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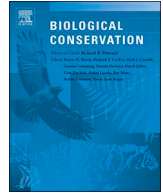
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Predicting valuable forest habitats using an indicator species for biodiversity

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ABSTRACT

Intensive management of boreal forests impairs forest biodiversity and species of old-growth forest. Effective measures to support biodiversity require detection of locations valuable for conservation. We applied species distribution models (SDMs) to a species of mature forest, the northern goshawk (*Accipiter gentilis*, goshawk), that is often associated with hotspots of forest biodiversity. We located optimal sites for the goshawk on a landscape scale, assessed their state under intensified logging operations and identified characteristics of goshawks' nesting sites in boreal forests. Optimal sites for the goshawk covered only 3.4% of the boreal landscape and were mostly located outside protected areas, which highlights the importance of conservation actions in privately-owned forests. Furthermore, optimal sites for the goshawk and associated biodiversity were under threat. Half of them were logged to some extent and 10% were already lost or notably deteriorated due to logging shortly after 2015 for which our models were calibrated. Habitat suitability for the goshawk increased with increasing volume of Norway spruce (*Picea abies*) peaking at 220 m³ ha⁻¹, and with small quantities of birches (*Betula* spp.) and other broad-leaved trees. Threats to biodiversity of mature spruce forests are likely to accelerate in the future with increasing logging pressures and shorter rotation periods. Logging should be directed less to forests with high biodiversity. Continuous supply of mature spruce forests in the landscape should be secured with a denser network of protected areas and measures that aid in sparing large entities of mature forest on privately-owned land.

1. Introduction

Boreal forests in Northern Europe have been subjected to intensive utilisation, causing habitat fragmentation, dominance of homogeneous single layered forest stands, suppression of natural disturbances and loss of old-growth forests (Esseen et al., 1997; Löfman and Kouki, 2001). This has resulted in profound effects on forest biodiversity: forestry is now considered the greatest threat factor for the red-listed species in Finland and Sweden, especially for species requiring old-growth forests (ArtDatabanken, 2015; Hyvärinen et al., 2019).

Only 4–5% of forest land is protected in Finland and Sweden in southern and lowland areas where the most productive forests are situated (Vaahtera et al., 2018; Höjer and Hedeklint, 2018). Furthermore, pressures for intensive use of forests may increase in the future when Finland, as one of the European Union countries, executes the directive on the promotion of the use of energy from renewable sources (2018/

2001/EU) where increased logging operations and the use of wood-based biomass play a key role (Huttunen, 2017; Ministry of Agriculture and Forestry, 2019). In Finland, logging volume has already recently increased, from about 60 million m³ year⁻¹ in 2012 to 78 million m³ year⁻¹ in 2018 (National Resources Institute Finland).

The current protected area (PA) network alone is insufficient to conserve forest biodiversity and threatened species (Parviainen and Frank, 2003; Virkkala and Rajasärkkä, 2007). PAs have thus been complemented with other legislative measures and management guidelines applied in managed forests to support biodiversity (Parviainen and Frank, 2003). For instance, the concept of woodland key habitats (WKHs) has been introduced to provide suitable sites for specialist and red-listed species (Timonen et al., 2010). However, WKHs are small and thus rarely provide suitable habitat for species requiring forest interior conditions (Aune et al., 2005). Moreover, part of WKHs remain unnoticed in the field and in management planning (Yrjönen,

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2004; Timonen et al., 2010). This suggests that complementary methods to locate hotspots for biodiversity are needed.

The Finnish Government launched the Forest Biodiversity Programme for Southern Finland (METSO-programme) in 2008 in order to halt the decline of forest habitats and species (METSO programme, 2019). However, site prioritization in METSO, and in other similar conservation prioritization programs, relies on comprehensive data of good quality on species which are robust indicators of locations with potentially high biodiversity values.

Unfortunately, detailed information over large areas for such species is typically incomplete. Thus, spatial species data used in conservation prioritization exercises often need to be complemented with species distribution models (SDMs) which are widely used tools in developing maps of projected distributions (Elith and Leathwick, 2009). SDMs can be particularly useful in forecasting the best sites for indicator species whose distribution reflects environmental conditions of general conservation interest (Landres et al., 1988).

We used the northern goshawk (*Accipiter gentilis*, hereafter goshawk) as an indicator species to model the availability of valuable habitats for biodiversity in boreal forests. Nest sites of goshawks are useful surrogates for biodiversity as they host increased levels of birds, the Siberian flying squirrel (*Pteromys volans*), species of conservation concern and old-forest specialists such as polypores (Byholm et al., 2012; Burgas et al., 2014). Co-occurrence with polypores implies similar habitat preferences while mobile animals are heterospecifically attracted to breed close to goshawks in order to get protection from the powerful raptor against other predators (Pakkala et al., 2006; Mönkkönen et al., 2007; Byholm et al., 2012). Moreover, old nests of goshawks are frequently used by other birds of prey for breeding (Meller et al., 2017). Goshawks prefer mature spruce forests, the proportion of which has continuously declined in southern Finland (Björklund et al., 2015; Virkkala, 2016). Therefore, it is important to estimate the availability of potential habitats preferred by the goshawk in a landscape under increasing logging pressures.

Here, we (1) used SDMs to locate areas that are suitable for goshawk nesting on a wide scale. Moreover, using logging data, we (2) followed the state of the suitable areas for goshawk nesting and potential hotspots of biodiversity under recent forest cuttings. We also investigated (3) the characteristics of boreal forest that describe nest sites of the goshawk and can be used to recognize potential nest sites and areas of high biodiversity. With these measures, we estimated the state of managed boreal landscapes for biodiversity associated with old-growth forest.

