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Original Research Article

Hit or miss? Evaluating the effectiveness of Natura 2000 for conservation of forest bird habitat in Sweden

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A B S T R A C T

Biodiversity conservation often requires a landscape perspective. When establishing the Natura 2000 (N2k) network, the effectiveness of the sites and the influence of the surrounding landscapes for species of interest was often disregarded. We analyzed the effectiveness of N2k sites in Sweden for three forest bird species of conservation interest in the European boreal landscapes: lesser spotted woodpecker (LSW), Siberian jay (SJ) and hazel grouse (HG). Our objectives were to: 1) quantify effective suitable habitat area in N2k sites with and without consideration of the adjoining landscapes; 2) examine effective habitat area within N2k sites along the north-south vegetation gradient 3) analyze functionality of N2k sites and assess how forests outside the sites affect habitat suitability inside N2k. GIS-based habitat suitability index models were applied to calculate the amount of effective habitat within and outside N2k sites. N2k sites contributed with 10% (HG), 13% (SJ) and 51% (LSW) suitable habitat identified in Sweden. Functionality of forest environments as habitat was higher inside N2k sites for LSW within all vegetation zones, and for SJ in the Alpine and Middle Boreal zones; for HG habitat outside the sites was more functional in all zones accept Alpine and Middle Boreal. The majority of N2k sites were of quite small size (<500 ha) and the size influenced their functionality for LSW and HG, with larger N2k sites being more functional. For SJ, however, average functionality of N2k sites was not influenced by their size. The largest average habitat increase linked to considering the contribution of areas outside N2k sites for their functionality as habitat was for the N2k sites of smaller size (1-500 ha). Therefore, the presence and quality of forests outside of N2k sites are of a greater importance for smaller sites, and as such these should be carefully managed. To improve conservation efficiency of the N2k sites in Sweden, we call for incorporating them into the development and implementation of the regional Green Infrastructure plans.

Abbreviations: PAs, protected areas; N2k, Natura 2000; EU, European Union; LSW, lesser spotted woodpecker; SJ, Siberian jay; HG, hazel grouse; LSEA, landscape scale effective habitat area; PSEA, pixel scale effective habitat area.

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1. Introduction

Forests are among the most species-rich ecosystems on Earth (MEA, 2005). Despite recent gains in global net forest area (Song et al., 2018), land use change and forest management practices continue to cause extensive forest biodiversity loss and disruptions of ecosystem functions (Chapin et al., 2000; Kok et al., 2018). A key tool for counteracting these negative impacts is the setting aside of large-scale, functional networks of protected areas (PAs) (Rodrigues et al., 2004; CBD, 2018). Recent studies, however, point to the challenges that PAs are facing; for example, Jones et al. (2018) found that one third of global protected land is under intense human pressure, with smaller PAs being particularly affected. Thus, the actual conservation benefits of PAs, i.e., their functionality, are undermined (CBD, 2018; Jones et al., 2018).

There is a need, therefore, for improved biological forecasting to detect early signs of critical transitions into irreversible changes (Barnosky et al., 2012) including the analyses of the functionality of PAs in supporting biodiversity, particularly in the case of small and isolated areas surrounded by highly modified landscapes (Gaston et al., 2008). To improve PAs conservation planning, the spatial dimension should be considered (Poiani et al., 2000; Auffret et al., 2015). Moreover, spatial analyses need to be applied where landscape structure is described and quantified and have to consider both the conservation qualities inside the sites and the restoration needs in the matrix outside the sites. Biodiversity surrogates, such as land cover and vegetation, are commonly used to represent biodiversity values at the landscape scale (Sinha et al., 2014), whereas the conservation status of PAs is often assessed using species' status. Expert knowledge-based habitat suitability models, combining both vegetation cover data and the focal species approach are effective tools for biodiversity assessment in forest management (Edenius and Mikusiński, 2006).

Biogeographic variation, socio-economic diversity, and relatively dense human population with a long land-use history, pose many challenges to pan-European conservation (Henle et al., 2008; Kati et al., 2014). The Natura 2000 (N2k) network was established to protect the most valuable and threatened species and habitats in the European Union (EU) (CEC, 1992; Evans, 2012). Moreover, N2k is expected to form the backbone of the European Green Infrastructure, defined as network of areas designed and managed to mitigate fragmentation and increase the spatial and functional connectivity between protected and unprotected areas, as well as to deliver a wide range of ecosystem services (Maes et al., 2015; EC, 2018; Hermoso et al., 2020). Currently, the EU member states are in the process of implementing Green Infrastructure (Slätmo et al., 2019).

At present, N2k encompasses 18% (784,252 km^2) of Europe's landmass and 6% (551,899 km^2) of marine environment across all 28 EU member states (EC, 2019). It includes Special Protection Areas designated under the Birds Directive (EPCEU, 2009) and Special Areas of Conservation designated under the Habitats Directive (CEC, 1992). According to the Habitats Directive, EU member states are required to manage natural habitats and species to reach or maintain 'favorable conservation status' (Epstein et al., 2015; Orlikowska et al., 2016). The N2k network encompasses a wide diversity of protection levels (often linked to national-level formal protection designations) ranging from areas where all human activities are prohibited to areas where conservation is combined with sustainable management of natural resources (CEC, 1992; Orlikowska et al., 2016). N2k is critical for the implementation of the countries' international obligations, in particular the Convention on Biological Diversity (CBD, 2018) and the EU Biodiversity Strategy to 2020 (Dudley et al., 2005; COM, 2011).

The establishment of the N2k network in Sweden began in 1993 and currently there are 4539 sites encompassing ca. 13% of the total land area (57,909 km^2 including inland waters) and 20,036 km^2 of marine environment (SCB, 2019). The terrestrial N2k site selection has largely built upon the network of previously existing PAs formally protected at the national level. Currently, 86% of the terrestrial N2k areas in Sweden overlap with nationally designated PAs (SCB, 2019). Overall, the Swedish N2k network encompasses ca. 18,834 km^2 of forest, corresponding to about 7% of the total forest area in Sweden. To date, the actual effectiveness of the N2k network in Sweden has not been studied quantitatively. Spatial considerations concerning its functionality as habitat of species of conservation interest is particularly relevant since the Swedish terrestrial N2k sites vary greatly in size, with the largest site of 554,675 ha (SE0810080 Vindelfjällen) corresponding to the combined area of the 3800 smallest sites. Such great variation obviously requires developing object-adjusted management strategies to secure favorable conservation status of habitats and species in particular sites.

