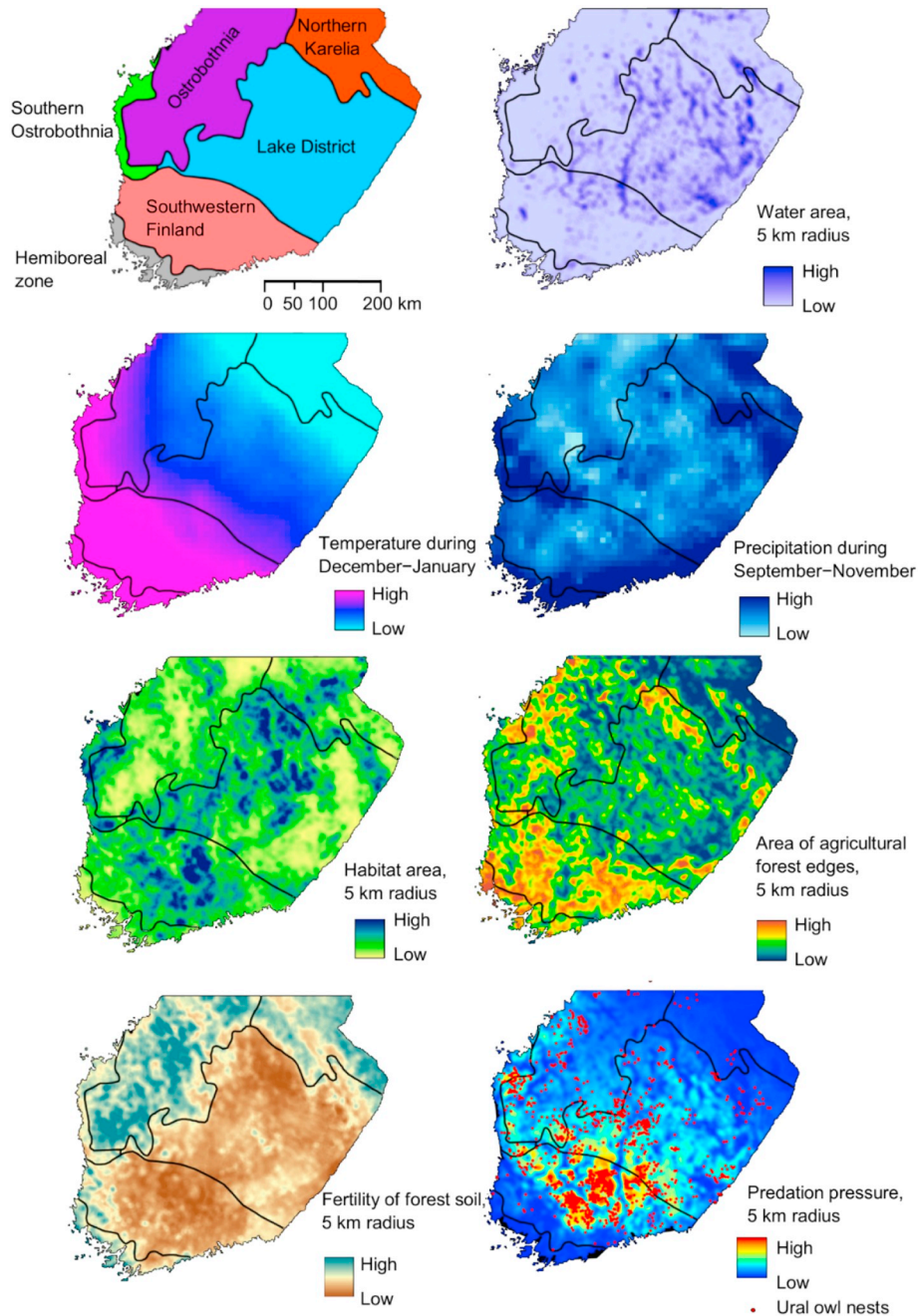
Fig. 3. Maps showing vegetation zones and landscape-level distributions of some environmental variables and modelled predation pressure.