2. Material and methods

2.1. Study area

Our study area was Central Finland, a region of 19,950 km². Central Finland is dominated by forestry land (72% of the area), while waterbodies cover 16% and agricultural areas 5% of the region. Forests are dominated by Scots pine (*Pinus sylvestris*, hereafter pine, 45% of the growing stock volume), Norway spruce (*Picea abies*, hereafter spruce, 35% of the volume) and birches (*Betula pendula* and *B. pubescens*, 16% of the volume; Anonymous, 2017; Vaahtera et al., 2018).

2.2. Study species

The goshawk is a middle-sized bird of prey that feeds on birds, e.g. forest grouse, corvids *Corvidae*, thrushes *Turdus* spp. and pigeons *Columba* spp., and mammals such as European red squirrels *Sciurus vulgaris* (Törnberg, 2001; Sulkava et al., 2006).

Goshawks prefer mature forests for nesting in Europe (Penteriani and Faivre, 1997; Penteriani, 2002; Hakkarainen et al., 2004), and old forests dominated by spruce are important for the breeding success of goshawks in northern latitudes (Björklund et al., 2015). Forest

management potentially impairs the breeding possibilities of the goshawk. Thus, changes in forest landscapes may contribute to the decline of the species, resulting in its classification as nearly threatened species in Finland (Meller et al., 2017; Hyvärinen et al., 2019).

On their territory, goshawks construct one or several alternative stick nests that they use for breeding in different years (Björklund et al., 2016). Adult goshawks are sedentary (Saurola et al., 2013).

We used the goshawk as an indicator species to model the habitat availability for biodiversity in boreal forests. The use of indicator species for conservation prioritization has been criticized as it is often not clear which species should be chosen as an indicator, whether it really indicates the relationship as assumed, and in case of environmental change, whether the indicator and the indicated biodiversity respond in a similar manner (Lindenmayer et al., 2000, 2006). However, the association of the goshawk with various taxa of mature spruce forest has been shown in many studies (Pakkala et al., 2006; Mönkkönen et al., 2007; Byholm et al., 2012; Burgas et al., 2014), and both the goshawk and associated species are known to suffer from logging that devastates their habitat.

2.3. Nest data

Nest sites of the goshawk have been monitored in Central Finland since 1989 as part of the Finnish Common Birds of Prey Monitoring. We used location data on occupied nests of the goshawk gathered in spring and summer 2015 and 2016 from an area that covers 43% of the study area (calculated as a minimum bounding geometry with the convex hull in ArcGIS). Nests from the two years matched temporally with the forest data (see Section 2.4) that represent a snapshot of the landscape whose changes we monitored. We assumed that closely (< 1000 m) situated nests belong to the home range of the same hawk pair and are thus alternative nests in a territory. When a territory had two or more alternative nests, we randomly chose one of the nests in order to avoid pseudoreplication as nests from the same territory are likely to have more similar habitats than nests from different territories. Finally, our data included 78 nests.

2.4. Multi-source national forest inventory data

Forest stand and tree characteristics are important in determining the nest site selection of the goshawk (Penteriani, 2002). Our forest data used in the modelling were based on a multi-source national forest inventory (MS-NFI) of the Natural Resources Institute Finland. The MS-NFI data combine information from field plots of Finnish national forest inventories (NFIs), satellite images (Landsat Thematic Mapper), elevation models and other georeferenced digital data. We used the nationwide MS-NFI based on field data of the 11th and 12th NFIs from 2009 to 2016 and satellite images from 2015 and 2016. Satellite images in our study area were mainly from August 2015. The data with 44 variables contain information on forest characteristics such as mean growing stock volume and canopy cover at the resolution of 16 m × 16 m (Mäkisara et al., 2019). We omitted variables (e.g. biomass of roots or dead branches by tree species) that, based on previous research, were not expected to determine the nest site selection of the goshawk. Finally, we had 32 variables.

2.5. Other environmental data

We extracted data on annual logging in 2000–2018 from the Global Forest Watch (hereafter GFW) that uses multispectral Landsat satellite imagery to measure areas of tree cover loss (Hansen et al., 2013). In GFW, tree cover is determined as an area where vegetation is higher than five meters, and tree cover loss is defined as stand replacement disturbance or a complete removal of tree cover canopy that can result from human activities (timber harvesting, fire) or natural causes (storm, disease, fire). Annual forest loss due to storm, disease and fire are very

sporadic in the study area (Nevalainen et al., 2018) so we concluded that tree cover loss results mainly from logging. The original resolution of the GFW data (30 m × 30 m) was resampled to 20 m × 20 m to match with other environmental data. We classified the GFW data into two logging periods: 1) 2000–2014 (logging before modelling), and 2) 2015–2018 (logging after modelling).

We used false colour orthophotos from 2008 to 2018 (National Land Survey of Finland, accessed by open data interface) and Corine land cover data of 2018 (Härmä et al., 2019) to verify the suitability of the modelled nest sites for the goshawk and to assess unlogged areas at the nest sites (see Section 2.6.2). Of the national Corine classification with 50 classes, 47 land use classes occurred in the study area (Appendix A). The resolution of the Corine data is 20 m × 20 m.

We also used geospatial data from the Finnish Environment Institute on PAs (on privately or state-owned lands, e.g. strict nature reserves, national parks, herb-rich forest areas, mire and shore conservation areas, old-growth forest areas) with the resolution of 20 m × 20 m to unravel the proportion of modelled nest sites that situate on PAs.