In this study, we used habitat suitability index modelling to assess the effectiveness of the Swedish N2k sites in providing suitable habitat for selected typical bird species of the EU Habitats Directive's 'Western Taiga' habitat type (EU-code: 9010; SEPA, 2011): lesser spotted woodpecker (LSW; *Dryobates minor*), Siberian jay (SJ; *Perisoreus infaustus*) and hazel grouse (HG; *Tetrastes bonasia*). As per the Habitats Directive (CEC, 1992), the conservation status of a habitat's typical species is considered a measure of the conservation status of a natural habitat. Our choice of species was based on the fact that the Western taiga is the habitat type covering the relatively largest proportion (21%) of the Swedish N2k sites' area (SEPA, 2011) and that these species represent a range of different forest environments (see Angelstam et al., 2004). Moreover, they have been used as focal species in modelling of forest management impact on biodiversity in Fennoscandia, and in practical forestry planning (e.g. Manton et al., 2005; Öhman et al., 2011).

The objectives of this study were to: 1) quantify effective suitable habitat area in N2k sites in Sweden for these typical species with and without accounting for the neighborhoods' habitat quality; 2) examine effective suitable habitat area within N2k sites along the north-south vegetation gradient and calculate their proportional contribution to the total amount of habitat in Sweden; and 3) assess the functionality of N2k forest habitats and how forests outside the sites affect habitat functionality inside N2k. We discuss the results in relation to the PAs sizes and the existing regional conditions as important prerequisites for attaining a functional Green Infrastructure.

2. Materials and methods

2.1. Study area and model approach

The study area encompassed all terrestrial N2k sites in Sweden. The habitat suitability index models used in this study were readily available for the three selected species (Edenius and Mikusiński, 2012; see also Table 1) and incorporated into the Heureka forest planning system of the Swedish University of Agricultural Sciences (Wikström et al., 2011; SLU, 2018a). These models are being increasingly implemented as tools in forest management in Sweden (Nordström et al., 2013). Similar modelling approaches for assessing habitat amounts for forest birds have been applied in earlier studies, e.g. by Manton et al. (2005) and Naumov et al. (2018) in Sweden and boreal Europe.

2.2. Input data

2.2.1. N2k sites

To delineate the N2k sites, GIS shapefiles of non-aquatic Sites of Community Importance and Special Protection Areas (SEPA, 2016a, 2016b) were used. Files were re-projected and merged in ArcGIS (ESRI Inc., 2015) into one combined file, and then converted into a raster with a final resolution of 25 m × 25 m to match the Swedish University of Agricultural Sciences' Forest Map projection and resolution (hereafter SLU Forest Map; SLU, 2016). The raster was then re-classified to value "1" for pixels located inside N2k sites and "0" for pixels located outside. Then we used the raster as a mask to extract habitat data within the N2k sites later to be used by our models.

To detect whether the size of habitat area differed between regions of Sweden, we assigned each N2k site to a vegetation zone (Alpine, Northern Boreal, Middle Boreal, Southern Boreal, Hemiboreal and Nemoral) according to Gustafsson and Ahlén's (1996) classification.

2.2.2. Forest variables

To identify suitable habitat, we used the SLU open-access Forest Map data (SLU, 2016). It was created by the Remote Sensing Laboratory of the Department of Forest Resource Management, Swedish University of Agricultural Sciences, by combining data from the Swedish National Forest Inventory with satellite image data using the k-Nearest Neighbors (kNN) method described in detail by Reese et al. (2003). The SLU Forest Map provides information in raster-based format (25 m × 25 m) about the forest's age, height, and tree species' standing volume for major tree species (SLU, 2016). Reese et al. (2003) assessed the accuracy of the SLU Forest Map's forest variable estimates at the stand level for an area in southwestern Sweden. It showed 33% overall root mean square error for the estimates of total wood volume, and 23% for the age estimates.

In our models, we used the following SLU Forest map estimates of forest variables: stand age and standing timber volume (cubic meter stem volume per ha) for Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), lodgepole pine (*Pinus contorta*), European beech (*Fagus sylvatica*), birch (*Betula* spp.), oak (*Quercus* spp.) and, collectively, other deciduous tree species. Using ArcGIS (ESRI Inc., 2015), we computed (in raster format) standing volume for three groups: first for all tree species combined,

Table 1
Parameter values based on typical bird species habitat requirements (as defined by [a]Manton et al., 2005;[b]Wiktander et al., 1992;[c]Edenius et al., 2004;[d]Angelstam et al., 2004;[e]Åberg et al., 2003;[f]Åberg et al., 1995;[g]Jansson et al., 2004;[h]Wiktander et al., 2001; [i]200 ha as used by HEUREKA and also being intermediate value of reported Siberian jay's year-round home ranges (0.4–5 km^2; Bradter et al., 2018) used for creation of the habitat suitability models (Edenius and Mikusiński, 2012) based on the SLU Forest Map data (SLU, 2016)).

Parameters	Typical species		
	lesser spotted woodpecker	Siberian jay	hazel grouse
Pixel scale requirements (25 m × 25 m)	Habitat score 1.0	Habitat score 1.0	Habitat score 1.0
Stand age	≥60 years[a]	≥60 years	≥20 years[e]
Proportion of deciduous trees	≥50%[b]	n/a	≥15% and <40%[e]
Proportion of coniferous trees	n/a	≥70%	n/a
Proportion of spruce	n/a	≥25%[c]	≥25%[e]
Pixel scale requirements (25m × 25m)	Habitat score 0.5	Habitat score 0.5	Habitat score 0.5
Stand age	≥60 years[a]	≥30 and < 60 years	≥20 years[e]
Proportion of deciduous trees	≥25% and <50%[b]	n/a	≥5% and <15%[e]
Proportion of coniferous trees	n/a	≥70%	n/a
Proportion of spruce	n/a	n/a	≥25%[e]
Landscape scale requirements			
Habitat networks	≥40 ha[b]	≥50 ha[d]	≥20 ha[f,g]
Neighborhood window size	200 ha[h]	200 ha[i]	100 ha[a,g]

then for conifer and deciduous species separately. Secondly, we developed raster (25 m × 25 m) maps with proportions of coniferous species, deciduous species, and also spruce treated separately.

