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RESEARCH ARTICLE

Identifying functional landscapes in Sweden for semi-natural grasslands and old-growth oaks (*Quercus robur*) based on habitat thresholds

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Abstract

Context The loss of biodiversity due to habitat destruction has been identified as a critical global issue. There is an urgent need for landscape-based guidelines for critical levels of habitat amount in conservation work.

Objectives The aims were to identify habitat amount thresholds for species associated with old oaks and semi-natural grasslands, and to map functional areas and areas with habitat mismatch to guide conservation and restoration planning.

Methods We used spatial data on the distribution of old oaks (*Quercus robur*) and semi-natural grasslands in southern Sweden, combined with an extensive dataset of occurrence records for species associated with these habitats. Presence and absence of 102 species in grid cells in relation to habitat amount were analysed using binomial GLMs weighted by survey effort.

Results A total of 86 species showed a significant positive relationship between occurrence and habitat amount and these relationships were used to identify habitat thresholds. Species-specific threshold values within each habitat type ranged from low to high, showing considerable variation in habitat requirements. The mapping of functional areas showed clear patterns in the study area with large differences between regions. However, there were also large regions showing a habitat mismatch, i.e., occurrence of species in areas with habitat amounts below the estimated thresholds suggesting potential extinction debts. Our analysis shows that by prioritising habitat restoration sites it is possible to make them fully functional in the future, offering tools for cost-effective nature conservation.

Conclusions The approach here, using extensive, partly citizen science data and relatively simple models to provide conservation practitioners and planners with decision support maps, can be a useful tool to tackle biodiversity loss. However, threshold values should be interpreted as minimum targets, and complementary consideration of habitat connectivity and climate change is recommended.

Keywords Habitat thresholds · Biodiversity · Functional landscapes · Cost-effective conservation · Spatial conservation priority

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Introduction

Loss of biodiversity has been identified as one of the critical global problems, threatening ecosystem functioning and thus the basic life support for humanity (Cardinale et al. 2012; IPBES 2019; Jochum et al. 2020). Steffen et al. (2015) identified biodiversity loss as one of the crucial Earth-system processes, and they concluded that there is a high risk that the current extinction rate of species is beyond the planetary boundaries for a stable Earth system. The current species extinction rate is estimated to be 1000 times higher than natural background rates and is likely to be 10,000 times higher in the future (de Vos et al. 2015). Among the major drivers behind the high extinction rate are human-caused habitat loss and degradation (Newbold et al. 2016; Powers and Jetz 2019) resulting in fragmentation of natural habitats (Haddad et al. 2015), alongside other threats such as climate change and overexploitation (Maxwell et al. 2016). In fragmented landscapes affected by habitat loss, carrying capacity decreases, reducing the number of individuals of a species (Foley 1994). This population decline increases extinction risk, which is further exacerbated by decreasing fragment area and increasing isolation between fragments (Andrén 1994; Bergman & Landin 2001; Chase et al. 2020), ultimately leading to extinction from stochastic events in small populations (Lande 1993). Several theoretical and empirical studies have shown that this decrease in survival probability is non-linear (Lande 1987; With and King 1999; Swift and Hannon 2010). At a certain threshold of habitat within the landscape, any further decrease leads to a rapid decline in survival rates. It has been shown that extinctions come well before the disappearance of the last habitats (Fahrig 2002). An empirical example of this is the white-backed woodpecker (*Dendrocopos leucotos*) in Sweden and Finland, where the extinction risk accelerated once the landscape consisted of less than 17% of suitable habitats, and extinction occurred if the level went below 9% (Carlson 2000). Similar patterns of non-linear habitat thresholds have been shown for butterflies in semi-natural grasslands (Bergman et al. 2004), woody plants on islands (Zhang et al. 2021) and for forest birds (Ocampo-Ariza et al. 2019). Identifying such habitat thresholds for species survival is crucial for conservation efforts in landscapes experiencing habitat loss and suffering from local species extinctions (e.g., Ceballos and Ehrlich 2002). Another important aspect of species conservation in fragmented landscapes is to identify the relevant spatial scales to which species respond to habitat features (Bergman et al. 2012; Monroe et al. 2022). The resulting response of a species to a particular spatial scale is a combination of the species' traits and underlying ecological processes (Stuber and Fontaine 2019). Identifying the spatial scale of species-landscape relationships is thus also vital in identifying functional areas for conservation planning and management measures (Boyd et al. 2008; Jarzyna and Jetz 2018).

Europe is one of the regions most affected by habitat loss, resulting in significant regional declines in species and an urgent need for conservation policies (Van Swaay et al. 2006). Several habitats have been affected in Europe, e.g. temperate broadleaf forest and semi-natural grasslands with only a fraction left undisturbed (Hannah et al. 1995; Picó and Van Groenendael 2007). Determining how much habitat within a landscape is sufficient for species survival is a question frequently posed by conservation practitioners. However, answering this question requires data that are both time-consuming and expensive to collect (Balmford and Gaston 1999; Hermoso et al. 2013), which makes conservation work difficult. Furthermore, most conservation work is done by practitioners with limited budgets and time for complicated data analyses. A large proportion of the conservation work done by practitioners may, therefore, be unsupported by scientific evidence partly due to the lack of data and the difficulty of accessing and processing the published scientific literature (Pullin & Knight 2005; Cook et al. 2010).

There is clearly a need for readily available data and simple but sound analysis methods that practitioners can use. In this study, we use an extensive dataset of species occurrence records for taxa associated with old oaks (*Quercus robur*) and semi-natural grasslands, combined with spatial data on the distribution of these habitats across a large region in southern Sweden. This novel approach can provide cost-effective and transparent guidelines for practitioners on where and at what spatial scales conservation actions should be focused. We do this by identifying functional landscapes for species, defined here as regions where habitat amount exceeds the threshold associated with a 50% probability of species occurrence (drawing on the functional landscape concept

of Poiani et al. 2000). While occurrence probability is a proxy that may not fully capture demographic viability, it provides a practical and scalable metric for landscape-level assessment. Furthermore, we aim to identify regions with a habitat mismatch—where species richness is higher than expected from habitat amount, indicating a potential extinction debt (Kuussaari et al. 2009)—that may be targeted for restoration. We use relatively simple models of species occurrence in relation to habitat amount, based on extensive data on species associated with old oaks and semi-natural grasslands.

Materials and methods

Study area

The study area encompasses a significant portion of southern Sweden, spanning 65,504 km^2, of which 54,908 km^2 is comprised of land (Fig. 1). The area belongs to the boreo-nemoral zone and is dominated by forests and agricultural areas (European Environment Agency, 2012). About 70% of the area consists of forests, where the majority are production forests dominated by *Picea abies* and/or *Pinus sylvestris* including deciduous trees as *Betula* spp. and *Populus tremula*. Small forest fragments of *Quercus robur*, *Fraxinus excelsior*, *Ulmus glabra* and *Acer platanoides* are also present. Arable fields cover 14% of the study area and semi-natural grasslands constitute 3.4% of the area.

