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ORIGINAL PAPER

Large-scale habitat model reveals a key role of large trees and protected areas in the metapopulation survival of the saproxylic specialist *Cucujus cinnaberinus*

Michał Bełcik[1] · Jakub Goczał[2] · Michał Ciach[3]

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Abstract

Deforestation for agricultural purposes and logging over centuries has resulted in a significant loss of forest cover and the deep structural and functional simplification of persistent European woodlands, which has led to a large-scale decline in biodiversity. Despite recent reforestation efforts in many regions of Europe, populations of numerous forest species remain unrecovered. Due to the loss of ecological continuity and the simplification of the ecosystem structure and functionality, the value of secondary forests in sustaining habitat specialists is being questioned. Here, we build a large-scale habitat suitability model to predict the current potential of forests to host populations of the flagship European saproxylic beetle *Cucujus cinnaberinus*. Our maximum entropy model revealed that the distribution of suitable habitats strongly corresponds to the occurrence of large and well-preserved forest complexes that are characterized by an ecological continuity of the stands. Among the analysed environmental variables, the mean tree diameter and distance to protected areas were the most important suitable habitat contributors. The optimum habitats were identified almost exclusively within some parts of the Carpathians and the northeastern part of the country, particularly in the Białowieża Forest, which include the best preserved European forests. Although a large number of small habitat patches was revealed across the country, these patches were highly scattered and had low predicted suitability. This study demonstrates that most woodlands are unsuitable for *C. cinnaberinus*, which points to the limited value of secondary forests for habitat specialists. Our findings emphasize the importance of large and intact forests with undisrupted ecological continuity as key areas for the persistence of the rare saproxylic beetle, which provokes questions about the effectiveness of reforestation as a tool for the conservation of forest habitat specialists.

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✉ Michał Bełcik
belcik@iop.krakow.pl

[1] Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland

[2] Institute of Forest Ecosystem Protection, Faculty of Forestry, University of Agriculture in Krakow, 29 Listopada 46, 31-425 Kraków, Poland

[3] Department of Forest Biodiversity, Faculty of Forestry, Institute of Forest Ecology and Silviculture, University of Agriculture in Krakow, 29 Listopada 46, 31-425 Kraków, Poland

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Introduction

In recent centuries, human agricultural activity has led to the deforestation of the temperate region (Hanski et al. 1994; Glatzel 1999; Paillet et al. 2010). As a result, large parts of Europe have experienced a total loss of natural forest coverage, and the remaining fragments have become highly isolated. Furthermore, the current forest area primarily encompasses managed forests or tree plantations, which are characterized by a simplified and unified tree species composition, age and spatial structure (Glatzel 1999; Bengtsson et al. 2000). Another consequence of human activity in European forests is an interruption in the continuity of key ecological processes related to tree mortality, which causes the temporary or permanent depletion of dead wood resources (Kolb and Diekmann 2004; Fritz et al. 2008; Lassauce et al. 2011; Nordén et al. 2014). The abovementioned alterations of forests have resulted in biodiversity loss, which is manifested in reduced species richness, local species extinctions, changes in community structure and interruptions in meta-population connectivity (Rukke 2000; Kouki et al. 2001; Brunet and Isacsson 2009; Ranius and Roberge 2011).

After an era of intensive deforestation, the forest coverage in Europe has increased gradually. Forests were extended by 17.5 million ha between 1990 and 2015, i.e., approximately 0.33% per year (Forest Europe 2015), mainly due to intensive planting efforts led by the European Union (Gamborg and Larsen 2003; Bauhus et al. 2013; Forest Europe 2015). Moreover, forest management policies have been subject to a major paradigm shift through decades of intensive forest utilization to more sustainable and multifunctional forestry (Gamborg and Larsen 2003; Rametsteiner and Mayer 2004; Siry et al. 2005). Despite these positive trends, secondary growth forests still differ significantly from primeval conditions in terms of ecological complexity and biodiversity (Kuuluvainen et al. 1996; Weslien and Schroeder 1999; Grove 2002; Liira et al. 2007; Brumelis et al. 2011; Bouget and Parmain 2016). Such differences are a consequence of the disruption of ecological continuity and limitations of dead wood resources.