2.3. Calculations of effective habitat area at pixel and landscape scales

Our models calculated effective habitat area, defined as an area containing habitat necessary to meet the species' requirements as determined by the habitat suitability index model parameters (Table 1). Since LSW and HG are distributed throughout the whole country (ArtDatabanken, 2018), we used the entire area of Sweden for calculations of their effective habitat area. As the SJ range is limited to central and northern Sweden (ArtDatabanken, 2018), we estimated the final effective habitat area for SJ only within that region.

To calculate species-specific effective habitat area at both the pixel and the landscape scales, we ran our models entirely in ArcGIS environment (ESRI Inc., 2015), outside the SLU Heureka forest planning system. However, we used the same species-specific habitat suitability parameter values (Table 1) as in the Heureka system (Edenius and Mikusiński, 2012; SLU, 2018b).

For each species, the effective habitat area was calculated at two spatial scales: 1) individual pixels; 2) landscape scale. The spatial scale of individual pixels was defined as based solely on parameters from SLU Forest Map data (SLU, 2016) concerning 25 m × 25 m pixels and not taking into account the neighborhoods' habitat quality. The landscape scale was defined by applying landscape filter selecting only those pixels that in addition to fulfilling habitat quality were also located in the areas that fulfilled species' requirements at the landscape level (Table 1).

In the first step, we calculated pixel scale effective habitat area (PSEA), in the form of raster maps, at the spatial scale of individual pixels, for the habitat scores 1.0 representing good conditions and 0.5 representing moderately good conditions (Table 1), which we then combined into one raster (Fig. 1a and 1e). For example, for LSW the following conditions had to be fulfilled for a pixel to be given the habitat score 1.0: stand age >60 years and deciduous tree proportion of volume >50%, and for habitat score 0.5: stand age >60 years and deciduous tree proportion 25–50% (Table 1).

In the second step, the effective habitat at the landscape scale was calculated by applying species-specific measure of neighborhood using ArcGIS Focal Statistics tool (ESRI Inc., 2016) for a circular moving window with a radius of 798 m for LSW and SJ, and 564 m for HG (Fig. 1b and 1 f; Wikström et al., 2011; Edenius and Mikusiński, 2012) to the raster with pixel-level habitat scores 1.0 and 0.5. The Focal Statistics tool computed an output raster where the value for each output pixel was calculated as a sum of the input pixel values located within a species-specific circular moving window centered on that pixel (ESRI Inc., 2016). The sizes of moving windows were defined by species' habitat requirements as indicated by best available knowledge provided by the species experts (Table 1). For conservation of LSW, Wiktander et al. (2001) recommended predominantly deciduous forest patch of a minimum 40 ha that can be fragmented over a maximum of 200 ha, thus we selected 200 ha (r = 798 m) for the LSW neighborhood window size. Also for SJ, we selected 200 ha (r = 798 m) large neighborhood used in Heureka even if smaller home ranges were discussed (see Angelstam et al., 2004). The species demonstrates large variation in the year-round home ranges (from 0.4 to 5 km^2; Bradter et al., 2018) and therefore we assumed that 200 ha, being an intermediate value, is appropriate. Jansson et al. (2004) and Manton et al. (2005) define HG's habitat requirements as forest stands of minimum 15 ha and a critical threshold minimum of 20% suitable habitat in a 1 km^2 area, thus we used the 1 km^2 (100 ha; r = 564 m) as HG neighborhood window size.

In the third step, in our post-Focal Statistics analyses of effective habitat area at landscape scale, we identified pixels that are part of habitat networks consisting of ≥40 ha effective area within a 200 ha window for LSW (Wiktander et al., 1992), ≥50 ha within a 200 ha window for SJ (Angelstam et al., 2004), and ≥20 ha within a 100 ha window for HG (Fig. 1c and 1g; Åberg et al., 1995; Jansson et al., 2004; Manton et al., 2005).

In the fourth step, we calculated the landscape scale effective habitat area (LSEA) as the number of pixels for habitat score 1.0 and 0.5 that are located within the habitat networks identified in step three. To do this, we overlaid the raster with identified habitat networks created in step three with the pixel scale raster maps made in step one containing habitat score 1.0 and 0.5, respectively (Fig. 1d and 1 h). Next, the original N2k shapefile was used to tabulate area for each habitat score within each N2k site. The area of the moderately good habitat (habitat score 0.5) was divided by 2 following Edenius and Mikusiński (2012) in order to calculate the input of this stratum into effective habitat area.

The models first calculated the total effective habitat area of all forest land in Sweden, without distinguishing between outside and inside of N2k sites, at both pixel and landscape scales. Then the total effective habitat area within N2k sites (at pixel scale without buffers and at landscape scale both without and with buffers) was computed. The effective habitat area outside of N2k sites at the pixel and landscape scales, was calculated as the difference between the total effective habitat area obtained for entire Sweden and the effective habitat area inside of N2k sites (without buffers at pixel scale and with buffers at landscape scale).

2.4. Calculations of habitat estimates

In our analyses, we use the term "functional habitats" or "habitat functionality" *sensu* e.g. Mikusiński and Edenius (2006), who define it as "the degree to which a given forest environment fulfils the spatial requirements of a given species in terms of composition, quantity, configuration and temporal dynamics." Several other authors have used these terms in that sense, e.g. for forest birds (Angelstam et al., 2003a; Lazdinis et al., 2005; Manton et al., 2005) or butterflies (Vanreusel and Van Dyck, 2007; Turlure et al., 2010).