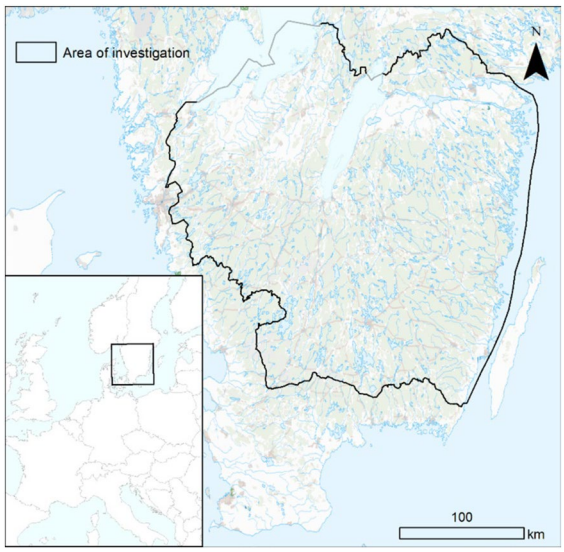

Fig. 1 The extent of the study area in southern Sweden

The study area was chosen due to its uniform ecological conditions and climate. However, there are large regional variations within the study area with regard to amount of agricultural and semi-natural grasslands areas and number of broadleaf trees due to the historical land use, which is a prerequisite for the analyses in this study. The coastal areas in the west, the islands Öland and Gotland and the very south of Sweden were considered too different regarding climate and bedrock, and were therefore omitted from the study area.

Habitat mapping

Two types of habitats were mapped in the study, one for species associated with old oaks (*Quercus robur*) (two subcategories, > 100 cm and > 150 cm in diameter respectively) and one for species dependent on semi-natural grasslands.

For oaks we used data from several regional mapping schemes of large individual oaks collected in the Swedish national species observation system (Artportalen.se, Project: Trädportalen, reported between 1980 and 2022). In these schemes, all oaks above 100 cm in diameter at breast height (dbh) have been mapped. In total, the data set contains 40,326 records of oaks larger than 100 cm in diameter and 3,626 above 150 cm. Almost the entire study area has been mapped for large trees, 42,152 km^2 (Figs. 5–7). Although records span a long time period, the majority were reported in recent years, and annual mortality of large oaks is low (Milberg et al. 2025). Some trees may have been lost or added over the survey period, but given the low turnover rate, we consider the cumulative data set a reliable representation of the current distribution of large oaks.

Areas of semi-natural grasslands were mapped using two sources, the Swedish National Meadow and Semi-natural Pasture Inventory database TUVA (https://jordbruksverket.se/tuva) and the Swedish Board of Agriculture database of EU subsidies to agricultural areas. The Swedish National Meadow and Semi-natural Pasture Inventory database contains data on the distribution of semi-natural grasslands in Sweden from a national survey that has been running since 2002 and contains data on 85,000 individual

semi-natural grasslands of high nature value (oligotrophic grasslands rich in plant species dependent on grazing or mowing) with a combined total area in Sweden of 340,000 hectares. All meadows and pastures were used in the analysis except those classified as "not restorable" (grasslands assessed during the national inventory as being too degraded for ecological restoration to a semi-natural state).

The Swedish Board of Agriculture database of EU subsidies to agricultural areas was used to identify additional grasslands receiving agri-environment payments. The subsidised grassland areas are classified in two classes: trivial grasslands and grasslands of higher conservation value. From that database (based on year 2014) we used only grasslands of higher conservation value (oligotrophic grasslands rich in plant species dependent on grazing or mowing). The two sources are complementary: TUVA offers comprehensive ecological site assessments, while the subsidy database captures additional grasslands of higher conservation value that may not yet have been identified and surveyed under the national inventory. The TUVA grasslands and the grasslands of higher conservation value from the subsidy database were merged into a single spatial layer for use in the analysis.

Species data

Data on species occurrences of terrestrial plants, lichens, fungi, and invertebrates were obtained from several different sources and cover the period from 1980 to 2014. In total, 5,700,341 species records were obtained from the different sources. The majority of the records came from the database Swedish Species Observation System (https://www.artportalen.se/). The others came from a number of sources: a private fungi database, County Administration Board surveys of semi-natural grasslands, municipality surveys, a plant species survey from the county of Småland and various scientific projects (Andersson et al. 2015). Observations with a precision lower than 5 km, or outside the focus area were excluded, leaving 4,898,150 observations. These background observations were used to account for spatial variation in survey effort when weighting species occurrence records in the analysis (see "Modelling of habitat thresholds" section, Modelling of habitat thresholds).

Selection of focal species

A list of species connected to oaks was compiled based on species information mainly from the Swedish Species Observation Centre (https://www.artportalen.se/). From this large list of species, a selection of focal species (Lambeck 1997) was made based on the following criteria: (i) heavily dependent on the tree species or habitat, (ii) well distributed and fairly common, (iii) well known (readily identifiable by both professionals and experienced citizen scientists, ensuring a higher rate of reliable reports).

For oak trees a total of 21 focal species were identified, all with > 80% of the records being on oaks in the Swedish Species Observation Centre. Two of the lichen species, *Buellia violaceofusca* and *Lecanographa amylacea* were 2018 identified as being the same species, based on the fungal component alone, but with different photobionts (Ertz et al. 2018). Although now considered conspecific, they are treated as separate functional units in this study owing to their distinct ecological requirements and association with oaks of different ages (Johansson et al. 2012).

For semi-natural grasslands, 81 focal species were identified using a national list of indicator plant species (Eneland 2017) together with butterflies and day-flying moths classified as grassland dependent (Van Swaay et al. 2006; Kuussaari et al. 2007; Krauss et al. 2010) and one red-listed grasshopper species highly dependent on semi-natural grasslands. These groups were selected based on their ecological relevance as grassland indicators and their good representation in the Swedish Species Observation System. Only one grasshopper species met the criteria of being both red-listed and strongly associated with semi-natural grasslands, as other Orthoptera in the region are more generalists. Other taxa such as birds were excluded because they respond to habitat at broader spatial scales or have insufficient data at the required resolution. The total number of observations for the focal species was 143,504.

Identification of relevant scale of response

In order to identify the relevant scale of responses for our species groups we reviewed the literature for multi-scale studies in northern Europe. We focused on landscape-level scales, as we aimed to assess the

effect of the surrounding landscape on species occurrence rather than site-level habitat quality, and therefore only included studies with scales larger than 100 ha, i.e. above site level (Supplementary material 1, Table S1). As expected, the scale of response varies between studies and species groups, from site level (field margin width) for vascular plants in one study (Dainese et al. 2015), to large regional scales up to a 64 km radius for oak-dependent lichens (Ranius et al. 2008). However, despite the limited number of studies (n = 9), spatial scales around 5–15 km radius dominate. Based on these results, habitat amount in the study area was mapped at two spatial scales, grids of 5 × 5 km and 15 × 15 km to address two relevant spatial scales.

Modelling of habitat thresholds

Species occurrences and habitat amount (measured as the number of oaks ≥ 100 cm dbh, the number of oaks ≥ 150 cm dbh, or the area of semi-natural grasslands in hectares) were aggregated in non-overlapping grids of 5 × 5 km and 15 × 15 km across the study area. The two oak diameter classes represent structurally different habitat resources, as larger oaks typically support greater abundances of cavities, dead wood, and complex bark structures important for distinct species assemblages (Ranius et al. 2008; Bergman et al. 2012). For each grid cell, the presence or absence of each focal species was recorded together with the amount of relevant habitat.