2.6. Analyses

2.6.1. Species distribution models, SDMs

Our data on goshawk nests represent presence-only data. Thus, we applied a maximum entropy method (Maxent), considered particularly useful for presence-only data, for modelling and predicting the areas suitable for goshawk nesting (Phillips et al., 2006; Elith et al., 2011). Maxent utilizes values of environmental variables, in our case the MS-NFI data, on known occurrence sites to predict suitable conditions for the species elsewhere in the study area (background) based on the environment. No climatic variables were included as our study area is rather small and we expected no weather conditions to affect goshawk's nest site selection.

Correlation between environmental variables may hamper the interpretation of Maxent results (Phillips, 2017). We calculated Pearson correlations between the continuous environmental variables (31) at the nest sites and considered values of $|r| \geq 0.7$ too high (Dormann et al., 2013). We aimed to keep as many variables as possible but in a number of cases, we needed to select between highly correlated variables. We then chose those variables which are known to be important for the goshawk based on earlier research (e.g. variables related to timber volume, Björklund et al., 2015), which are useful for generalization in other areas, or whose impact was of specific interest. Finally, our selected set of predictor variables included one class variable, site fertility class (with seven classes), and nine continuous variables (abbreviation, unit; see Appendix B for more details): growing stock volume of the spruce, pine, birches, and other hardwood (spruce, pine, birch, other hardwood volume, respectively, $\text{m}^3 \text{ha}^{-1}$), canopy cover (%), canopy cover of broad-leaved trees (hardwood cover, %), saw timber of other broad-leaved trees than birches (other hardwood logs, $\text{m}^3 \text{ha}^{-1}$), pulpwood volume of the birches (birch pulpwood, $\text{m}^3 \text{ha}^{-1}$) and the biomass of the stem residual of the spruce (spruce stem residual, 10 kg ha^{-1}). As an alternative to spruce volume, we tested the effect of the total growing stock volume (total volume, $\text{m}^3 \text{ha}^{-1}$), a variable highly correlated with spruce volume.

The original resolution of the MS-NFI data (16 m × 16 m) was too high to describe the quality of the forest stand around the nest tree from the “goshawks' perspective” (Penteriani, 2002). Thus we resampled the MS-NFI data to resolutions of 80 m × 80 m and 160 m × 160 m to represent one potential nesting stand, and the nest and MS-NFI data were then tested using Maxent to detect potential differences in model performance between the two resolutions (Parkkinen, 2019).

In Maxent, model accuracy is tested with cross-validation, i.e. by leaving out each group in turn, and using the omitted group for evaluation (Phillips, 2017). We split the data into 10 groups for cross-validation. Based on cross-validation, Maxent calculates an average AUC-value (area under the receiver operating characteristic (ROC) curve)

across the models (Fawcett, 2006). With presence-only data, AUC depicts a probability that a sample of positive instances (presence locations) and a sample of negative instances (random background locations, pseudoabsences) are correctly ordered (Phillips et al., 2006). Performances of the alternative Maxent models (with the spruce volume or the total volume, and with the two resolutions) were compared using their AUC-values, and the model with the higher AUC was selected for further analysis.

The relative importance of the variables was measured by variable contribution and model deterioration measures which show how much model accuracy would deteriorate if values of a variable were randomly allocated on the training presence and background data. Maxent also performs jackknife-tests to determine the variables that provide the largest unique contributions to the models (Phillips, 2017).

Maxent yields for each square a cloglog-transformed index value ranging from 0 to 1 that describes the relative suitability of the square to goshawk nesting, given the environment (Elith et al., 2011; Merow et al., 2013). We classified squares with index values of 0.69–1.00 as optimal, 0.46–< 0.69 as typical and < 0.46 as poor for goshawk nesting (following approximately Phillips, 2017; see Appendix B for details). For further analyses, we divided optimal squares into ‘best’ goshawk squares (index values 0.92–1.00 corresponding to a high probability of suitable conditions, Phillips, 2017) and ‘good’ goshawk squares (index values ≥ 0.69 and < 0.92).

2.6.2. Logging in the optimal squares

Our Maxent models were based on the situation in the forest landscape in 2015. After this, goshawk squares may have been degraded due to logging (Byholm et al., 2020). To assess this threat, we measured the proportion of best and good goshawk squares that were located in ‘safe sites’ in PAs and those that were situated in unprotected managed forests and were possibly logged in recent years.

In order to investigate the state of best and good goshawk squares, we used the GFW data to measure in each square the unlogged area in 2019 (after SDMs), in 2015 (during the SDMs) and in 2000 (to determine the logging history of the square; details in Appendix C). We used the following thresholds to define the status of the squares in 2019: a) a 50 m-radius of mature forest (7854 m^2) which goshawks at least require around a potential nest tree to consider the stand as suitable for nesting (Penteriani et al., 2002), and b) a 20 m-radius of forest (1257 m^2) as being the minimum buffer to be left in logging around a nest tree of any forest-dwelling hawk (Appendix C, the Finnish forest raptor project, METSO-petolintuhanke, 2017). The first threshold differentiated between squares that can or cannot provide nesting sites for the goshawk on their own. If the first threshold criterion was not met, a square could still be a potential nesting site provided that the unlogged area continued outside the square (see Figs. C.1 & C.2, c–d). However, when the remaining unlogged area in a square was smaller than the second threshold, we classified the square totally unsuitable for nesting (Fig. C.2b). Thus based on these criteria, we considered best and good goshawk squares fully unsuitable for the goshawk (‘destroyed’) in 2019 if the unlogged area was < 1257 m^2 , ‘vulnerable’ if the unlogged area was $\geq 1257 \text{ m}^2$ –< 7854 m^2 , and ‘preserved’ if the unlogged area was $\geq 7854 \text{ m}^2$ (examples of best and good goshawk squares in the Appendix C).