East: Lake district, North Karelia and Kainuu

Forests (71% within a 5-km radius) and lakes (16% within a 5-km radius) dominate the landscapes. Agricultural land can still be an important feature in some areas. Forests are dominated by pine in the east and north. Soil is less fertile in Northern Karelia and Kainuu than in the Lake District.

Northwest: Southern Ostrobothnia and Ostrobothnia

In general, the landscapes are dominated by forests (73.3% within a 5-km radius), but agricultural lands (14.1% within a 5-km radius) and mires dominate some landscapes. Soil is less fertile than in other regions, and forests are mostly dominated by pine.

Southern Ostrobothnia is relatively small and narrow area (see Fig. 3). Because of mild winters it belongs to Southern boreal zone

together with Southwestern Finland. However, the border of Southern Ostrobothnia and Ostrobothnia divides an area of especially high flying squirrel density. To avoid the arbitrary division of this high-density area between two separate regions, we included the area in both the Southwest and Northwest regional models.

3. Results

In the model for the whole study area, mean winter temperature was the variable with the highest permutation importance and highest gain when used in isolation (see Fig. 5). Winter temperature also decreases the gain the most when it is omitted (training gain without the variable is smallest), and thus it appears to have the most information that is not present in the other variables. Generally flying squirrels seem to prefer warmer regions of Finland, but the response curve (see Fig.6) indicates that there might be an optimum temperature for the species.
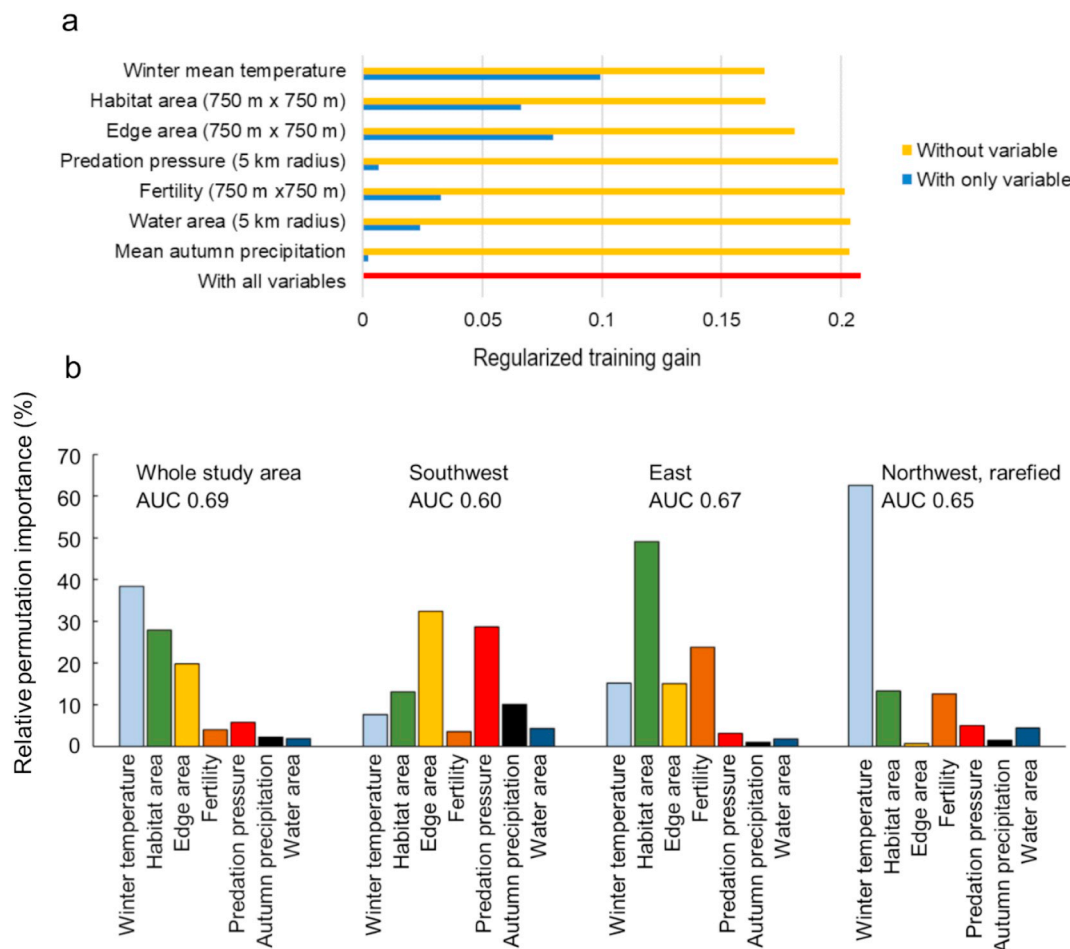
Fig. 4. a) Relative predictive power of different environmental variables based on the jackknifing of regularized training gain for the study area model. Values shown are averages of 15 replicate runs for the model. b) AUC values and relative permutation importance for the variables for all flying squirrel models.