Using species data from the Swedish Species Observation System and other sources means that there is some spatial bias in survey coverage and effort. To account for this, we calculated background observations of species belonging to the same broad taxonomic group as the focal species: insects (Hymenoptera, Hemiptera, Orthoptera, Coleoptera, Lepidoptera), epiphytes (bryophytes and lichens), vascular plants and fungi. These 4.8 million background observations were used to weight species occurrence records following the ignorance function of Ruete (2015):

$$I = \text{threshold} / (\text{observations} + \text{threshold}),$$

where 'observations' is the number of background observations in a given grid cell and 'threshold' is the number at which there is a 50% probability that absence of a focal species reflects true absence. We set the threshold to 20, meaning that 20 background observations yield an ignorance score of 0.5 (Ruete 2015). This choice was evaluated by repeating analyses with alternative threshold values (10 and 50), which showed that the rank ordering of species thresholds was consistent, though model coefficients shifted slightly and z-values decreased for most species at higher threshold values (Supplementary material 2, Table S2). The spatial distribution of survey effort (background observations per grid cell) is shown in Supplementary material 3, Fig. S1.

Presence and absence of each species in each grid cell was analysed using a binomial GLM with a logit link, with habitat amount as the explanatory variable and I as weight. The habitat amount required for a 50% probability of occupancy (the 50% habitat threshold) was calculated. Sensitivity was assessed using 1,000 bootstrap resamples; the 5th and 95th percentiles illustrate the uncertainty interval. We defined the habitat threshold as the habitat amount at which the probability of occurrence equals to 0.5, following the LD50 analogy of Rueda et al. (2013), while acknowledging that this is a conventional rather than ecologically derived threshold. To assess sensitivity, we calculated thresholds also at P = 0.25 and P = 0.75 (Supplementary Table S2). Rueda et al. (2013) proposed using the inflection point (P ≈ 0.2) as an alternative threshold. However, for several species the predicted occurrence at zero habitat already exceeded 0.2, rendering this threshold inapplicable. In practice, the choice of threshold should reflect the conservation objective and the acceptable level of risk. Low thresholds (e.g., P = 0.2) risk underestimating the habitat amount needed to sustain a species, while very high thresholds (e.g., P = 0.75) may set unrealistically demanding targets. The conventional P = 0.5 threshold represents a reasonable compromise, balancing the risk of underestimation against practical feasibility. Model performance (AUC, sensitivity and specificity) is reported in Supplementary Table S2. All analyses were performed in R v. 4.2.2 (R Core Team 2022).

Mapping of habitat thresholds and habitat mismatch

The functionality of the landscape was estimated using the habitat thresholds for individual species and the spatial distribution of habitat amount. Landscape

functionality was mapped using four threshold levels, representing a gradient from less sensitive species (requiring low habitat amounts) to very sensitive species (requiring high habitat amounts). For oak-dependent species, for example, regions were mapped based on the number of oaks ≥ 100 cm dbh within 15 × 15 km grid cells needed to fulfil the habitat thresholds for a minimum of 2, 6, 13 and 18 species, respectively. We used fixed, non-overlapping grid cells; we acknowledge that this may underestimate habitat availability for species near cell boundaries, as suitable habitat in adjacent cells is not accounted for. However, this approach ensures spatial independence among sampling units and is consistent across the analysis.

Habitat mismatches were defined as areas where sensitive species occurred but the habitat amount was below their estimated threshold. These areas were generated by first mapping occurrences of all species with habitat requirements above a common threshold shared by many sensitive species. This produced a Boolean map indicating whether any such species was observed within a given grid cell. The actual habitat amount was then compared to the threshold, generating habitat mismatch maps showing where habitat was sufficient (positive values) or deficient (negative values).

Results

Threshold values for individual species

Of the 102 analysed species' responses to habitat amount at different spatial scales, 86 (84%) showed a significant positive relationship between occurrence and habitat amount. These relationships were used to identify habitat thresholds. Two typical curves for habitat thresholds for species with different accuracy in their responses are shown for two oak-dependent species: the fungi *Grifola frondosa* and the epiphytic lichen *Cliostomum corrugatum* (Fig. 2). For a 50% occurrence probability, *G. frondosa* had a threshold value of 135 trees above 100 cm in diameter within 2500 ha (5 × 5 km grid). The corresponding value for *C. corrugatum* was 46 trees. The bootstrap intervals for *G. frondosa* were larger than those of *C. corrugatum*, indicating a more consistent pattern for occurrences and absences in relation to the number of trees for *C. corrugatum*.

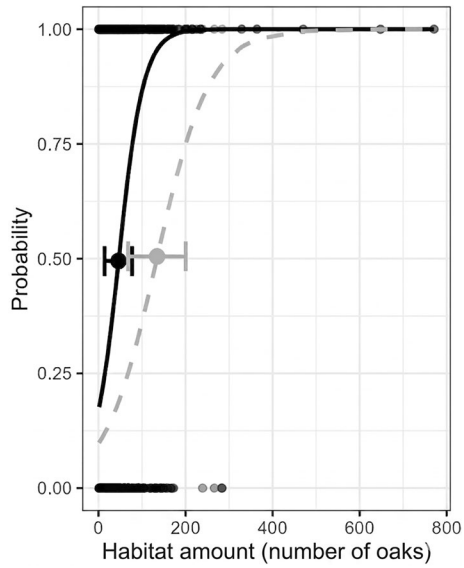

Fig. 2 Probability of occurrence for *Cliostomum corrugatum* (black lines) and *Grifola frondosa* (grey lines) in relation to the number of oaks above 100 cm in diameter within 2500 ha (5 × 5 km grid). The horizontal line at 50% probability shows an interval representing 5–95% of the bootstrapped values (see Fig. 3)

Threshold values for the focal species for each habitat showed similar patterns, ranging from species with lower thresholds to species with higher thresholds (Fig. 3). The most sensitive species have thresholds several orders of magnitude higher than the less sensitive species. For example, threshold values for oak-dependent species range from a minimum of 32 oaks above one meter in diameter within 5 × 5 km for *Chaenotheca phaeocephala* up to 512 oaks for *Gymnopus fusipes*.

Oak-dependent species show overall threshold values that are well within the available amounts of large oaks, while species dependent on semi-natural grasslands show a clear pattern of threshold values at the top end of the available area of grasslands. The discriminatory ability of the habitat models (AUC) was overall acceptable to excellent (Supplementary Table S2), but higher for oak-dependent species (mean = 0.77, range 0.58–0.91) than for semi-natural grassland species (mean = 0.67, range 0.40–0.90), consistent with the weaker habitat responses observed for the latter group.