We used ArcGIS Desktop programs (10.3.1 and 10.5.1; ESRI, Redlands, CA, USA) and QGIS 3.6.2-Noosa (QGIS Development Team) to process and manage the environmental data. We used MaxEnt 3.4.1 (Phillips, 2017) for maximum entropy modelling and R version 3.5.2 (R Core Team, 2018) for the calculation of correlations.

3. Results

Maxent models with spruce volume performed better than those with total volume. Furthermore, models developed at the 160 m resolution had a higher predictive power than the 80-m resolution

models. The averaged AUC-value \pm standard deviation for the models with spruce volume was 0.895 ± 0.046 at the 80 m resolution and 0.903 ± 0.044 at 160 m (Appendix D) while for the models with total volume it was 0.888 ± 0.052 at the 80 m resolution and 0.896 ± 0.048 at 160 m. Therefore, the other model results are presented only for the models with spruce volume and the 160 m resolution. The averaged AUC-value of these models was high (Swets, 1988) indicating that our focal variables had a high explanatory power.

The outperformance of the 160-m resolution in modelling habitat suitability compared to the 80-m resolution (Appendix D) was in agreement with some earlier results. Fine-scale resolutions may not have produced the highest model performances (Arnone et al., 2016), probably because they provided overly detailed prediction maps that indicated small isolated forest stands (Fig. D.1a). Coarse resolutions captured bigger entities of suitable habitat that can describe more accurately the nesting habitat requirements of a species, as was shown here for the goshawk (Fig. D.1b).

3.1. Habitat suitability at the landscape level

The outputs of our Maxent models suggested that optimal 160-m-squares covered 3.4%, typical 4.0% and poor 75.4% of the study area, respectively (Fig. 1). Squares that consisted totally of waterbodies were not included in this classification.

The first step in the analysis of the optimal goshawk squares was excluding 212 squares which had too small quantities of potential nesting habitat (see Appendix C). After this, the set of optimal squares included 6895 (cover 0.9% of the study area) best goshawk squares and 19,421 (cover 2.5%) good goshawk squares (Fig. 2).

Best and good goshawk squares were mostly located in unprotected areas, as 6552 (95.0%) of the best and 18,638 (96.0%) of the good goshawk squares were completely outside the PAs. Conversely, 343 (5.0%) of the best and 783 (4.0%) of the good goshawk squares included PAs to some extent (Table 1). Of these, 134 (1.9%) of the best and 234 (1.2%) of the good goshawk squares were situated completely within PAs (e.g. Fig. 1c).

3.2. State of the optimal goshawk squares

In total, 11% of best and over 9% of good goshawk squares were destroyed or vulnerable in 2019 (Table 1). Some of these squares included PAs at least to some extent (Table 1); in these cases logging were mostly carried out outside the PAs in the square (logging is allowed in some of the PAs). Importantly, rather substantial logging operations have occurred during the few recent years (Table 1). Most of the destroyed squares (230 (97%) of best and 435 (98%) of good goshawk squares) had over 7854 m² of unlogged area in 2015, i.e. the time point for which our SDMs were calibrated. The same applies to vulnerable squares (Table 1) of which 440 best (84%) and 1138 good (79%) goshawk squares contained more than 7854 m² of unlogged area in 2015.

Approximately 90% of the best and good goshawk squares were preserved, i.e. they still included enough unlogged area for the goshawk. Of these, 2771 best and 6580 good goshawk squares were completely preserved (unlogged area 25,600 m² in 2019) corresponding to 40.2% and 33.9% of best and good goshawk squares, respectively. However, only 338 (5.5%) of the preserved best and 756 (4.3%) of the preserved good goshawk squares included PAs (Table 1).

On the other hand, both vulnerable and preserved squares may have been subjected to logging to some extent (Appendix C). Altogether, logging occurred in 3062 (44%) of best goshawk squares and 9846 (51%) of good goshawk squares during the logging periods.

3.3. Characteristics of nest sites

Spruce volume was the most important variable in defining habitat

suitability for goshawk nesting (Table 2, Fig. E.1). Hardwood cover, other hardwood logs and site fertility class contributed to some extent to habitat suitability while the rest of the variables were of minor importance. However, while birch volume only had a slight contribution to the model performance, its exclusion decreased the prediction ability of the model almost by 10% (Table 2).

Habitat suitability for the goshawk increased with increasing spruce volume. The relative suitability of habitat exceeded 0.8 with spruce volume of 150 m³ ha⁻¹ and peaked at 220 m³ ha⁻¹ after which it remained on a high level (Fig. 3). For the variables of moderate importance, the highest habitat suitability was reached at 2–3% of hardwood cover, < 1 m³ ha⁻¹ of other hardwood logs, site fertility class 3 (mesic forests) and about 18 m³ ha⁻¹ of birch volume. For the other variables, the peak was typically at low values (Fig. E.2) except for canopy cover which showed a sharp increase in suitability for cover values higher than 60%.

Taken together, Maxent results indicated that the best nest sites for the goshawk are typically stout spruce forests mixed with small quantities of birches and other broad-leaved trees with rather closed canopy cover at mesic sites.

4. Discussion

We identified characteristics of mature forests that describe suitable nesting sites for the goshawk, an indicator species of forest biodiversity, in an intensively managed boreal forest landscape. Such suitable sites were sparse in our study area and a remarkable proportion of them was already deteriorating or lost in a short period.