The term ecological continuity was adopted by Rose (Rose 1974) and has subsequently been widely applied as an indicator of forest ecological value. Although the definition of this term differs (Nordén and Appelqvist 2001), ecological continuity is most often used to describe forests characterized by long-term uninterrupted persistence and a low level of human-induced disturbance (Nordén and Appelqvist 2001; Kolb and Diekmann 2004; Nordén et al. 2014). Since both ecological continuity and dead wood abundance are considered crucial factors for biodiversity protection in forests (Grove 2002; Lassauce et al. 2011; Mikusińska et al. 2013; Kunttu et al. 2015), newly planted forests are expected to exhibit lower values for various forest species than for old-growth forests remnants. Although this hypothesis has been proven for various taxonomic groups (Bremer and Farley 2010; Paillet et al. 2010; Brumelis et al. 2011; Pawson et al. 2013; Bradshaw et al. 2015; Lachat and Müller 2018), there is a strong belief that secondary forests may help in biodiversity restoration.

Due to the large number of taxa, precise estimations of forest biodiversity represent a serious methodological problem and a consensus has not been reached on the indices that are reliable. Several different indicators of forest biodiversity at various levels have been proposed, including the total volume of dead wood, number of species, ecological continuity, habitat heterogeneity, habitat fragmentation, structural complexity and connectivity or occurrence of focal species (Barbati et al. 2014; Gao et al. 2015). Currently, one of the most frequently proposed concepts in biodiversity assessments involves the use of indicator species, i.e., habitat specialists or umbrella species (Roberge and Angelstam 2004; Sattler et al. 2014; Breckheimer et al. 2014; Mikoláš et al. 2015). Such an approach has several benefits, including a reduction of costs and clarity of management and conservation goals. Moreover, an indicator species approach may be advantageous because it is based on real species' responses to the quality of the environment quality and not technical estimators, such as habitat structure (e.g., dead wood volume). For forest biodiversity evaluations, saproxylic organisms, especially saproxylic beetles, are widely used as indicators (Jonsson and Jonsell 1999; Jonsell and Nordlander 2002; Ranius 2002; Smith et al. 2008; Lachat et al. 2012). Some wood-inhabiting beetles have specific habitat requirements and life-history traits that make them particularly sensitive to human-induced forest changes. Moreover, the occurrence of saproxylic beetles is well correlated with the presence of several other indicators, such as fungi (Linnakoski et al. 2012; Floren et al. 2015), other insects (Vindstad et al. 2014) and woodpeckers (Wesołowski 1995; Mikusiński et al. 2001; Tomiałojć and Wesołowski 2004).

Due to economical and historical circumstances, some forest fragments located mainly in the eastern part of Poland did not lose their ecological continuity over time (e.g., Białowieża Forest, Carpathian forests), whereas forests located in the western part of the country were markedly degraded or deforested by intensive utilization during World War II and now primarily include secondary forest planted after World War II. The aim of this study is to estimate the large-scale distribution pattern of suitable habitats of the flagship saproxylic species *Cucujus cinnaberinus* (Scopoli 1763). Given that the spread of the beetle has recently been observed in some parts of the species range, we investigated whether the results of large-scale forest habitat restoration could be beneficial for *C. cinnaberinus* and may enable the recovery of its population.

Materials and methods

Targeted species

Cucujus cinnaberinus constitutes a flagship species for saproxylic beetle conservation in Europe. The species is listed in the Bern Convention and strictly protected by law in most European countries across its distribution range. The species is listed as Near Threatened and close to qualifying for Vulnerable (Nieto et al. 2010). *C. cinnaberinus* is also included in the II and IV annexes to the Habitat Directive, and the status of its population and habitat has become crucial for the identification and monitoring of protected areas included in the Nature 2000 network across the entire European Union.