The effect of autumn precipitation remained small in the model for the whole study area.

The positive effect of the amount of habitat was clear (Fig. 4) and appeared quite linear (Fig. 5). Amount of edge habitat also had a clear positive effect on the occurrence of flying squirrels (Figs. 4, 5). Fertility did not bring much additional information to the model of the whole study area (Fig. 4, but see below regional models).

The effect of modelled predation pressure was negative, but low in the model for the whole study area (Fig. 4). There was a narrow region of positive effect at the lowest values of predation pressure (Fig. 5), which is likely explained by the fact that the Ural owl and flying squirrel are both absent from similar areas. Details of the Ural owl model (predation pressure) can be found in Supplement 1. According to the model, predation pressure would be highest in the forest-dominated areas of southwestern Finland (see Fig. 3 and Supplement 1).

The model predicted the highest occurrence probabilities for the flying squirrel in the western and southern regions of the country (Fig. 6a). The same pattern was also produced by the regional models (Fig. 6b), despite the differences in relative importance of explaining variables (Fig. 4b). We also projected the whole area model for 2016 by updating only the habitat data. Note that the projection is a raw-output and thus indicates only relative differences in the occurrence probability. Reduced resolution maps are provided as KMZ files (Whole study area: Supplement 4, Northwest: 5, Southwest: 6, East: 7 and 8 (whole study area projected model for 2016: 8).

The prediction success of the models for the whole study area and regions were mostly low (0.60–0.69, see discussion about the low AUC values). The highest AUC value was for the regional model for the

Northwest region (0.84), but rarefying the data affected results in this area by dropping the AUC value to 0.65, indicating that spatial autocorrelation affected the model. Rarefying, however, did not influence the relative role of environmental variables in the model. Rarefying did not affect the results (AUC values and effect sizes of explanatory variables) in the other regional models or in the model for the whole study area, and therefore we present only the nonrarefied models (Figs. 4, 6), that is, the models in which all data points in the dataset were used.

In the above models, the background points are based only on sites visited during the survey. To test the effect of the background points on the AUC values, we ran the whole study area model using all forest land as the background (> 50% of 250 m × 250 m cells was forest land). AUC for the full model was 0.752 and thus considerably higher than for the model using a background consisting only of sites actually visited (AUC 0.69). Adding information on nearest occurrence observation improved the AUC value of the model for the whole study area from 0.69 to 0.74. The permutation importance of this variable was as high as 65%. This variable did not, however, affect the results for the environmental variables, and it was dropped from the final models. More information on model fit and performance can be found in Supplement 3, where we assessed the predicted probabilities of occupancy separately for the true locations of presence and absence in the data and also compared model predictions to species' monitoring program data.