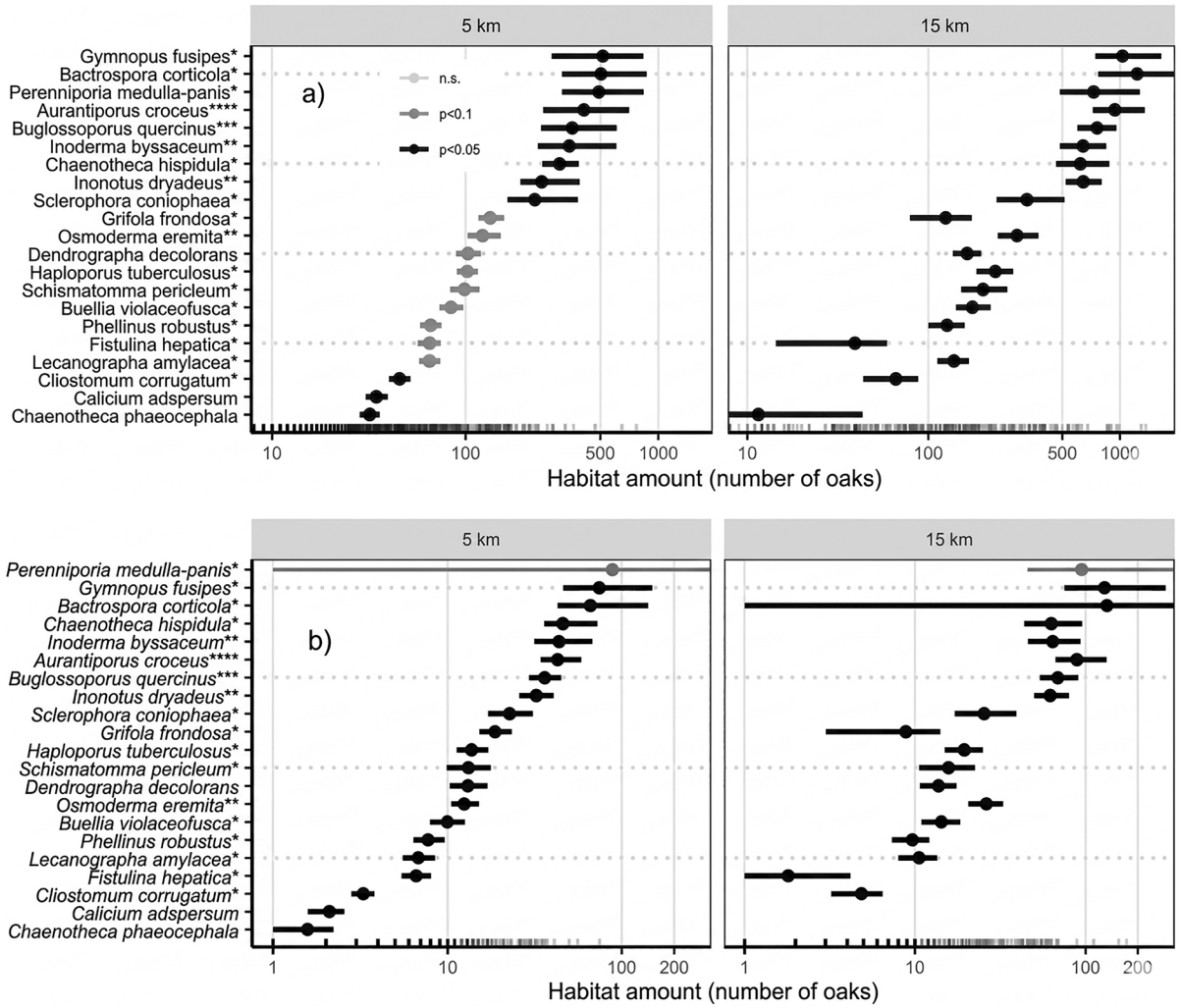

Fig. 3 The habitat amount required for 50% probability of occupancy and 5/95 percentile of bootstrap replicates for different habitats and spatial scales. **a** oaks > 1 m dbh, **b** oaks > 1.5 m dbh, **c** semi-natural grasslands (ha). The rug-plot at the bottom of each panel indicates observed amounts of habitat. Swedish Red List categories (SLU Artdatabanken 2020) are indicated by asterisks: NT=*, VU=**, EN=***, CR=****

Mapping of functional areas and areas with habitat mismatch

Using results from the habitat threshold, conservation value pyramids (Holmer and Stenlid 1997) were constructed exemplified in Fig. 4. The pyramid follows the concept of nestedness where communities of species in smaller habitat fragments are subsets of those in larger fragments (Diamond and Gilpin 1982; Patterson and Atmar 1986). If the landscape fulfils the habitat requirements for a species that requires a high number of oaks > 150 cm, for example *Aurantiporus croceus* in the top of the pyramid, the landscape for all other species with lower demands such as *Osmoderma eremita*, *Grifola frondosa* and *Cliostomum corrugatum* is considered to be functional (Fig. 4).

The mapping of functional areas and areas with habitat mismatch shows clear patterns in the study area with large differences between regions (Figs. 5–7). The mapping of oaks > 100 cm dbh at the 15 × 15 km scale shows that the north-eastern part of the study area has large functional areas for oak-dependent species. However, in some areas in the south and west, the number of oaks is too few to reach