Prior to the twenty-first century, knowledge of the distribution and ecology of *C. cinnaberinus* was limited and the species was perceived as an extremely rare "relict beetle" associated with natural or even primeval forests (Speight 1989; Eriksson 2000). However, in recent years, large-scale spreading of the species was observed in Western and Southern Europe. The species markedly expanded its range in Germany (Reibnitz 2008; Esser and Mainda 2015; Hörren and Tolkiehn 2016) and Austria (Eckelt et al. 2014), entered the Netherlands (Teunissen and Vendrig 2012; Noordijk et al. 2013) and Belgium (Crevecoeur et al. 2017) and reached Northern France (Fuchs et al. 2014). *C. cinnaberinus* was found to inhabit anthropogenic habitats, such as abandoned poplar plantations and non-native black locust *Robinia pseudoacacia* stands (Vrezec et al. 2017). However, these latter findings resulted in their exclusion from a recent list of "primeval forest relict beetles" (Eckelt et al. 2018). Recent changes in European forest management policy, including the application of close-to-nature silviculture, increased the dead wood resources and promoted reforestation and rewilding efforts, which have had a positive effect on saproxylic organisms, such as *C. cinnaberinus*. Nevertheless, empirical data clearly documenting this effect are still insufficient.

Cucujus cinnaberinus is considered an umbrella species, and its protection serves to protect a wide community of co-occurring saproxylic organisms (Mazzei et al. 2011; Horák et al. 2012). Currently, the occurrence of *C. cinnaberinus* has been confirmed in most European countries (Horák and Chobot 2009; Nieto et al. 2010; Horák et al. 2010), including newly discovered populations in Southern Europe (Kovács et al. 2012; Fuchs et al. 2014; Šag et al. 2016; Vrezec et al. 2017). The species inhabits various types of deciduous and mixed forest, both in the mountains and lowlands. *C. cinnaberinus* prefers large and sun-exposed dead wood of various deciduous and coniferous trees characterized by a moderate to high moisture content and an intermediate stage of decay (Horák et al. 2010, 2012; Goczał and Rossa 2017; Vrezec et al. 2017).

Although *C. cinnaberinus* is no longer considered a relict species, it still serves as an indicator of forest biodiversity. As a saproxylic specialist, this species tends to perish rapidly with forest alterations due to interruptions in the dead wood supply. On the other hand, current data from Western and Southern Europe suggest that their populations may be restored if an appropriate rewilding method is applied. Furthermore, its occurrence is relatively simple to detect, and surveys can be conducted throughout entire seasons (Buchholz 2012). These characteristics make *C. cinnaberinus* a proper candidate for a model species to assess the effect of structural changes of forest habitats on saproxylic organisms.

Study area

Poland is a central European country (312,679 km^2) with high forest coverage (Fig. 1). At the end of the 18th century, forests accounted for as much as 40% of the Polish territory (The State Forests Information Centre 2010). Nevertheless, due to intensive exploitation during World War II between 1939 and 1945, forest cover dropped by half to approximately 21% in 1946 (The State Forests Information Centre 2010). Large parts of old-growth and natural deciduous forest were replaced with fast-growing coniferous monocultures, although this trend this varied markedly between regions across the country, with intensive forest utilization and structural alterations occurring in the western parts of the country and vast tracts of old-growth natural forest with a long ecological continuity remaining in eastern and southern Poland. After World War II, the first National Plan of Afforestation was established to support the most degraded and completely deforested areas. Since that time, the forest area in Poland has increased and currently encompasses 29.5% of the country (Central Statistical Office 2015). As a result, previously ecologically degraded western parts of Poland currently present the highest forest coverage nationwide (Central Statistical Office 2015). However, these restored forests still represent heavily transformed secondary managed woodlands. Although eastern Poland has lower forest coverage than western Poland (ca. 30% *vs.* 39%), it includes the best preserved old-growth and primeval forests in Europe.