4.1. Habitat suitability and deterioration in the landscape

Optimal sites for goshawks were infrequent as best and good goshawk squares together covered only 3.4% of our study area. Very clearly, mature forests have become scarce and young forests more widespread in landscapes under intensive forest management (Björklund et al., 2015; Vaahtera et al., 2018). This development is adverse for the goshawk which avoids hunting in dense young forests (Widén, 1989). Difficulties in predation and finding nest sites in landscapes of managed forests are suggested reasons for the goshawk's decline also in Sweden (Artfakta, 2020).

The key reason for the low habitat suitability for the goshawk is that the majority of forests in the study area are younger than 60 years old and the mean spruce volume is 50 m³ ha⁻¹ (Vaahtera et al., 2018). Such a landscape is challenging for a species whose optimal habitat in the European boreal zone, mature spruce forests, should be over 70–80 years old (Saga and Selås, 2012; Äijälä et al., 2014) and have high volumes of spruce (optimally 220 m³ ha⁻¹). Moreover, we may even have overestimated the quantity of the optimal goshawk squares in 2019 as the GFW data are only available from 2000 onwards. Forests logged just before 2000 are still too young as nesting habitats for the goshawk but they could not be accounted for in our suitable habitat measurements.

It is also noteworthy that not all squares projected to be suitable are available for the goshawk due to intraspecific competition, i.e. raptors do not tolerate conspecifics close to their nest sites (Penteriani and Faivre, 1997; Tornberg, 2001; Katzner et al., 2003). Suitable habitats closer than 3–4 km to occupied goshawk nests are unavailable to other goshawks (Tornberg, 2001; Hakkarainen et al., 2004). Therefore, the actual number of optimal sites for the goshawk is smaller than what is indicated in our Maxent outputs. However, all sites projected to be optimal are potentially good for other biodiversity preferring mature spruce forests. Whether these species occupy the optimal sites likely depend most on their dispersal abilities.

Logging activity is high in the study area and evidently mature forests are targets for regeneration felling (Hansen et al., 2013; Äijälä et al., 2014; Vaahtera et al., 2018; Byholm et al., 2020). Most of the