4. Discussion

In this study, we produced predictive maps to identify areas of high suitability and occurrence probability for a species protected by *the*
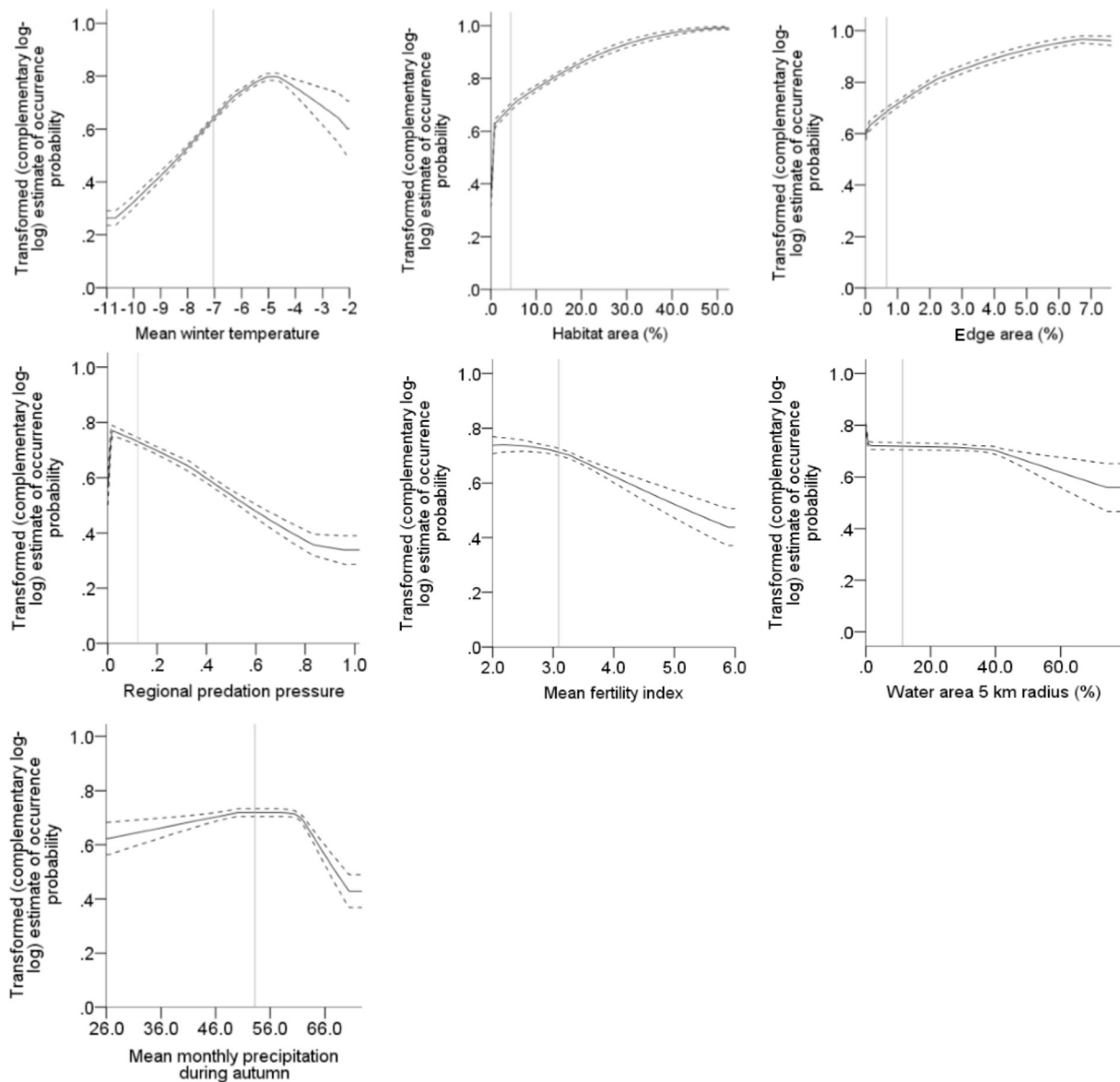
Fig. 5. Marginal response curves showing how the predicted probability of presence changes as each environmental variable is varied, assuming all other environmental variables remain constant at their average sample value (prevalence set for 0.5). The curves show the mean response of the 15 replicate MaxEnt runs (black line) and the mean ± one standard deviation (dotted lines). Vertical line shows the average value of the variable in the whole data. Note the scale of the fertility index: 1 = most fertile, 8 = least fertile.

system of strict protection in the EU (92/43/EEC). We observed that occurrence was difficult to predict at the site and annual level, which complicates the conservation of the species. We also identified that climate is an important determinant of species occurrence and found support for the hypothesis that predation affects the flying squirrel population.