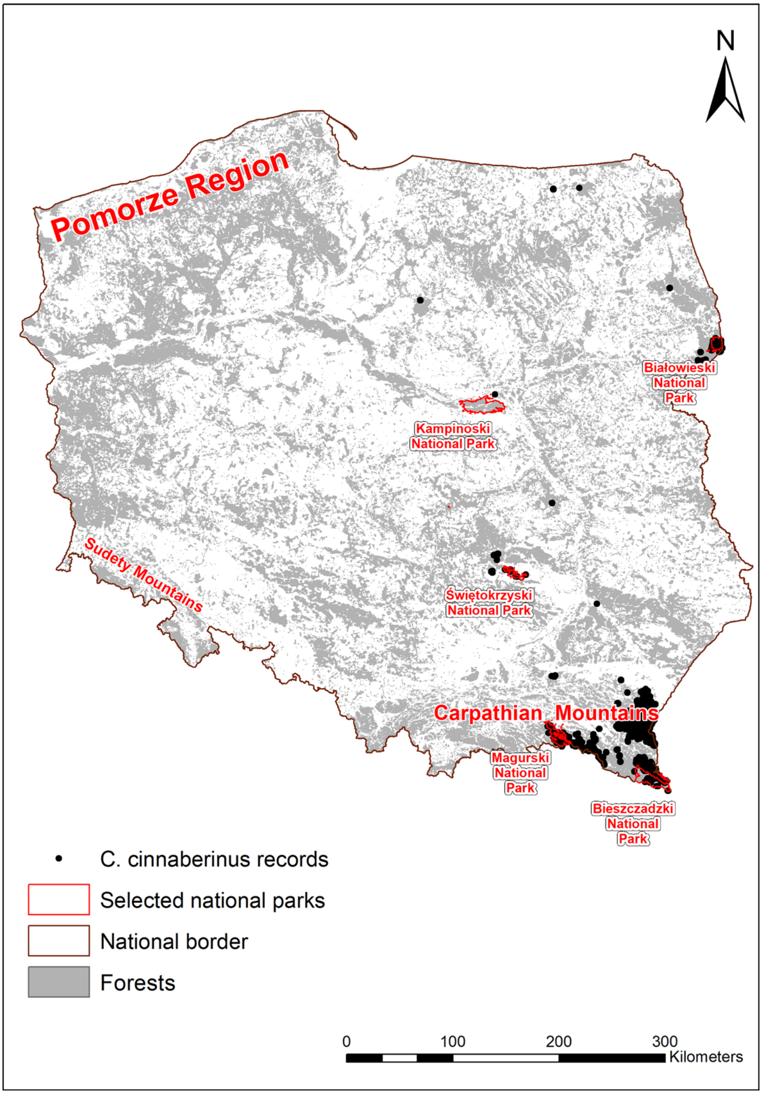

Fig. 1 Forests in Poland, *Cucujus cinnaberinus* presence records and the most important locations mentioned in the text

Presence data

We used all available sources of *C. cinnaberinus* presence records, including published articles and reports (Trzeciak 2011; Miłkowski 2012; Smolis et al. 2012; Buchholz et al. 2013; Olbrycht et al. 2014; Plewa et al. 2014; Marczak 2016), and unpublished data from governmental agencies (Regional Directorates for Environmental Protection), State Forests National Forest Holdings and national park authorities, which are obligated by law to collect data on the species' occurrence. Due to the implementation of the Habitats Directive (Official Journal of the European Communities 1992) and establishment of the Natura 2000 network of protected areas in Poland, potential habitats have been surveyed since 2004 for the purpose of preparing management plans. Due to the conservation value of the species and legal requirements, *C. cinnaberinus* was one of the targeted species. All conducted surveys provided reliable data on the current distribution of *C. cinnaberinus* in Poland. In total, 794 records collected up to 2016 were used in the analyses (Fig. 1).