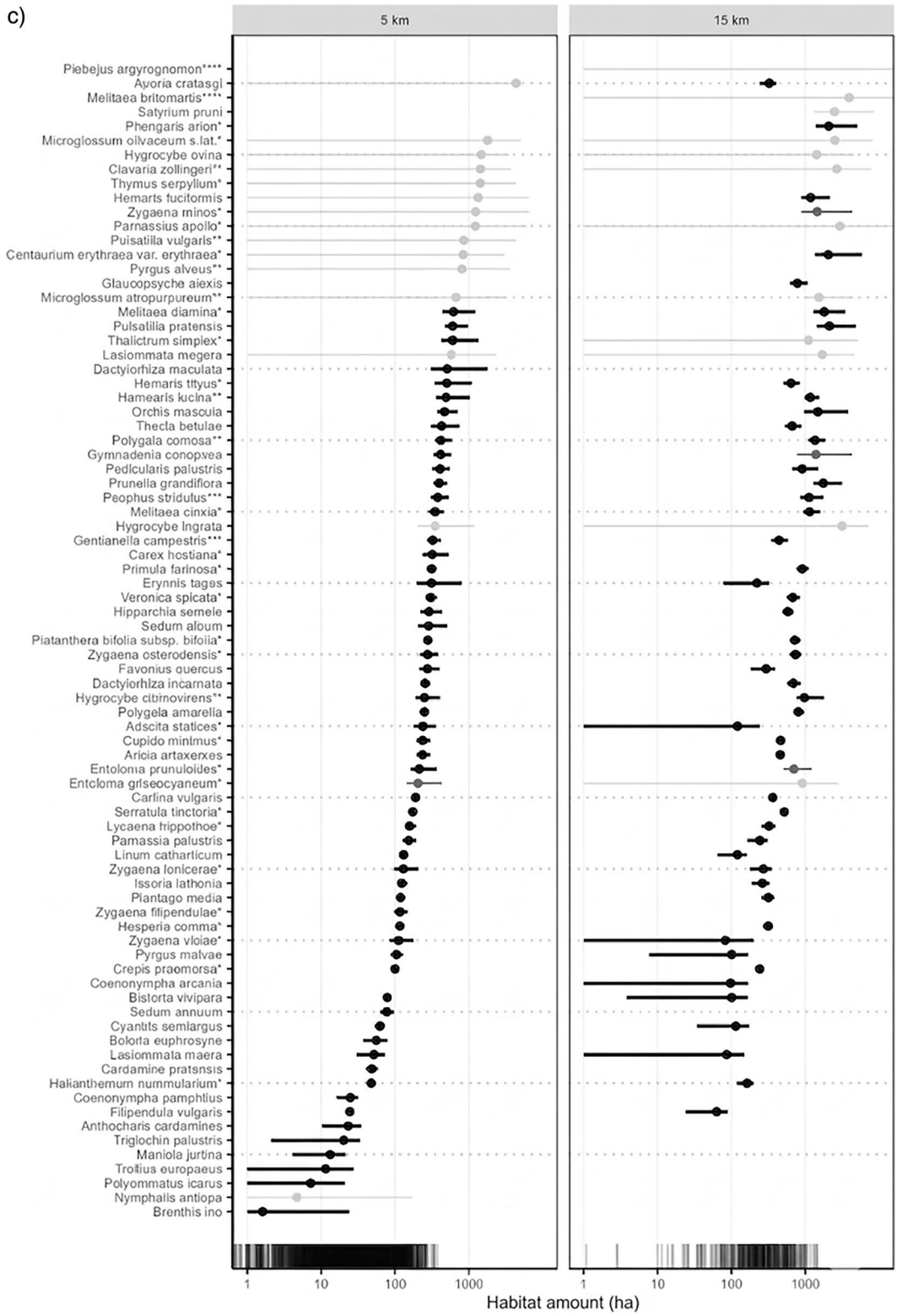

Fig. 3 (continued)

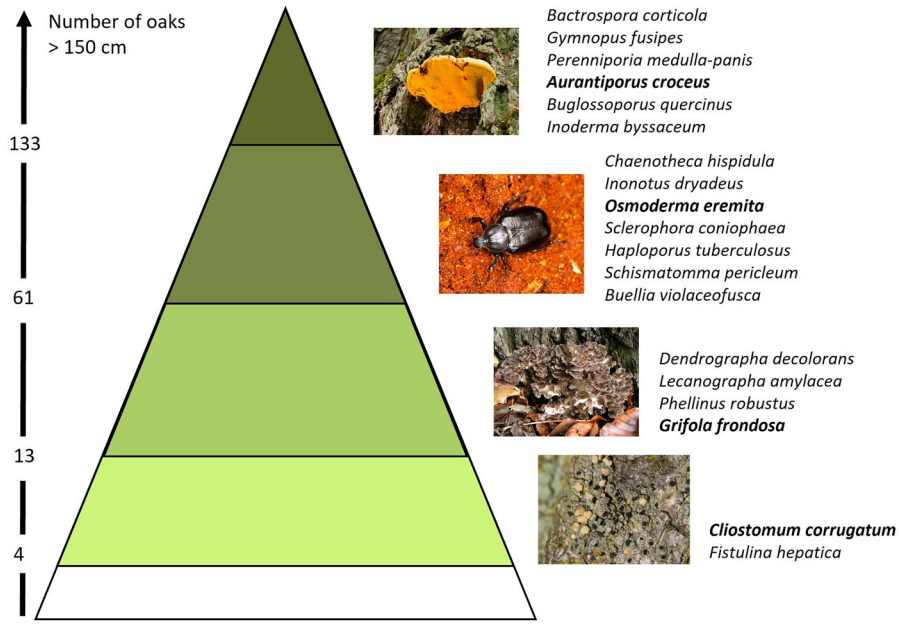

Fig. 4 A conservation value pyramid for species dependent on oaks > 150 cm dbh within 15x15 km. If the landscape fulfils the habitat requirements for a species that requires a high number of oaks > 150 cm dbh the landscape for all other species with lower demands is considered functional. Species name in bold indicates the species in the photo. Photo credits: Karl-Olof Bergman except *Grifola frondosa* by Pethan CC BY-SA 3.0

the threshold values for harbouring any of the oak-dependent species. On the other hand, a few distinct regions in the north-east have enough habitat to hold also the most sensitive species (Fig. 5). The smaller spatial scale of 5 × 5 km shows similar patterns, but with smaller regions.

The habitat mismatch maps show that sensitive species occur both in areas where the number of oaks is above their threshold values and in many areas well below. In many areas in the south and west, the negative habitat mismatch is 200–300 oaks, meaning that the areas that the species occur in have 200–300 oaks fewer than their threshold values. In some areas, the negative habitat mismatch is more than 300 oaks. The functional areas for the sensitive species, with no negative habitat mismatch, are mainly in the north-eastern regions.

The patterns are similar on the smaller spatial scale of 5 × 5 km, with a negative habitat mismatch in the south and west and functional areas in the north-eastern region.

The mapping of functional areas for the largest oaks above 150 cm dbh, at the 15 × 15 km scale, shows that there are mainly areas in the north-east with enough oaks to be functional for the most sensitive species (Fig. 6). However, also an area in the south-east is functional. Similar to the habitat pattern for the smaller oaks > 1m dbh, some areas in the south and west, contain too few oaks to reach even the lowest threshold values. The smaller spatial scale at 5 × 5 km shows similar patterns, however, showing smaller regions.

The mapping of functional areas for semi-natural grasslands at the 15 × 15 km scale shows several functional regions in the study area (Fig. 7). The functional areas are situated mainly in the northern part with some additional areas in the south-east. The habitat mismatch maps show that sensitive species occur both in areas with grassland areas above their threshold values and in many areas well below the threshold. In many areas in the south and west, the negative habitat mismatch is 200–450 ha. In some areas, the negative habitat mismatch is more than 450 ha. The functional areas for the sensitive species, with no negative habitat mismatch, are mainly in the northern and south-eastern regions.

Discussion

For almost all the species examined in the study, the occurrence probability increased significantly with increasing habitat amounts, either the number of host trees or habitat area. The general pattern of increasing species richness or probabilities for the occurrence of individual species with increasing habitat amount has been shown empirically across biomes