The predictive ability of our models seemed poor at first glance (AUC 0.6–0.7), but the selection of the modelling area and the background influenced the rate of well-predicted absences and, thus, the AUC scores (Lobo et al., 2008). Our model's AUC scores would have been higher (> 0.75, generally considered as acceptable performance) if we would have not had information on, and therefore used, actually surveyed sites as the background. In our case, low AUCs also seem to reflect the ecology of this short-lived species: the annual survival of adult individuals ranges from 0.43 to 0.76 (Lampila et al., 2009; Brommer et al., 2017; Mäkeläinen et al., 2016) and, therefore, survival and colonization dynamics of the species create empty territories constantly (Brommer et al., 2017). This is also seen in the species

monitoring data, in which occupancy or detection status changed from 2006 to 2007 in 18% of the monitoring plots (n = 853, Jokinen et al. unpublished). According to analysis presented in Supplement 3, our models are better in indicating high quality sites than sites where the species is only occasionally observable. One should also remember, that we did not use the exact coordinates of the observations, but rather we explained occurrence on the scale of 300 m × 300 m survey plots and 750 m × 750 m forest variables. This likely affected the maximal AUC scores that we could realistically expect to achieve.

Although the model was built with 13-year-old data, this should not affect the conclusions of the effect of explanatory variables. However, projecting the model likely increases the uncertainty of resulting predictions for species occurrence. For example, climate change can produce some uncertainties. Out of the tested environmental variables, the average winter temperature had the largest predictive power for flying squirrel occurrences. Movement of the temperature cline has already been observed to cause bird species turnover in Finland (Virkkala and Lehikoinen, 2017). We do not currently know what mechanisms
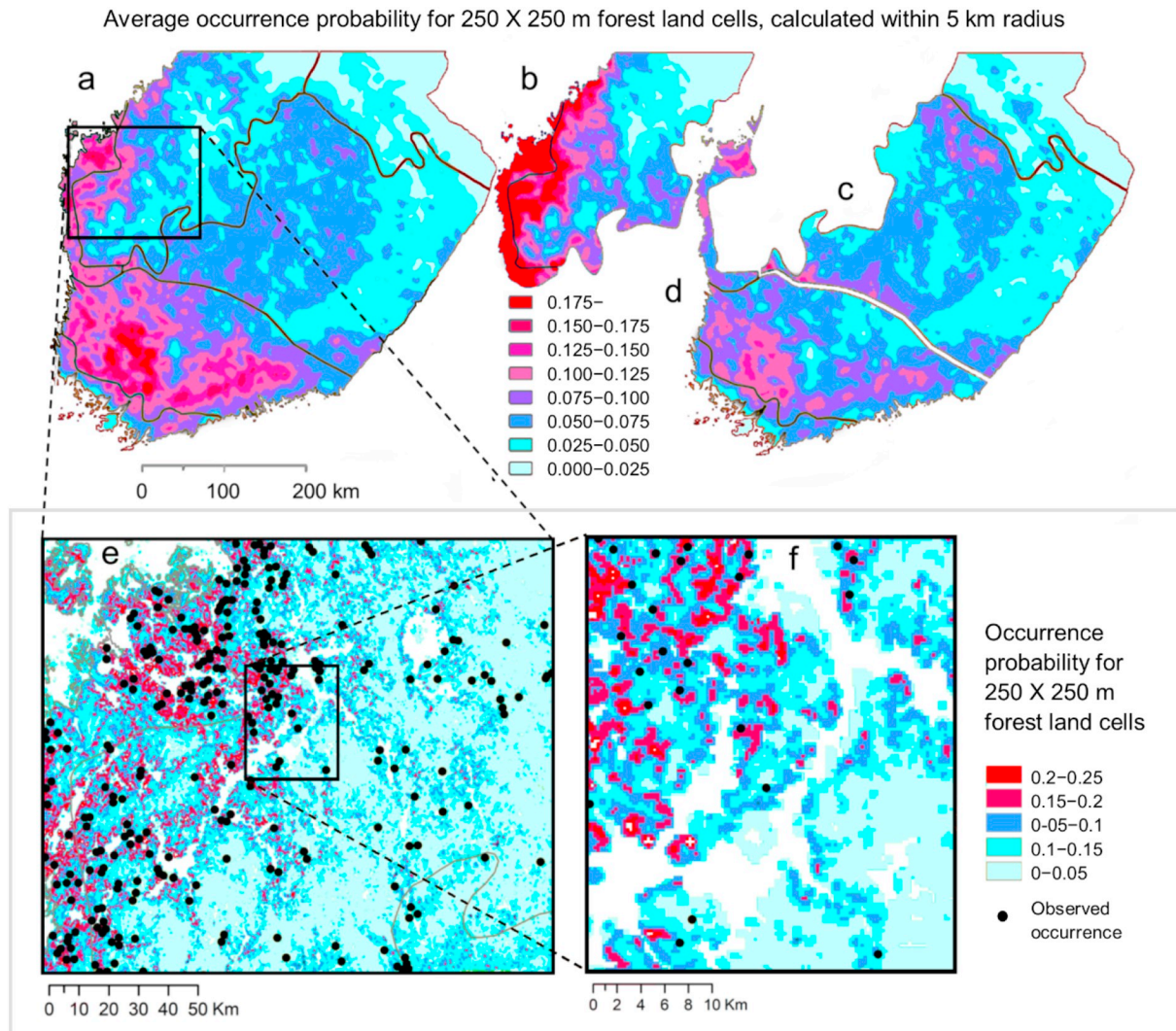
Fig. 6. Occurrence probabilities of a) the model for the whole study area, and b-d) of the three regional models, calculated as means for 250 × 250 m forest land cells within 5-km radius in 2005. Panels e) and f) are examples of a full resolution map of the whole area model.