Environmental background data

Based on an analysis of the ecological literature on saproxylic insects (Speight 1989; Franc et al. 2007; Bouget et al. 2014), a set of environmental variables was selected with the potential to affect the occurrence of *C. cinnaberinus* (Table 1). Layers representing distance to urban areas (as a land cover class), roads and protected areas (national parks and nature reserves) were created using the state spatial features geodatabase (BDOO, Polish central geodesy database, http://www.codgik.gov.pl), which includes vector layers for every major geographical and spatial feature in the country. A distance matrix was selected to account for the degree of human disturbance based on the raster resolution chosen for the analysis. For data describing tree stands, we have used the Bureau for Forest Management and Geodesy Forest data bank (https://www.bdl.lasy.gov.pl), which is a data repository that contains information about all state owned and private forests in Poland. These data have been collected for the preparation of Forest Management Plans and represent the official National Forest Inventory, which includes detailed descriptions of a wide variety of forest stand parameters, habitat types and soil parameters available at the stand scale. The data collection methodology is regulated by their official technical manual (The State Forests Information Centre 2012), which ensures that data collection is uniform for the whole country and the environmental data are a reliable source for country-wide analyses. Data from the BDOO database have similar characteristics and were collected from country-wide land use surveys; thus, this database is a reliable source of information at the landscape scale. Light pollution as a proxy of human presence and activity (Longcore and Rich 2004) was determined based on the visible infrared imaging radiometer suite supplied by the Earth Observations Group (NOAA National Geophysical Data Center). The raster layer contains the average radiance based on night-time data and was expressed in nanowatts per square centimetre per steradian ($nW/cm^2 \times SR$).

All layers used in the analyses were converted into ASCII file format with the same cell size (50 m) using ArcGIS software (ESRI, Redlands, USA). This size has been chosen to capture the spatial complexity of forest stands because rasters generated via this method accurately represent forest stand boundaries. An increase in cell size would produce a raster that would not spatially match the forest stand boundaries, thus resulting in a loss of information due to generalization. A total of 13 variables (Table 1) were used in modelling. The correlations between variables were evaluated via a Pearson correlation analysis ($r > 0.5$ for all variable pairs). To include the described complexity of Polish forests, our model has been created to reflect the extent of the country, including both forested and non-forested areas. All of the environmental layers (in PUWG 1992 coordinate system) were clipped to the boundaries of the country. In case of non-forested areas, all of the attributes concerning the forest stands (e.g., mean diameter at breast height, mean density, etc.) were assigned a value of zero.

Table 1 Description of the 13 environmental variables used to develop the *Cucujus cinnaberinus* habitat distribution model in Poland

Layer name	Layer source	Layer description
Stand characteristics		
Perimeter–area ratio of forest stand	Forest Data Bank	Perimeter–area ratio of forest complex
Diameter at breast height	Forest Data Bank	Mean diameter at breast (1.3 m) height for forest stand (in centimetres)
Height	Forest Data Bank	Tree canopy height (in m)
Density	Forest Data Bank	Mean density of forest stand (representing tree canopy density, see Table 3)
Forest site moisture	Forest Data Bank	Site moisture type (representing soil moisture—see Table 3)
Vertical stand structure	Forest Data Bank	Vertical stand structure type (see Table 3)
Stand density code	Forest Data Bank	Stand density code for forest site (representing ratio between a theoretical timber volume of a model stand to this particular stand, expressed in an integer ranging from 0 to 1.8 in this dataset)
Number of trees	Forest Data Bank	Number of trees per 1 ha
Understory vegetation cover	Forest Data Bank	Understory vegetation cover type (see Table 3)
Human presence and activity		
Distance to roads	BDOO	Distance to roads (in m)
Distance to urban areas	BDOO	Distance to urban areas (in metres)
Light pollution	NOAA National Geophysical Data Center	Degree of light pollution (can be seen as a measure of anthropopressure)
Distance to protected areas	BDOO	Distance to national parks and nature reserves (in metres)

Modelling approach and model validation

To determine the habitat parameters that can be used to predict the *C. cinnaberinus* distribution, we applied species distribution modelling using maximum entropy models in MaxEnt ver. 3.3.3 k software (Phillips et al. 2006). The following settings were used: a 15-fold cross validation with 5000 iterations, a logistic output to generate response curves and jackknife results, random seeding and a regularisation multiplier (fixed at 1).