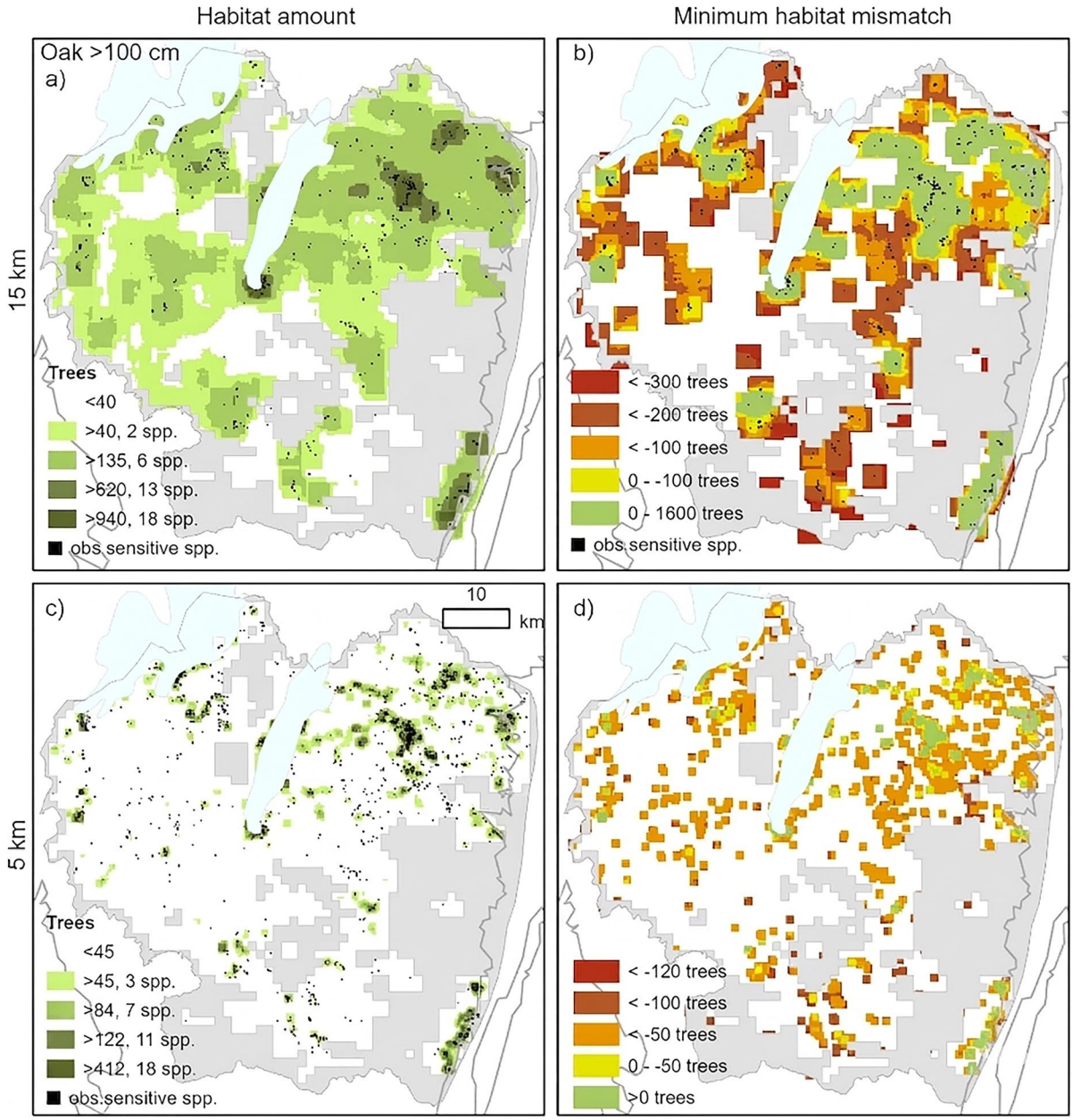

Fig. 5 Functional areas with enough habitat to harbour a certain number of species (**a**, **c**) and areas with habitat mismatch (**b**, **d**), for oak-dependent species based on oaks > 100 cm dbh. The number of species, seen in the legend (of **a** and **b**), for the different habitat amount classes correspond to habitat thresholds in Fig. 3. The habitat mismatch maps are based on the distribution of species requiring > 327 oaks at 15 km and > 122 oaks at 5 km, representing moderately sensitive species. As an example, red areas (in **b**) lack at least 300 oaks to be functional for the species occurring there, while green areas have a surplus of up to 1600 oaks. Grey areas lack tree data. The values for functional areas and habitat mismatch thresholds were chosen to illustrate the general pattern; alternative threshold values yielded similar spatial patterns

all over the world (Newbold et al. 2015) as well as for different species groups, e.g., small mammals and bats in Brazil (Estavillo et al. 2013; Muylaert et al. 2016), butterflies and beetles in Sweden (Bergman et al. 2004, 2012), and birds in Australia (Radford et al. 2005) and Sweden (Angelstam et al. 2004).