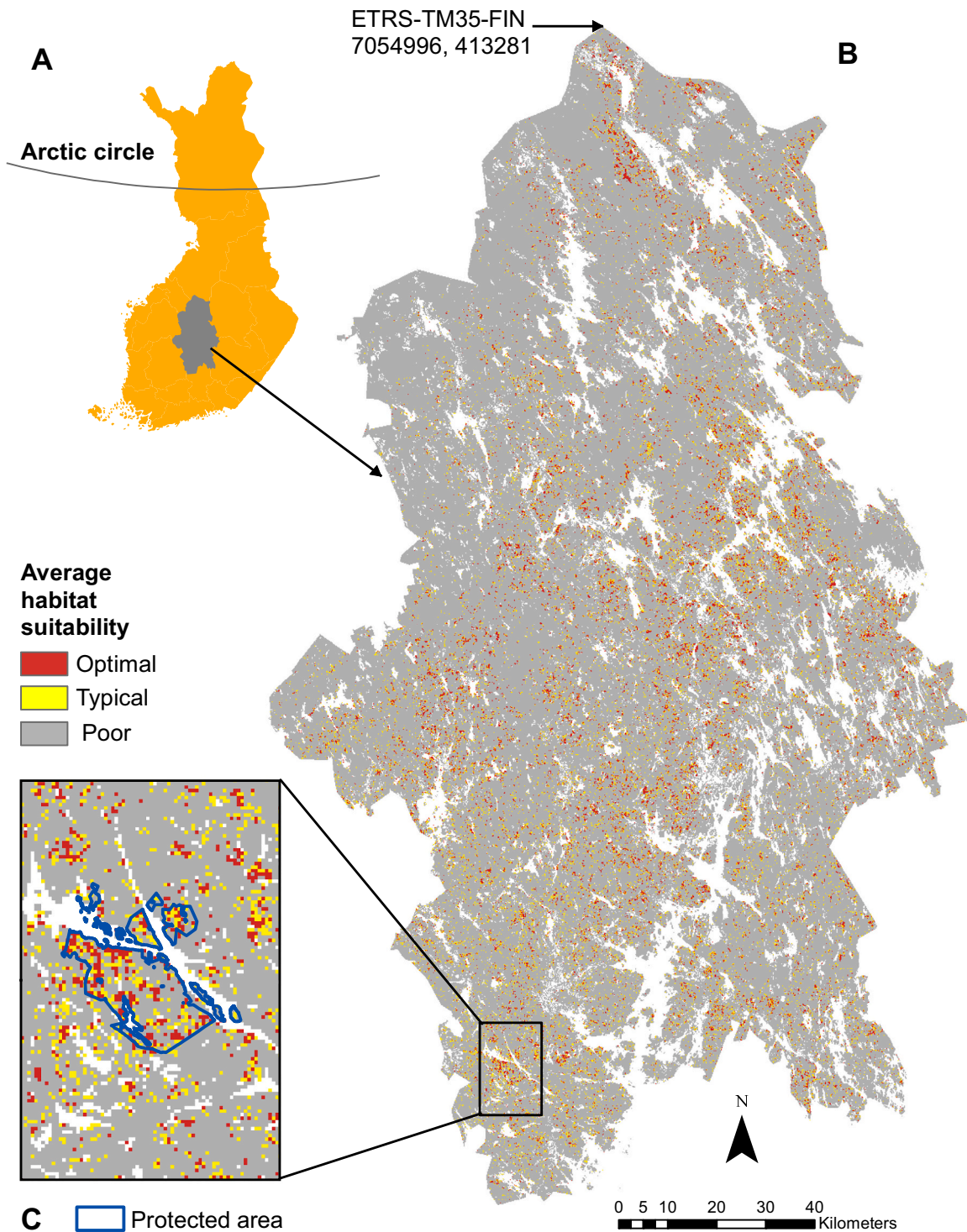


Fig. 1. a) The study area (Central Finland) in Finland. b) The distribution of the 160 m × 160 m squares predicted to be optimal (dark red; habitat suitability index of 0.69–1.00), typical (yellow; 0.46– < 0.69) or poor (grey; < 0.46) nesting habitat for the goshawk. White = waterbodies. c) A cluster of optimal and typical squares in a protected area, Isojärvi National Park. To increase visibility, the actual size of the goshawk squares is slightly enlarged. Map contains data from the Finnish Environment Institute: the Polar and Tropical Circles, Equator and International Date Line 2017; the National Land Survey of Finland: Administrative borders 2018 and General map 2008; and Metsähallitus: Nationally Designated Nature Protected Areas and Wilderness Reserves 2013, all with the Licence CC BY 4.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forestry land in Central Finland is privately-owned and most of the total removal of wood is from private forests (Vaahtera et al., 2018). This compares with other countries as most of the European forests are in private ownership (Parviainen and Frank, 2003). Of the roundwood removals in privately-owned forests, the quantity of spruce logs is

almost double the quantity of pine logs in the study area (1,447,000 m³ and 764,000 m³ in 2017, respectively; Vaahtera et al., 2018) even though pine forests are more widespread in the study area (see Section 2.1). Thus, these logging operations are focused especially on stout spruce forests (as in Norway; Saga and Selås, 2012), i.e. sites of high

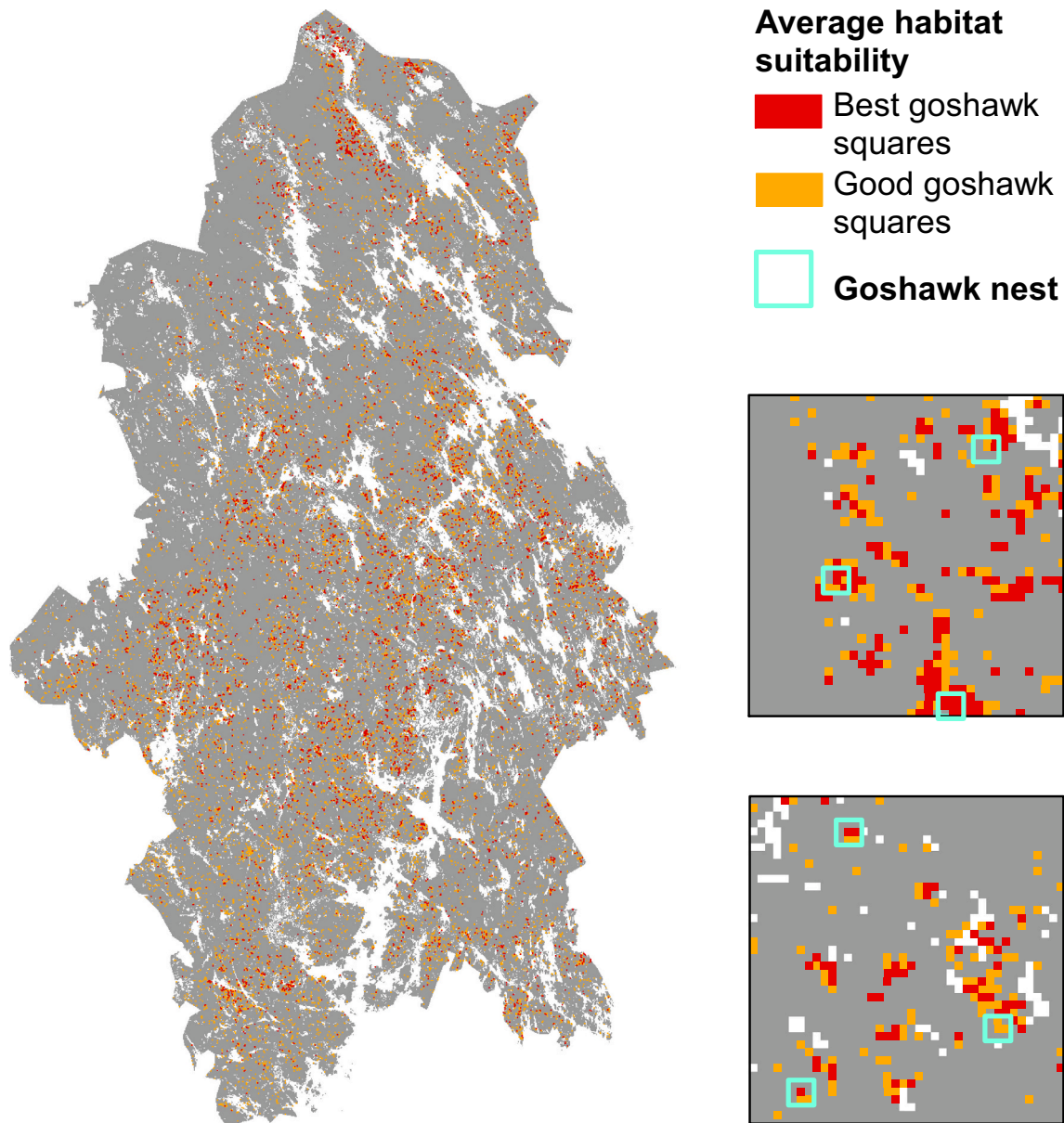


Fig. 2. The distribution of best (red; habitat suitability index ≥ 0.92 , $N = 6895$) and good (orange; $0.69 < 0.92$, $N = 19,421$) goshawk squares in the study area. To increase visibility, the actual size of the 160 m \times 160 m goshawk squares is slightly enlarged. White = waterbodies and grey = other than optimal nesting habitat for the goshawk. Two enlargements of the predicted map show turquoise squares that include a goshawk nest. Licences of the data in the map, see Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

State of best and good goshawk squares in 2019 (see Section 2.6.2), a few years after the species distribution model. PA shows the number and proportion of the destroyed, vulnerable and preserved goshawk squares that contained protected areas at least to some extent.