A Receiver Operating Characteristic (ROC) curve was evaluated to determine the model's predictive ability, and the evaluation focused on the Area Under the Curve (AUC) of the ROC curve. An AUC value close to 0.5 represents a totally random model, while an AUC value close to 1 represents perfect discrimination (Fielding and Bell 1997). To minimize the risk of over-fitting and obtain an unbiased prediction (Abid and Williams 2010), we applied jackknife tests to estimate the variables that were most important for model prediction. Predictor variables with a percentage of contribution exceeding 100/K (where K is the number of predictors) were considered to have high explanatory power (Mac Nally 2000, 2002).

Dealing with spatial autocorrelation

The Maximum Entropy method is among the most widely used modelling approaches in cases with sparse, irregularly sampled data and minor location errors (Phillips et al. 2009). Although the method focuses on presence-only data, the lack of systematic sampling of an area of interest may lead to a spatial bias (Kramer-Schadt et al. 2013) because of the overrepresentation of species records from carefully checked areas relative to the locations where no research was carried out. Because *C. cinnaberinus* is a targeted species for preparing the management plans for both protected areas and managed forests, potential habitats were carefully inspected for the species' occurrence by using the same methodology (Buchholz 2012). This approach minimizes the potential bias resulting from the omission of a large part of potentially occupied areas. As a result, data collected for the purpose of this study represent the current distribution of *C. cinnaberinus*.

To overcome the potential sampling bias effect caused by the spatial clumping of presence data, we applied the following widely used method designed to deal with a spatial autocorrelation: background manipulation with a bias file (Kramer-Schadt et al. 2013; Phillips et al. 2009). This approach relies on simulating a dataset that provides an independent means on predictive performance assessment (Kramer-Schadt et al. 2013). This dataset was created by generating a random point layer with the same amount of points as the original forest observations in 4 km buffer zones, and these layers were then rasterized and converted to ASCII file format. By generating random points, this approach minimizes the bias that may occur due to spatial autocorrelation between presence data and environmental layers, and it is recognized to improve the goodness of fit of the model (Syfert et al. 2013; Stolar and Nielsen 2014).

Selecting suitable areas

We have used the resulting Maxent modelling output to identify suitable forest patches as well as areas that could potentially be colonized by *C. cinnaberinus*. First, we identified forests occupied by the species by drawing a 50 m buffer (corresponding to the model raster resolution) around each of the known occurrence points and selected forest patches that fell within this buffer as occupied areas. To determine the potentially suitable forest stands for this species, we have selected areas where the Maxent predicted suitability was $>50\%$ (Yan et al. 2018). We also identified forests patches that could be potentially colonized by the species. Since the dispersal distance for *C. cinnaberinus* is not known, we have used an average distance between nearest known localities as a proxy of the movement ability (median = 517 m, quartile range: 258.1–1192.7). The received value corresponds well with known median dispersal distances for other saproxylic beetles of a similar size (Brouwers and Newton 2009; Zauli 2014). Every suitable forest stand that fell within this distance was considered to be potentially available for colonization.

Results

Species habitat distribution

Plotted model predictions indicated that the most suitable areas for *C. cinnaberinus* coincided with the largest and most intact forest complexes of the eastern part of Poland (Fig. 2), which were located mainly in the Carpathian Mountains and the north-eastern region (i.e., the Białowieża Forest). Suitable habitat patches were also identified in the southern-central part of the country (Fig. 2), including forest complexes of the Świętokrzyskie Mts National Park (see Fig. 1). A large number of small and highly scattered habitat patches across the country that could potentially be suitable to harbour *C. cinnaberinus* populations was also observed. However, most of these sites had low predicted suitability and were isolated and beyond the predicted movement abilities for the species (Fig. 2). Large parts of central and western Poland revealed no suitable habitats for *C. cinnaberinus* despite their relatively extensive forest coverage. The average AUC for the replicate runs was 0.943 ± 0.008 SD, indicating that the proposed model accurately predicted the actual species habitat distribution.