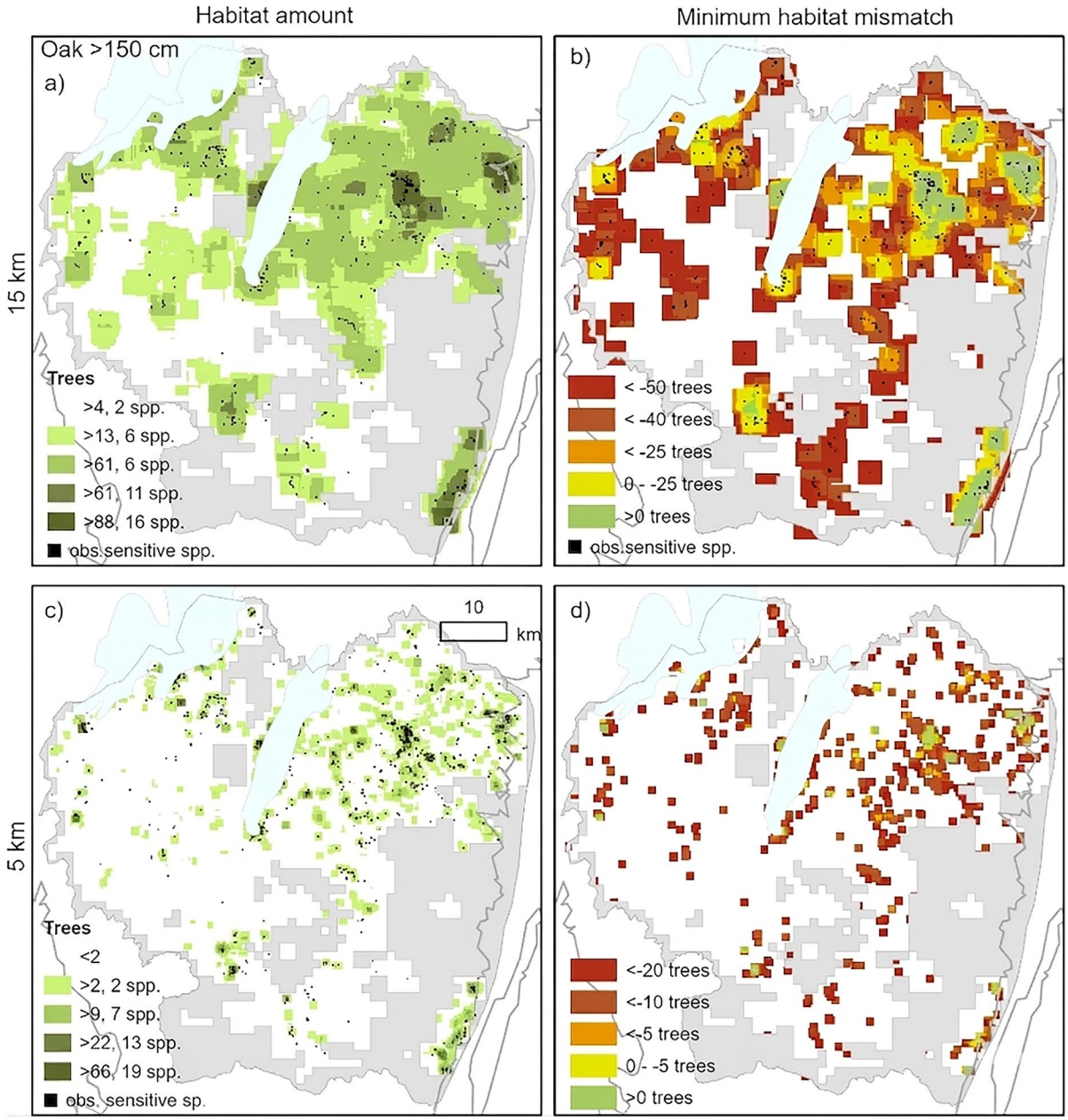

Fig. 6 Functional areas with enough habitat to harbour a certain number of species (**a**, **c**) and areas with habitat mismatch (**b**, **d**) for oak-dependent species based on oaks > 150 cm dbh. The number of species, seen in the legend (of **a** and **b**), for the different habitat amount classes correspond to habitat thresholds in Fig. 3. The habitat mismatch maps are based on the distribution of species requiring > 60 oaks at 15 km and species requiring > 22 oaks at 5 km, representing moderately sensitive species. As an example, red areas (in **b**) lack at least 50 oaks for being functional for the species occurring there, while green areas have a surplus of oaks. Grey areas lack tree data. The values for functional areas and habitat mismatch thresholds were chosen to illustrate the general pattern; alternative threshold values yielded similar spatial patterns

Thus, our results give strong support to the conclusion that the species observations in this study, based on a combination of citizen science data and professionals, provided data good enough to capture species

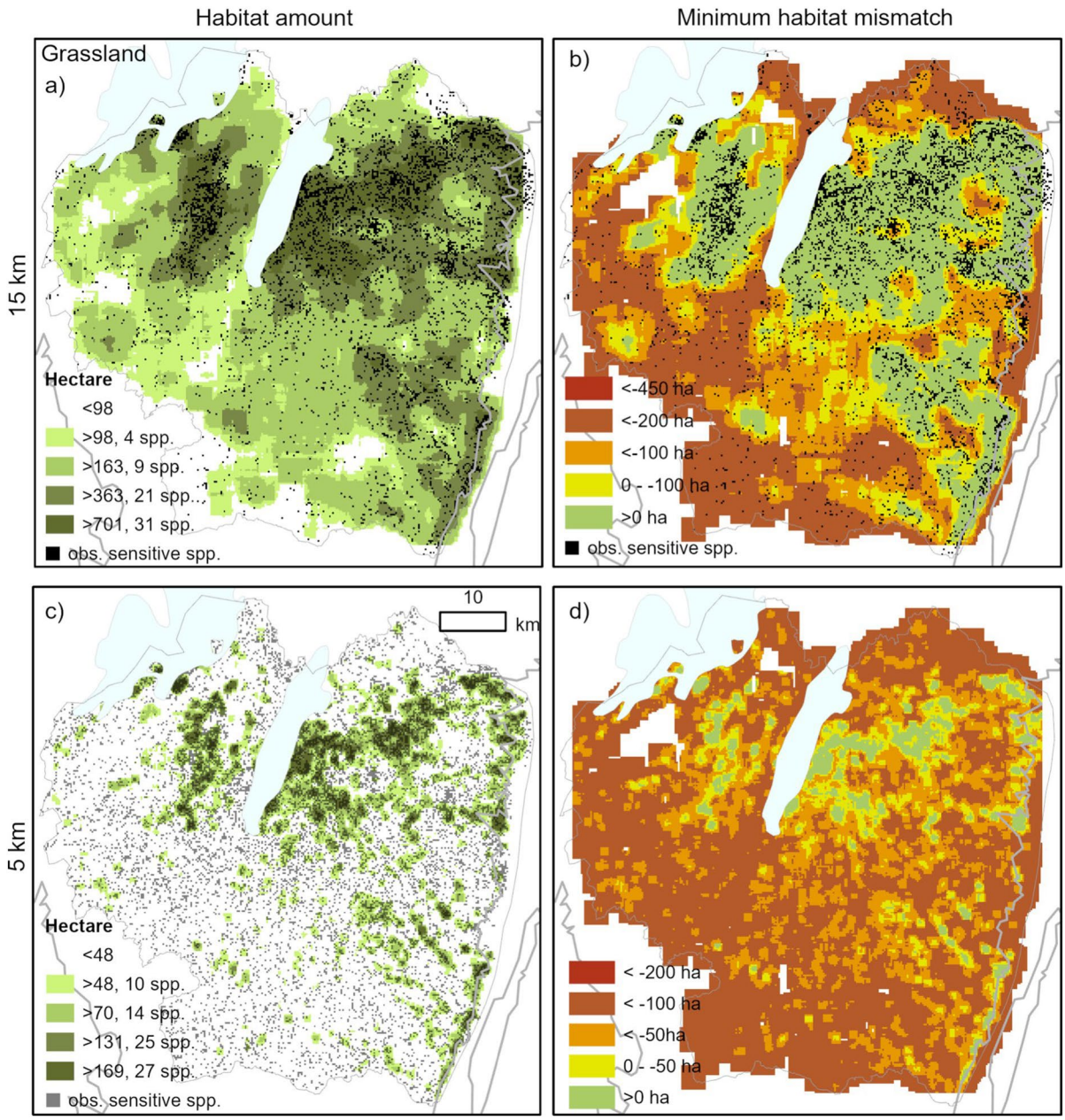

Fig. 7 Functional areas with enough habitat to harbour a certain number of species (**a**, **c**) and areas with habitat mismatch (**b**, **d**) for semi-natural grassland dependent species. The number of species for the different habitat amount classes correspond to habitat thresholds in Fig. 3. The habitat mismatch maps are based on the distribution of species requiring > 370 ha at 15 km and > 131 ha at 5 km, representing moderately sensitive species. As an example, red areas (in **b**) lack at least 450 ha for being functional for the species occurring there, while green areas have a surplus of grasslands. Grey areas lack grassland data. The values for functional areas and habitat mismatch thresholds were chosen to illustrate the general pattern; alternative threshold values yielded similar spatial patterns

occurrences and absences over regions. Furthermore, it shows that our habitat data were good enough to be relevant for the majority of our study species. That, in turn, made it possible to map functional regions for species, regions close to functional, and regions that may have an extinction debt. In the regions mapped

out as functional, we can expect species to survive and ecosystems to be maintained, including crucial ecological processes (Poiani et al. 2000).

Conservation actions need to target the relevant spatial scale for the long-term survival of species (Boyd et al. 2008). According to the literature data, the majority of the species in our study responded to larger spatial scales, which has important implications for conservation planning. The spatial scale of response for species is several orders of magnitude above the general patch area in the region, and it is clear that conservation plans need to cover larger regions. Species living in fragmented habitats like those in the studied region often exist in metapopulations where local populations are connected and where extinction probabilities are lower due to the rescue effect from neighbouring populations (Hanski and Gilpin 1991). In a fragmented landscape consisting of small fragments like in the study area, there seems to exist a minimum number of habitat fragments for species to exist. Four different butterfly species tended to survive in regions with 15–20 fragments and tended to be absent from regions with fewer than 10 fragments (Thomas 1994; Thomas and Hanski 1997; Bergman and Kindvall 2004). The spatial scales of response identified for many of the targeted species groups in this study may reflect the size of a region needed to harbour a viable metapopulation over time. The relatively large spatial scales identified here for species dependent on old trees, may also be due to the temporal dynamics over time for old trees as they change in quality over time, age, and die, and new suitable trees grow up. In such dynamic landscapes, models have shown that larger areas with more fragments are needed than in static landscapes (Ranius 2007; Perry and Lee 2019).