Squares in 2019		Best goshawk squares			Good goshawk squares		
State	Unlogged area (m ²)	N	%	PA (%)	N	%	PA (%)
Destroyed	< 1257	236	3.4	0 (0)	442	2.3	2 (0.5) ^a
Vulnerable ^b	$\geq 1257 - < 7854$	526	7.6	5 (1.0)	1445	7.4	25 (1.7)
Preserved	≥ 7854	6133	88.9	338 (5.5)	17,534	90.3	756 (4.3)
Total		6895	~100.0	343 (5.0)	19,421	100.0	783 (4.0)

^a Logging occurred outside the PAs but destroyed the suitable habitat for the goshawk in the square.

^b Vulnerable squares included 63 best and 190 good goshawk squares where the low quantities of unlogged areas had natural causes – such as forests on the lake shore – and no logging occurred during the logging periods. Nevertheless, all vulnerable squares are sensitive to any additional reduction in suitable habitat.

Table 2

Relative contributions of the environmental variables used in modelling the habitat suitability for the Goshawk, averaged over multiple Maxent runs. Model deterioration shows a percentual drop in the training AUC (area under the receiver operating characteristic curve) of the species distribution model if values of a variable are randomly re-allocated (see Section 2.6.1).

Variable	Variable contribution %	Model deterioration %
Spruce volume	72.7	64.6
Hardwood cover	7.7	12.0
Other hardwood logs	6.7	3.4
Site fertility class	5.4	1.5
Birch pulpwood	2.1	3.6
Spruce stem residual	1.6	0.9
Other hardwood volume	1.4	1.5
Birch volume	1.2	9.9
Canopy cover	0.8	1.8
Pine volume	0.5	0.6

habitat suitability for the goshawk and associated biodiversity. As nests in mature forests are often lost due to logging, goshawks need to switch their nesting site (Penteriani and Faivre, 2001; Saga and Selås, 2012; Byholm et al., 2020).

An important finding for forest biodiversity conservation is that the optimal habitats for goshawk are currently under accelerating risks. Roundwood removals have increased in Finland in recent years (Vaahtera et al., 2018; see also Virkkala et al., 2020). Consistently, we found that 9–10% of best and good goshawk squares were already lost or became vulnerable during the few years after modelling. It seems that optimal sites for the goshawk and associated biodiversity are at a notable risk to sudden and broad changes as most of the squares deemed as destroyed or vulnerable in 2019 still had enough unlogged area for the goshawk a few years earlier. Moreover, the GFW data showed that approximately half of best and good goshawk squares were logged at least to some extent.

Several resident forest birds, such as the willow tit *Poecile montanus*, crested tit *Lophophanes cristatus*, great spotted woodpecker *Dendrocopos major* and hazel grouse *Tetrastes bonasia* have declined in Finland in a recent period (2012–2018) of increased logging and roundwood removals (Virkkala et al., 2020) showing that the effects of logging procedures on many bird species are parallel with the decline of goshawk's nesting habitats. This further enhances the indicator value of goshawk for other biodiversity against environmental changes.