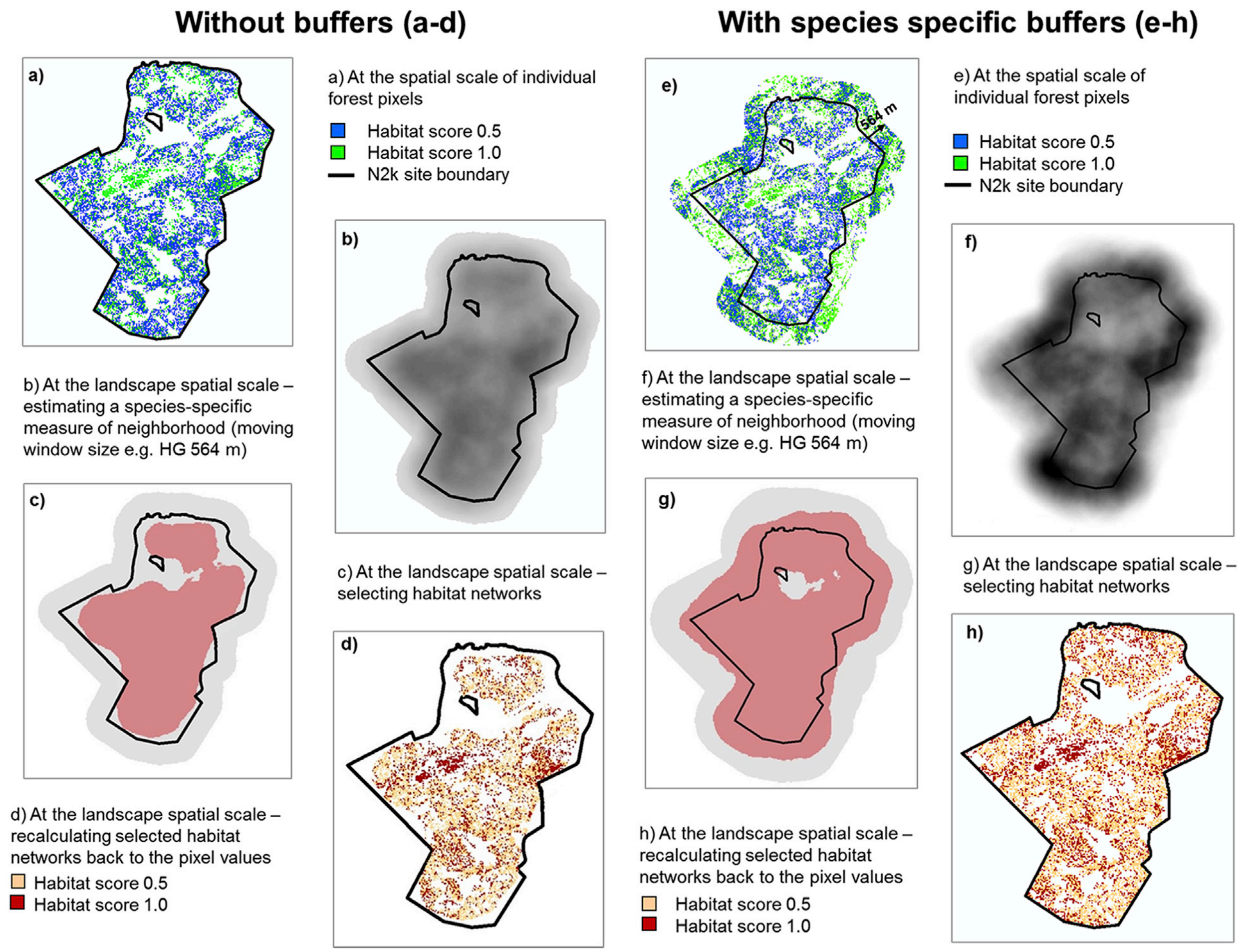

Fig. 1. Example of calculations of effective habitat area (here for hazel grouse (HG) for the N2k site SE0810096 Stenbithöjden) without species specific buffers (a-d) at a) the spatial scale of individual forest pixels (for habitat scores 0.5 and 1.0); at the landscape spatial scale - b) estimating a species-specific measure of neighborhood quality using ArcGIS Focal Statistics for a circular moving window (here for HG, r = 564 m, in grey); c) selecting habitat networks, here for HG consisting of ≥20 ha effective area (in coral) within a 100 ha window; d) recalculating selected habitat networks, here for HG, back to the pixel values for habitat scores 0.5 and 1.0; with species specific buffers (here for HG, r = 564 m; e-h) at e) the spatial scale of individual forest pixels (for habitat scores 0.5 and 1.0); and at the landscape spatial scale - f) estimating a species-specific measure of neighborhood quality using ArcGIS Focal Statistics for a circular moving window (here for HG, r = 564 m, in grey); g) selecting habitat networks, here for HG consisting of ≥20 ha effective area (in coral) within a 100 ha window; h) recalculating selected habitat networks, here for HG, back to the pixel values for habitat scores 0.5 and 1.0.

For the purpose of our analyses, we defined habitat functionality as the proportion of habitat which remains after applying a filter representing the species' landscape-scale requirements. Hence, we quantified habitat functionality for each N2k site by dividing its landscape scale effective habitat area (LSEA) by its pixel scale effective habitat area (PSEA) (online Appendix A1 Definitions and Formulas, Eq. (A.1)). In other words, this is the proportion of the initial number of habitat pixels which remains after filtering out pixels whose neighborhood pixels do not fulfill the species' requirements. We estimated the average habitat functionality for N2k sites located in the different vegetation zones. Moreover, we also calculated for each species habitat functionality at the vegetation zone level for areas inside and outside N2k sites. We defined habitat functionality inside N2k sites for each vegetation zone as the quotient of the sum of N2k sites' landscape-scale effective habitat area (LSEA) to the sum of N2k sites' pixel scale effective habitat area (PSEA) within the vegetation zone (Eq. (A.2)).

Then, we estimated the habitat functionality outside of N2k sites for Sweden as a whole as the quotient of the summed landscape-scale effective habitat area (LSEA) outside N2k to the summed pixel-scale effective habitat area (PSEA) outside N2k (Eq. (A.3)).

To assess the contribution of forest outside of the N2k sites to habitat suitability inside the N2k sites, we first used species-specific buffers (Fig. 1e), equal to 798 m (LSW, SJ) and 564 m (HG), to each N2k site (applied in GIS) and then administered the landscape filter representing the species' landscape-scale requirements (Fig. 1f). Next, we calculated the landscape scale effective habitat area for buffered N2k sites (LSEA_buffer_N2k); Fig. 1g and 1h). This was used for computing habitat increase defined as the increase in proportion of suitable habitat inside N2k sites after taking into account the quality of areas outside N2k (within buffers) measuring the effect of the neighborhood on the quality of habitat within N2k sites. It was calculated as a difference of landscape scale effective habitat area between buffered (LSEA_buffer_N2k) and non-buffered N2k site (LSEA_no_buffer_N2k), then divided by the landscape scale effective habitat of non-buffered N2k (Eq. (A.4)).

We estimated the proportion of habitat (%) for LSW, SJ and HG captured by the N2k sites by dividing the species' LSEA in N2k by the total LSEA in Sweden including N2k sites (Eq. (A.5)).