With a relevant spatial scale of response (Holland et al. 2004) established, the next crucial factor for applied conservation is to estimate a critical habitat amount for occurrence within the relevant scale. Identifying habitat thresholds below which species are lost in the landscape allows conservation planners to be proactive instead of reactive (Groves et al. 2002). It will be possible to establish measurable goals, identify priority areas for sensitive species, and identify areas in need of restoration to meet the goals. It is also important that the goals are science-based to maximise the probability of success (Tear et al. 2005). In this study, we could provide clear goals for species dependent on old oaks, allowing conservation planners to map and quantify functionality over their regions. For example, our results indicate that 400 oaks above 1 m in diameter within 25 km^2 would be associated with a 50% probability of occurrence for many oak-dependent species. However, this does not imply that current landscapes meeting this threshold are in a stable state; time-lag effects and extinction debts mean that species may persist temporarily in landscapes where habitat has declined below functional levels (Kuussaari et al. 2009; Hylander and Ehrlén 2013). Consequently, our threshold values should be interpreted as minimum targets rather than as confirmation that the current situation is adequate. Earlier studies over smaller regions in Sweden have indicated similar numbers. Species richness of beetles reached a plateau at about 250 oaks above ≥ 100 cm dbh in an area of 16 km^2 (Bergman et al. 2012). A study in Sweden estimated that at least eight ancient oaks ≥ 160 cm dbh were required within 12.5 km^2 to obtain 50% predicted occurrence on an individual ancient oak for *Ramalina baltica*, a red-listed (NT) oak-dependent lichen (Paltto et al. 2010). The threshold value for occurrence in a 25 km^2 area for another oak-dependent, red-listed lichen, *Cliostomum corrugatum*(NT), was four oaks >150 cm dbh in this study. In this study, we were also able to set targets for one of the rarest oak-dependent polypores, *Aurantiporus croceus*. The species is considered vulnerable in the IUCN Red List and critically endangered in eight European countries (Dahlberg 2019). The threshold for *A. croceus* was 43 oaks above 150 cm in diameter within 25 km^2, giving conservationists a guideline for functional landscapes for this species.

We could also estimate thresholds for species dependent on semi-natural grasslands. Semi-natural grasslands are one of Europe's most species-rich habitats (Bonari et al. 2017) and therefore of special interest. In Sweden, more than 30% of all species on the Red List occur in agricultural landscapes, the majority associated with semi-natural grasslands (Eide et al. 2020). It has been shown that populations in grassland-poor landscapes become extinct earlier compared to those in grassland-rich landscapes (Lennartsson 2002). This study could provide thresholds for several grassland plants and insects. The threshold for the red-listed burnet moth *Zygaena viciae* in this study was 7.9% grasslands within an area of 25 km^2. A study of burnet moths in Sweden indicated a threshold of

11% grasslands and deciduous forests within 78.5 km^2 (Bergman et al. 2004). The plant *Gentianella campestris* is another red-listed species, with a long history of decline in Sweden (Glav Lundin and Eriksson 2021) and a target for many conservation efforts. This study's threshold was estimated to be 8.7% of semi-natural grasslands within 25 km^2. The threshold estimated in this study can give a guideline for conservation efforts for this species on the landscape level.

In this study, we identified areas close to functional where small efforts could restore functionality for many species, which gives possibilities for cost-effective nature conservation. It has been shown that a systematic conservation planning approach like this is better at identifying the most cost-efficient combination of patches to be restored in order to reach a goal than ad hoc approaches (Margules and Pressey 2000; Petersen et al. 2016). Habitat restoration to lift a landscape above the threshold is likely to have much greater conservation benefits than restorations that fall clearly below thresholds (Radford et al. 2005).

We also identified areas with many sensitive species but with a habitat amount well below our estimated thresholds. It is possible that the species in these areas exist in an extinction debt (Tilman et al. 1994; Kuussaari et al. 2009). In these areas, there exists a window of conservation opportunity to avoid future extinctions (Wearn et al. 2012). To prevent and halt ongoing extinction processes in these regions, there is a need to increase the habitat amount and restore habitat connectivity (Deák et al. 2021). Even for species dependent on old oaks occurring in poor landscapes, it has been shown that it is possible to increase long-term persistence if conservation actions quickly address the need to increase tree regeneration rates (Johansson et al. 2013).

Conservation implications and limitations

This study aimed to test whether species data largely based on citizen science and habitat data could provide guidelines for practitioners on where and at what spatial scales conservation action should be focused. Using these data, we present quantitative and spatially explicit predictions of functional landscapes for species associated with old oaks and semi-natural grasslands, providing decision support maps crucial for environmental planning (Geneletti 2004).

Our models are relatively simple, taking only habitat amount into account after identifying the characteristic scale of response. In empirical studies, total habitat area has been shown to be more important than isolation of individual habitat patches (Fahrig 2003; Hodgson et al. 2011), and simple habitat amount goals can be as effective as more complicated models including isolation (Fahrig 2013). However, for less mobile species such as *Osmoderma eremita*, inter-patch distances may be critical (Hanski and Ovaskainen 2000), and for species requiring multiple habitat types (Dunning et al. 1992), effective habitat availability may be lower than suggested by a single-habitat approach. For example, several grassland butterflies require both larval host plants and nectar resources in adjacent habitats, meaning that grassland area alone may underestimate effective habitat availability.

Several further limitations should be acknowledged. We used species occurrence as a proxy for population viability, which does not capture demographic parameters; assessing true viability would require data on population sizes, trends, and demographic rates such as reproduction and survival. Our functional landscape designations should therefore be interpreted as necessary but not sufficient conditions for persistence (Poiani et al. 2000). The choice of $P = 0.5$ is conventional rather than ecologically derived; we provide results at $P = 0.25$, 0.5 and 0.75 to allow practitioners to select a threshold appropriate to their context (Supplementary Table S2). Species may also persist temporarily where habitat has declined below functional levels—an extinction debt (Tilman et al. 1994; Kuussaari et al. 2009) — meaning areas appearing functional may be losing species, while areas with habitat mismatch may still harbour species within a conservation opportunity window (Wearn et al. 2012).

Climate change will alter species distributions and habitat quality, so threshold values should not be treated as permanently fixed. In particular, climate-driven range shifts may render current thresholds inadequate in areas where species expand into new regions or contract from existing ones (Pecl et al. 2017). Despite these uncertainties, the current values provide an essential starting point, as habitat loss remains the dominant pressure on these species. The success of this approach relies on continued improvement of habitat data and species occurrence records, where citizen science campaigns could also increase

public engagement and encourage local conservation (McKinley et al. 2017).

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Author contributions Karl-Olof Bergman: writing—original draft, writing—review & editing, conceptualization, funding acquisition, visualization, project administration. Leif Andersson: data curation, conceptualization, resources, project administration. Markus Franzén: writing—review & editing, funding acquisition. Victor Johansson: writing—review & editing, funding acquisition. Lars Westerberg: data curation, formal analysis, methodology, investigation, visualization, software.

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Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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