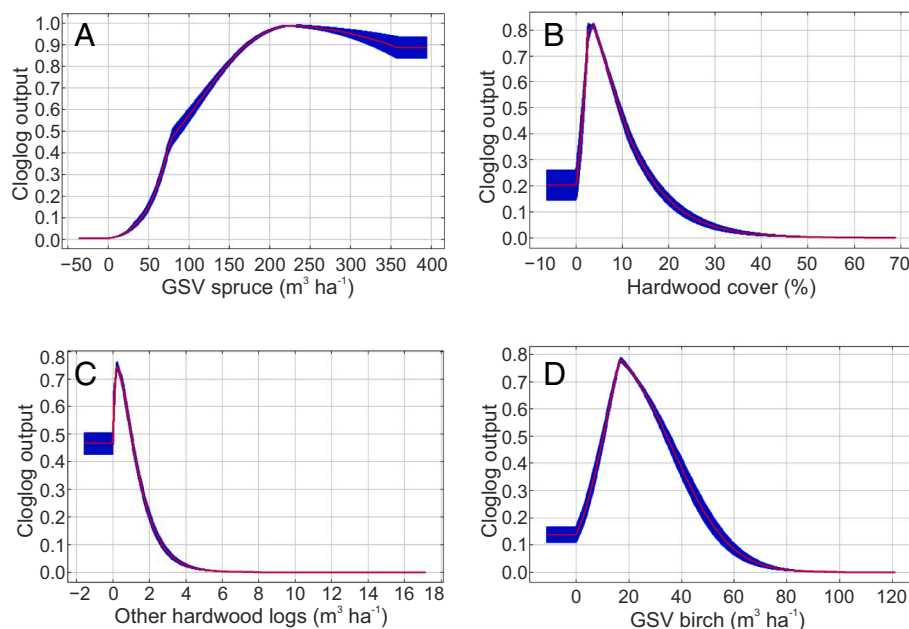


Fig. 3. The average probability (red line, ordinate) \pm standard deviation (blue) of habitat suitability for goshawk nesting along values of habitat variables (abscissa). The probability of suitable habitat for the goshawk was highest with a) spruce volume of $220 \text{ m}^3 \text{ ha}^{-1}$, b) hardwood cover of 2–3%, c) other hardwood logs less than $1 \text{ m}^3 \text{ ha}^{-1}$, and d) birch volume of $18 \text{ m}^3 \text{ ha}^{-1}$. Constant ('clamped') probabilities indicate negative values or large values that occurred in the study area but not at the nest sites in order to allow the modelling of their suitability for the goshawk. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Characteristics of boreal forest at suitable sites

Spruce volume was a key predictor for the habitat suitability of the goshawk. The importance of mature stout forest for the goshawk has been shown in Europe and North America (Penteriani and Faivre, 1997; Penteriani, 2002), and particularly the importance of spruce in the European boreal coniferous forests (Selås, 1997; Saga and Selås, 2012; Björklund et al., 2015; Parkkinen, 2019). Spruce provides good shelter for nests (Selås, 1997) which is probably why spruce volume outperformed total volume.

Areas where spruce volume exceeded $150 \text{ m}^3 \text{ ha}^{-1}$, with a peak at $220 \text{ m}^3 \text{ ha}^{-1}$, represented forest stands with high probability for suitable nest sites for the goshawk. Goshawks need large trees to support their stick nests that become heavy after multi-annual use (Löhmus, 2006). Congruently, large trees and old-growth forest are also important for many red-listed species (Hyvärinen et al., 2019). The subsequent slight decrease in habitat suitability after the peak value in spruce volume may imply that with very high volumes, forests become too dense for hunting (Widén, 1989). Alternatively, very high values of spruce volume may be so rare in the landscape that most of the goshawks must accept forests with lower spruce volume.

The highest habitat suitability values were positively related with small quantities of birches and other broad-leaved trees indicating that spruce-dominated mixed forests are the most optimal nest sites. Goshawks construct their nests both in big conifer and broad-leaved trees throughout the Holarctic region (Penteriani, 2002). Nevertheless, the nest tree is usually a spruce or pine in European boreal forests while birches or European aspen (*Populus tremula*) are occasional choices (Meller et al., 2017), aspen being also important as a host for many threatened species (Hyvärinen et al., 2019). In addition, habitat suitability in our results increased with canopy cover of over 60% which is in line with previous studies (Bosakowski et al., 1992; Reich et al., 2004). Closed canopy shields from the weather and avian predators (Penteriani and Faivre, 1997; Selås, 1997; Saga and Selås, 2012).

4.3. Conservation perspectives

Most of the optimal nesting sites for the goshawk were still preserved but they are under risk as they were mainly situated outside PAs. This stresses the importance of conserving biodiversity with complementary measures in privately-owned managed forests. It would be

crucial for the goshawk and associated biodiversity to secure a continuous supply of mature spruce forests in managed boreal landscapes. A denser network with more PAs for forest-dwelling species should be secured in areas with intensive forestry, e.g. in southern Finland where PAs currently cover a smaller proportion of land compared to northern Finland (Virkkala et al., 2020).

Our predicted optimal sites for the goshawk may importantly complement other data used for conservation prioritization (Mikkonen et al., 2018). One potential system to conserve the most optimal forests could be financial compensation for their protection to the forest-owners through the METSO-programme (Syrjänen et al., 2016). Forest-owners and managers can also be informed about the forests optimal to the goshawk. The Finnish Forest Centre can provide guidelines for setting them aside from intensive management.

Using the goshawk as an indicator species, our aim was to model potential areas of forest biodiversity and demonstrate the current state of managed boreal landscape for species of mature forest. The state was worrying as logging in recent years were focussed on spruce forests. This is especially harmful as spruce volume was more important a predictor than total volume even though spruce forests comprise only a third of the growing stock volume in the study area. Logging should be more evenly distributed over the tree species and directed less to forests with potentially high biodiversity values.

Pressures for increased use of biobased renewable resources should not compromise with obligations to conservation. Intensive forestry conflicts with biodiversity and non-timber ecosystem services of forests, and it may take a long time for them to recover (Pohjanmies, 2018). Our results show that the increase of logging volume may have detrimental effects on boreal biodiversity (see also Virkkala et al., 2020) if logging practices and preserving forest habitats are not properly taken into account.

5. Conclusions

This study revealed that an indicator species associated with mature spruce forests has sparsely distributed optimal habitats in boreal landscapes modified by intensive forestry. Optimal habitats are further reduced if the rotation period of harvesting gets shorter than presently. Our Maxent results show the importance of stout spruce forest for the indicator species, goshawk, and help in identifying sites that are likely hotspots of biodiversity and species of conservation concern that inhabit old-growth mixed spruce forests. These forests are under continuous threat of logging and 10% of them was already lost or degraded in a short time period. The small quantity of optimal habitats and the apparent high risk of their disappearance suggest that current measures to halt the loss of old-growth forests are insufficient. The conservation of mature spruce forests at the landscape level should thus be urgently prioritized, and new tools and incentives are needed to spare large entities of mature forests on privately-owned lands.

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Glossary

Forestry land includes e.g. productive and poorly productive forest land, unproductive land and forest roads.

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Data statement

Modelled data are stored in Zenodo: doi.org/10.5281/zenodo.3926626.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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