connect flying squirrel occurrence to mean temperature, and thus we cannot say how quickly the effect of climate change could be observable. It could be that thermoregulatory costs are significant for a small animal consuming low-energy food (but see Selonen et al., 2014). Also, leaf-out and masting of deciduous trees depend on temperatures and determine food availability for flying squirrels (see e.g. Hoset et al., 2017). If these factors are important, species abundance patterns should follow temperature cline with a short time lag. On the other hand, if the effect comes through connection to forest composition, forest vegetation zones move slow. According to our results, a rise in temperature will increase the quality of habitat in central and northern areas, but potentially decreases it in southwestern and coastal areas, which are most densely populated by the species. Along the southern coast, a larger proportion of autumn and winter precipitation will come as rain, and less in the form of snow, which may negatively impact the species, as cold rain can be energetically unfavourable for small mammals (Conley and Porter, 1986).

Some uncertainty of the predicted map (both the original and the projection) arises from the forest inventory data; it is not so detailed that it could capture all aspects of habitat quality, such as changes in availability of food and nest sites. On the positive side, we used the same forest data used by the forestry administration and organizations, which is available for conservation authorities. Thus, our results can easily be applied, e.g., for monitoring and evaluation. Our definition of

a suitable habitat for flying squirrels differs from, e.g., that of Remm et al. (2017), who found that an increase in the area of a > 50-years-old spruce-deciduous forest in 250-m radius had a positive effect until it exceeded 40% of the area, after which increase in area actually decreased the occurrence probability of flying squirrels. In our model, an increase in old forest (> 80 years) continued to increase the occurrence probability until the observed maximum value of 49.9% of the 750 m × 750 m area. It seems that the exact proportion of spruce or the stock volume seems to be less important for the species than the stand age. Spruce plantations/monocultures in the fertile and moist land of southern Finland can gain high volumes at a relatively young age, but they still lack important resources for the species. Our observation, that the positive effect of agricultural lands on flying squirrel occurrence (Santangeli et al., 2013; Remm et al., 2017; Turkia et al., 2018) did not disappear when we included climate, predation pressure and fertility in our models further, supports the notion that Finnish forests may lack important resources for the species. Deciduous trees, providing food and nesting sites, can be more common and produce more catkins (important food source, Hoset et al., 2017) on edges that are on fertile soil and have favourable microclimate (lightning conditions and temperature). In North America, northern flying squirrels seem to respond more to stand-level microclimate and food availability than to forest type or age (Wheatley et al., 2005). Habitat heterogeneity can be important for the flying squirrel as different resources can be located in

different types of habitats. Future research should test whether functional response models (Mysterud and Ims, 1998; Matthiopoulos et al., 2011) would be more suitable.

The regional abundance is also partly explained by the differences in predation pressure. Based on earlier studies it is known that Ural owls affect the flying squirrel locally, as flying squirrels often are absent from the close proximity of nest sites of the Ural owl (Byholm et al., 2012; Turkia et al., 2018). However, it has been thought that the Ural owl does not play a major role in explaining flying squirrel density in the landscape (Selonen et al., 2010; Selonen and Mäkeläinen, 2017; Turkia et al., 2018). Our results imply that Ural owls may affect flying squirrels also at the population level. An analogous situation has been observed with the Northern flying squirrel (Carey et al., 1992; Forsman et al., 1984). Our results seem to support those by Turkia et al. (2018) and indicate that strong predation pressure can override the effect of habitat availability in southwestern Finland (see Figs. 2, 6).

5. Conclusions and implications for species conservation

Inadequate information on species occurrence and stochasticity in occupancy of high-quality habitats are problems for the effective implementation of the system of strict protection of species (92/43/EEC). The distribution area of the flying squirrel is also much too large to be completely surveyed by conservation authorities, but forest managers and owners still have to comply with the protection legislation. The occurrence probability maps provided in this study can inform authorities and managers on the likelihood of finding flying squirrels in different areas. On the other hand, the knowledge on the distribution of the species and regional differences in the role of predators and habitat structure (see also Remm et al., 2017) explaining occurrence can be used for planning more effective conservation actions. Our models indicate that increasing the area of old forest habitat would increase the occurrence probability of the species in most sites, but also that resources for the species should be increased in the general forest matrix. In other words, we recommend developing forest management to increase important resources for the species on a landscape scale independently of its observed occurrence. In addition, in certain areas with a high density of Ural owls, we agree with Turkia et al. (2018) and recommend coordination between flying squirrel protection and an effort to promote the Ural owl nesting with nest-boxes.

Our observation that the regional abundance of the flying squirrel depends mostly on climate has two implications for species conservation. It means that 1) we could consider targeting the conservation efforts according to expected gain, in those areas with the most favourable conditions for the species. However, at the same time it means that 2) we should take into account the possibility that the changing climate will affect the species. Thus, our study indicates that also mammalian species like the flying squirrel can be sensitive in the face of future climate change, such as has been observed, for example, in birds (e.g. White, 2008; Virkkala and Lehikoinen, 2017). Climate change has not been considered to be a major threat for the flying squirrel (Liukko et al., 2016), but we recommend that the existing species monitoring programme is developed and its data analysed from this perspective as well.

The effects of climate change will increase the need of European and continental-level cooperation in the protection of biodiversity. Our results show that we would need additional tools and measures in the EU for achieving a favourable conservation status of those species that occur in commercial forests. Scientific papers are not the most used information sources for decision makers and managers in the first place (Pullin et al., 2004), and Guisan et al. (2013) have suggested that more useful SDMs could be developed through dialog between modellers and the decision makers and managers, and by practice-oriented case studies. So, we represent our results as a starting point for the dialog between modellers and users of the information.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.biocon.2018.12.008. These data include the Google maps of the most important areas described in this article.

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