3. Results

Based on our LSEA calculations of effective habitat area, N2k sites contributed 10% (456,710 ha) of HG, 13% (535,520 ha) of SJ, and 51% (292,276 ha) of LSW suitable habitat in Sweden (Fig. 2). For comparison, figures obtained by using PSEA calculations were 9% (577,675 ha) of HG, 12% (673,259 ha) of SJ, and 27% (427,176 ha) of LSW suitable habitat in Sweden (Fig. 2). These figures can be compared to the total of 7% (1,883,447 ha) of Swedish forest land area within delineated N2k. Hence, the network can be considered highly effective at capturing LSW habitat and somewhat effective at capturing HG habitat. In northern Sweden, where SJ occurs, N2k sites capture 12% (1,688,913 ha) of the Swedish forest land area. Therefore, N2k sites are not more effective at capturing SJ habitat than north-Swedish forests in general: the proportion of the SJ habitat captured in N2k is roughly the same as the general proportion of forest captured by N2k in northern Sweden. Summed at the national level, the effective habitat area within N2k sites did not increase considerably when we accounted for the contribution of the forest located outside the N2k sites (based on the species-specific buffers; Fig. 2a). Adding the landscape filter yielded landscape scale effective habitat areas that were 32%, 20% and 21% smaller than effective habitat areas for the LSW, SJ, and HG at pixel scale, respectively (Fig. 2b).

The number of pairs of each species that could be supported by the effective habitat area at the landscape scale, obtained from our models for the whole country, differed from the estimated population sizes reported in Sweden (BirdLife Sverige, 2018) by +3% (LSW), −22% (SJ) and −4% (HG) (online Appendix Table A1).

We observed an obvious contrast between the northern and southern vegetation zones in their relative contributions to suitable habitats. The effective habitat area within N2k sites was largest for the Northern Boreal vegetation zone (Fig. 3) for all three species, followed by the Alpine zone. The Middle Boreal zone also contained relatively large effective habitat areas

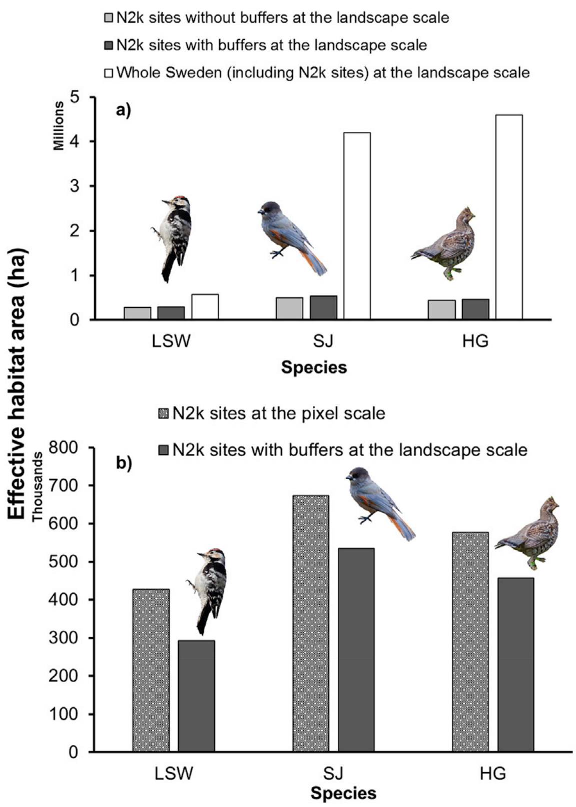

Fig. 2. Effective habitat area for lesser spotted woodpecker (LSW), Siberian jay (SJ) and hazel grouse (HG) at the landscape-scale (a) within N2k sites (light grey), within N2k sites accounting for the contribution of forest located outside the N2k sites (dark grey) and in whole Sweden (including N2k sites; white); (b) effective habitat area at the pixel (patterned) spatial scale without accounting for the contribution of forest outside the sites and at the landscape (dark grey) spatial scale accounting for the contribution of forest outside the sites for LSW, SJ and HG within N2k sites,. Data for SJ is restricted to its geographical range only (northern and central Sweden). Photos of LSW, SJ and HG are provided by Anders Tedeholm, Krister Melkersson and Thomas Österholm, respectively.

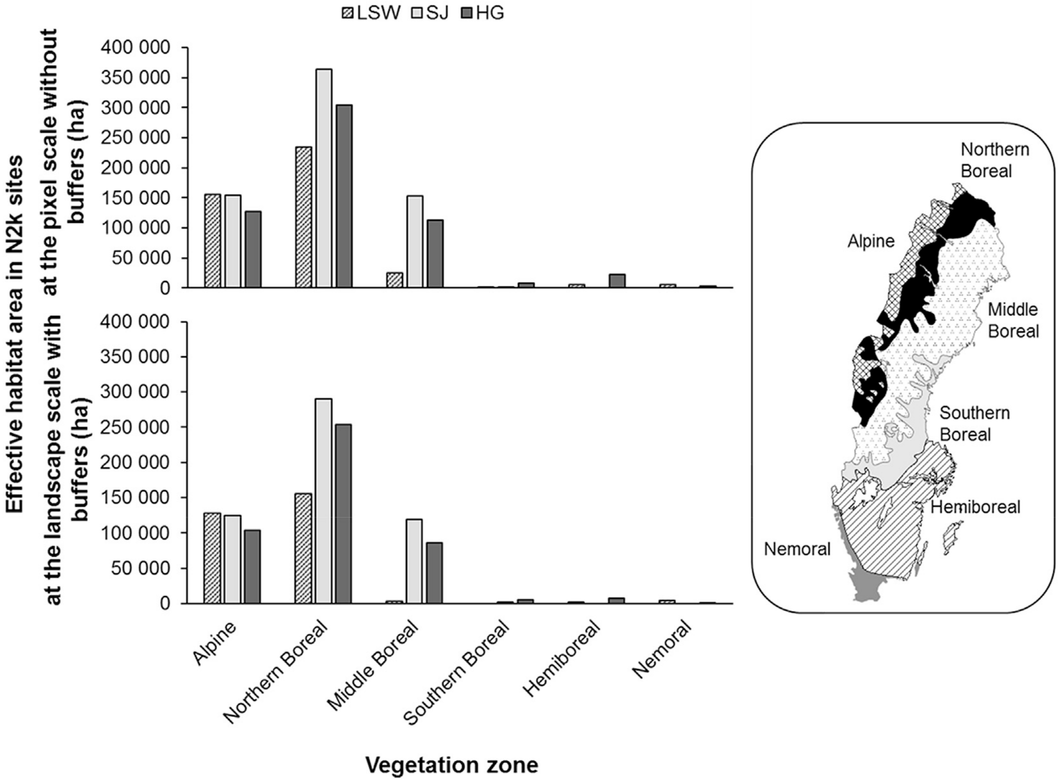

Fig. 3. Effective habitat area (ha) in N2k sites within six vegetation zones for the lesser spotted woodpecker (LSW), Siberian jay (SJ) and hazel grouse (HG) in the N2k sites at different spatial scales - pixel (i.e. not accounting for landscape-scale species requirement) and landscape (accounting for landscape-scale requirements) scales, with accounting for the contribution of forest located outside the N2k sites. Data for SJ is restricted to its range that does not include Hemiboreal and Nemoral zones.

within N2k for the SJ and HG, but little suitable habitat area for the LSW, especially when considering its landscape-scale requirements. The Southern Boreal zone provided very little suitable habitat for SJ and HG, and no suitable habitat at all for LSW, within N2k sites. The Hemiboreal and Nemoral zones contributed with very limited amount of suitable habitat for LSW and HG.

The habitat functionality of the N2k sites varied between vegetation zones (Fig. 4). Average functionality of the N2k sites for LSW was highest in the Alpine zone, followed by the Nemoral and Northern Boreal zones. For HG, the average functionality was higher in northern than southern vegetation zones. For SJ, average functionality was generally high, especially in the Middle Boreal zone. Moreover, the size of the N2k sites influenced their functionality for LSW and HG, with larger N2k sites, mostly present in Alpine, Northern and Middle Boreal zones, being more functional (Fig. 5a). For SJ, however, average functionality of N2k sites was not influenced by their size. Most of the N2k sites with suitable habitat for LSW and HG were of small size (1-500 ha) and of low functionality (3.1% and 26.1% respectively; Fig. 5a). For all three species, the largest average habitat increase resulting from taking into account the contribution of forest areas outside N2k (within species-specific buffers) was observed for N2k sites of 1–500 ha area (Fig. 5b).

Comparisons of habitat functionality within and outside N2k sites showed that for LSW, N2k sites were clearly more functional than areas outside N2k sites in all vegetation zones (online Appendix Fig. A1). For SJ, habitat functionality was quite similar inside and outside N2k sites, albeit somewhat higher inside than outside in the Alpine and Middle Boreal zones. For HG, habitat functionality was quite similar inside and outside N2k in the northernmost vegetation zones, but higher outside than inside N2k in the southern vegetation zones, especially in the Hemiboreal.

4. Discussion

Our study revealed important species-specific patterns superimposed on geographic and vegetation zone differences. For LSW, functionality was higher inside than outside N2k sites within all vegetation zones where the model identified suitable habitat. In contrast, for HG, the areas outside N2k had higher average functionality than the N2k sites in southern Sweden. The majority of N2k sites were of small size (<500 ha) and low functionality for LSW and HG. For SJ, however, the average habitat

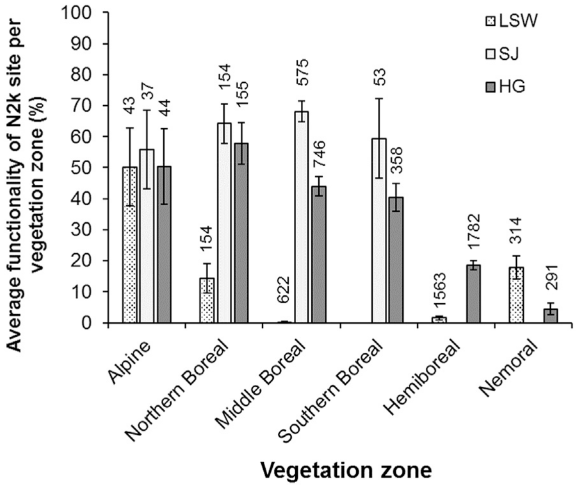

Fig. 4. Average functionality of the Swedish N2k sites per vegetation zone for lesser spotted woodpecker (LSW), Siberian jay (SJ) and hazel grouse (HG) with accounting for the contribution of forest located outside the N2k sites. The bars indicate 95% confidence intervals of the average functionality in each vegetation zone. The numbers above bars indicate the number of N2k sites in each vegetation zone. SJ does not occur in Hemiboreal and Nemoral vegetation zones. Sites with mean habitat functionality = 0 are included.

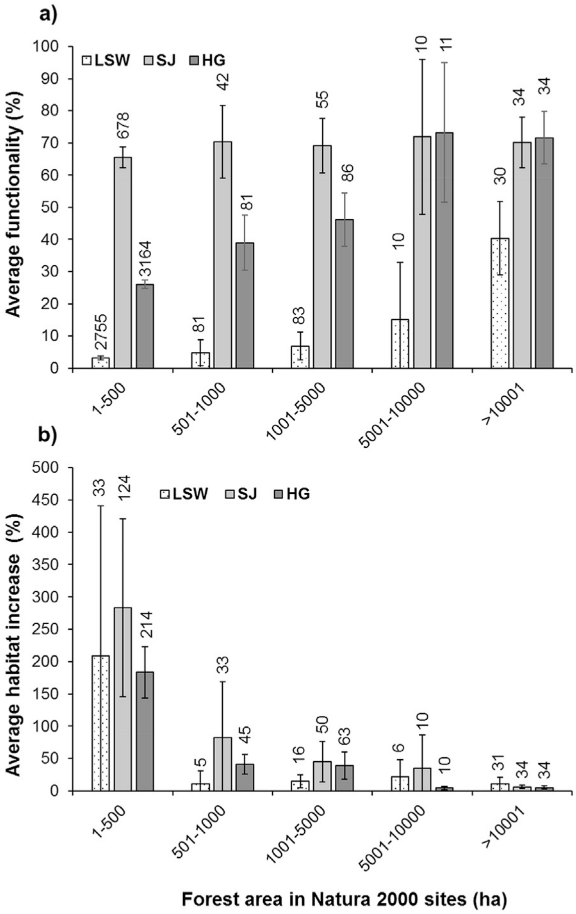

Fig. 5. Average functionality (a) of the Swedish N2k sites per forest area class (ha) with accounting for the contribution of forest located outside the N2k sites for lesser spotted woodpecker (LSW), Siberian jay (SJ) and hazel grouse (HG), and average habitat increase (b), defined as a the increase in the proportion of suitable habitat inside N2k sites after taking into account the contribution of the forest areas outside the sites' borders, per forest area class (ha) in each N2k site in Sweden at landscape scale. Sites with less than 1ha of effective habitat area at the landscape scale were removed from calculations of (b). Sites with habitat increase = 0 are included. SJ data is restricted to its range only. The bars indicate 95% confidence intervals of the average functionality (a) and average habitat increase (b) in each class of forest area. The numbers above bars indicate number of N2k sites in each forest area class.

functionality was generally high and did not vary much between N2k size classes or vegetation zones. The largest contribution of the areas outside N2k sites to habitat proportion within N2k was for the smaller sites.

The patterns of habitat suitability, contribution of N2k network, and functionality inside and outside of the network, varied among species. Since the N2k sites were more functional for LSW than the areas outside N2k sites in all vegetation zones, and since half of this species' habitat in Sweden is predicted to occur within N2k sites, effective conservation management of the sites can play a crucial role for delivering positive outcomes for this species (ArtDatabanken, 2018). For SJ, the generally high level of habitat functionality both inside and outside N2k is somewhat surprising and requires further investigation. It is possible that our model for SJ overestimates habitat availability, especially outside N2k, as it does not consider vertical stratification of the forest vegetation, an important factor for SJ protecting their nests against visually oriented corvid predators and extreme weather (Eggers et al., 2005). The higher functionality of HG habitat outside than inside N2k sites in southern Sweden, particularly in the Hemiboreal zone, suggests that today's south-Swedish managed forest landscapes offer relatively good potential for maintaining favorable habitat conditions through appropriate management.

Habitat suitability index models have been employed in many studies addressing historical, current and future habitat availability (e.g. Angelstam et al., 2003b; Öhman et al., 2011; Zohmann et al., 2013; Naumov et al., 2018). However, the results of such modelling are sensitive to parameter values and to the quality of the input data (e.g. Manton et al., 2005). In our study, this challenge is apparent in the case of LSW. Although the amount of LSW habitat calculated by our model for the whole of Sweden was sufficient to support the current population estimate of 7000 pairs (online Appendix Table A1), the predicted spatial distribution is somewhat questionable. Indeed, Ottosson et al. (2012) showed that the majority of LSW individuals occurs in Nemoral, Hemiboreal and Southern Boreal zones, while our model detected most suitable habitat in N2k sites of the Alpine and Northern boreal zones. This discrepancy may be partly due to the fact that vast areas of mountain birch forest (dominated by *Betula pubescens* ssp. *czerepanovii*) occur in the Alpine zone. This is an ecosystem with much lower productivity than south-Swedish deciduous forests, thus probably supporting fewer LSW pairs per unit area. Also in the Northern Boreal zone, deciduous forests have much lower productivity on average than the southern deciduous forests where the habitat suitability model for LSW was developed. Moreover, other factors, e.g. climate, and low temperatures in winter increasing adult mortality, may restrict LSW's occurrence in the northern regions (Selås et al., 2008). In our LSW model, Wiktander's et al. (1992) threshold of >40% deciduous tree cover was used as a guidance and not a firm threshold for the assessment of habitat value at the pixel level with proportion of deciduous trees $\geq$50% for the habitat score 1.0 and $\geq$ 25% and <50% for the habitat score 0.5 (Table 1). Moreover, older stands with $\geq$25% deciduous trees are officially used in Sweden (e.g. in Swedish National Environmental Objective "Sustainable Forests"; Swedish Forest Agency, 2019a) to define deciduous-rich forests. Further research will be necessary to explore regional variation in habitat requirements of LSW.

In addition, as shown by Grahn (2008), LSW is able to utilize landscapes with less deciduous component than used in the Heureka model. Moreover, LSW can use habitats outside of the forest land mapped by the SLU Forest Map (SLU, 2016), such as deciduous-dominated rural/peri-urban parks and other habitats with sparsely distributed, but large and old deciduous trees. As demonstrated by Mikusiński et al. (2003), the distribution of deciduous stands and trees in forest landscapes of Sweden is highly skewed towards settlements and their boundaries, while contiguous forests, except for southernmost Sweden, have a very small deciduous component. Deciduous trees and deciduous-rich stands of smaller size or close to settlements are not included in Heureka model nor in the SLU Forest Map data (Manton et al., 2005; SLU, 2016) we used, since it is largely limited to the forest land and is most accurate for areas larger than few hundred hectares. Reese et al. (2003) point out that the SLU Forest Map data (SLU, 2016), used in our study, does not perform well in detecting deciduous vegetation. Our results may be also influenced by the fact that the SLU Forest Map tends to underestimate the age of "old" forests and overestimate the age of "young" forests, making it challenging to distinguish, e.g. 80 year old and 180 year old forests (Mats Nilsson, personal communication, 2018).

Another aspect to consider is that some deciduous-rich forest stands form linear landscape features (e.g. riparian habitats). When applying a landscape filter in the form of a circular moving-window tool, such landscape features, even if spatially connected, are often omitted because there is not enough habitat measured in the circular neighborhood window i.e. within the 798 m radius. According to Lazdinis and Angelstam (2005), riparian habitats are quite rare in the production forest landscape of Sweden compared to naturally dynamic boreal landscapes.

Grahn (2008) ran LSW habitat model for forests along Ume River, northern Sweden, and compared the LSW-model generated effective habitat area with the species' inventory in the same region. She concluded that there was a good match between the models and the LSW inventory results for that area. Sensitivity analysis of the LSW habitat model, used in the Heureka planning system, conducted by Norman (2015) showed larger effective habitat area in northern Sweden (Västernorrland) than in central parts of the country (Örebro and Gävleborg). Manton et al. (2005) carried out sensitivity analysis for modelling habitat suitability for LSW and HG using SLU Forest Map (SLU, 2016; a.k.a. kNN) and concluded that the data concerning deciduous component was not very accurate. Palmgren (2016) found that locally available detailed Vegetation Map was much more efficient than SLU Forest Map (SLU, 2016) in detecting areas with LSW observations in south-west Sweden. Further research will be necessary to improve the accuracy of the model for LSW, perhaps using newly available data Forestry Maps (Swedish Forest Agency, 2019b) obtained through laser scanning of Sweden's forest land possibly in combination with the new National Land Cover data (Ahlcrona et al., 2019).

There is an apparent geographical bias in the distribution of N2k sites, in particular with respect to large and more functional sites being predominantly located in the sparsely populated Scandinavian Mountains. This distribution is linked to the distribution of nationally designated PAs largely overlapping with N2k sites (Nilsson and Götmark, 1992): many of the largest nature reserves and national parks which are part of N2k are concentrated in northwestern Sweden. Nevertheless, the intensified use of the unprotected matrix in northern Sweden as a whole has largely disrupted connectivity in forest landscapes, which challenges the establishment of functional green infrastructure (Svensson et al., 2019). The future of the currently unprotected, but still largely intact forests of this region is currently being debated (Jonsson et al., 2019).

Our results show that smaller N2k sites are much less effective in providing habitat for forest species of conservation interest. The impact of the outside matrix becomes more apparent in small sites due to edge effects (Svensson et al., 2019). This is problematic, because these small sites strongly dominate in number (e.g. 83% of sites providing habitat for SJ, 93% for LSW and 94% for HG are smaller than 500 ha). We also found that the forest areas outside N2k site boundaries but within species-specific buffers are very important for securing the conditions for the analyzed species in small N2k sites. This means that the way the forest-neighboring N2k are managed is of crucial importance for the effectiveness of smaller sites in providing habitat for those species. The Habitats Directive clearly states that activities outside a N2k site should, with few exceptions, only be allowed if they do not adversely affect the integrity of the site (CEC, 1992). It also urges the EU Member States to "endeavor to improve the ecological coherence of N2k by maintaining, and where appropriate developing, features of the landscape which are of major importance for wild fauna and flora" (CEC, 1992). Therefore, although there is no legal requirement for buffer zones around N2k sites, we suggest that the areas outside N2k sites should be managed in ways that maintain and possibly enhance the value of these PAs (while simultaneously acknowledging the importance to improve or maintain habitat quality within the PAs; see Häkkilä et al., 2018). This suggestion is particularly applicable in the case of smaller, forest-dominated sites surrounded by production forests. There is a variety of alternatives to traditional clearcut forestry measures that could be applied in such buffer zones (e.g. Lindenmayer et al., 2006). The size of such zones could be related to the spatial key species' requirements at particular site. While the quality of the habitat outside of the N2k site is more important for the smaller than for the larger sites, larger areas can also be greatly influenced by the habitat outside when they are of elongated shape, consist of several smaller areas or contain non-forest areas, e.g. mires, lakes or rivers.

The forest land in Sweden is dominated by largely modified landscapes consisting of many small remnants of natural areas of high conservation value embedded in a matrix of human-made or semi-natural habitats (Jongman, 2002; Svensson et al., 2019). N2k sites are strongly influenced by this matrix (Orlikowska et al., 2016). In the present study, we show that by including landscape requirements, the habitat quality for LSW, SJ and HG in N2k sites in Sweden is lower than if only local (pixel) level quality is considered, exemplifying the impact of increasing habitat fragmentation. Enoksson et al. (1995) revealed that fragmentation of deciduous forest within coniferous forest landscape can have serious detrimental effects on forest-living species dependent on deciduous trees. This raises important concerns for forest management practices and conservation. For the species covered in our study, such habitat fragmentation is especially important for LSW and HG, since both depend on deciduous tree species for foraging and/or nesting (Angelstam et al., 2004). Moreover, HG may be especially vulnerable to forest fragmentation, because of its poor dispersal capacity and requirement of closely located (0.2–2 km) habitat patches of minimum 25 ha in size (Åberg et al., 1995). Fragmentation may hinder colonization of isolated patches of suitable habitat even in forested landscapes, especially intensively managed (Åberg et al., 2003), leading to establishment of small and isolated populations particularly vulnerable to extinction for demographic reasons (Harris, 1984). Similarly, the SJ is sensitive to forest habitat fragmentation due to poor dispersal capacity and reluctance to crossing open areas (Fabritius, 2010). Creating strong dispersal barriers may lead to restricted gene flow between subpopulations, especially for species with high site fidelity such as SJ (Uimaniemi et al., 2000).

Currently, we are witnessing considerable progress towards achievement of the Aichi Target 11 globally, with only 2% of PA coverage needed to achieve the global target (CBD, 2018). In the EU, the N2k network has expanded notably in number and area of sites and thus greatly contributed to the global target. However, achievement only in terms of PA area coverage is not sufficient to stop the ongoing biodiversity decline. What is most important in assuring effective protection of species and habitats is the functionality of these PAs and this is still lacking for a large proportion of PAs (Angelstam et al., 2003a; Hedwall and Mikusiński, 2015). A key aspect of the habitat functionality of PAs is their connectivity (sensu Hanski, 1999, 2011); according to Saura et al. (2018), worldwide only 30.5% of countries currently meet the Aichi Target 11 connectivity requirement. Saura et al. (2018) also show that the protected connected land (% of biome land area) for the boreal forests/taiga biome is only 4.8%; for Sweden the values range from <30% in the southern, <2% and <5% in the central parts and <17% in the northwestern mountain region. This is particularly problematic in the light of ongoing climate change, as its impacts are more severe in fragmented landscapes (Mantyka-Pringle et al., 2012). Identifying gaps in the functionality and effectiveness of the N2k network for protecting particular species, as done in the present study, could be seen as a starting point when designing functional Green Infrastructure, with the key aim of improving connectivity and functionality of small and isolated N2k sites.

5. Conclusions

Based on our results, we argue that while the N2k network in Sweden has a potential for conserving suitable habitat for typical bird species, its quality and favorable conservation status are affected by the matrix outside the PAs. Hence, management plans for the sites should also include conservation and restoration measures in the matrix, especially when the site's size is small. We recommend creation of buffer zones around N2k sites. Their spatial extent and management should be determined using the specific landscape level requirements of the habitat's typical species and employing the best available habitat data. The spatial aspects of habitat suitability should be incorporated in national and regional Green Infrastructure implementation.

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Declaration of competing interest

The authors declare no conflict of interest (financial, personal or other relationships) with other people or organizations within three years of the beginning of the submitted work that could inappropriately influence or be perceived to influence our work.

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Appendix A. Supplementary data

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