Potential for dispersion

The mean area of the forest complexes occupied by *C. cinnaberinus* was 32.02 ha (SD =37.93, range: 0.01–346.72, median = 23.04) and did not significantly differ ($F = 182.2$, $p = 0.89$) from the mean area of suitable forest patches at 25.20 ha (SD = 232.89, range: 0.002–17,192.78, median = 4.39 ha). The median distance between occupied forest complexes was 407.77 m (quartile range: 99.75–1136.98) and differed significantly ($F = 144.1$, $p = 0.01$) from the median distance between the suitable forest patches at 69.87 m (quartile range: 11.59–239.21). Although the mean distance between suitable habitat patches was smaller than the mean distance between occupied forest complexes, most clusters of suitable habitat patches were located over the current species distribution and outside the potential movement range (Fig. 2).

Contribution of environmental variables to the model

The maximum entropy model indicated that the most important variables ($\geq 10\%$ of contribution) in both the training and final models were the mean diameter at breast height of the forest stand, distance to the protected areas, amount of light pollution and amount of moisture of the forest stand (Figs. 3 and 4 and Table 2).

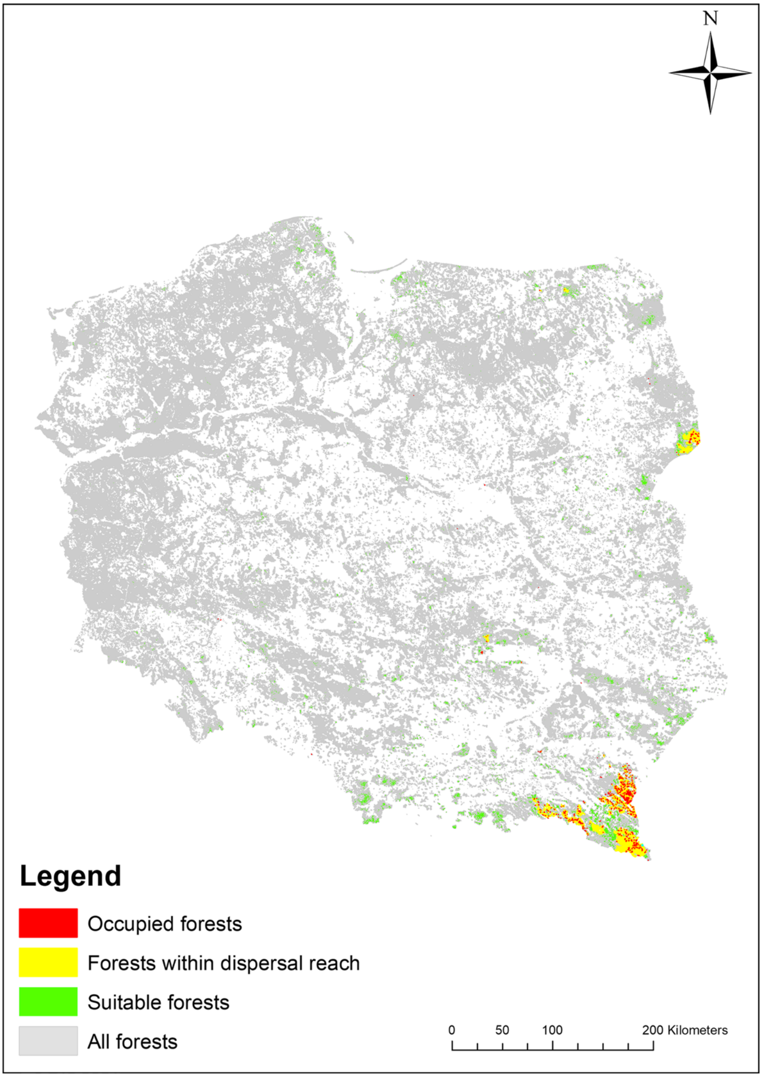

Fig. 2 Predicted suitable forest patches and areas for colonization for *Cucujus cinnaberinus* in Poland derived from a maximum entropy model

Single environmental variables response

The habitat suitability for *C. cinnaberinus* increased with the mean diameter at breast height and reached its highest value at above 50 cm (Fig. 3). The probability of the occurrence of suitable habitats decreased rapidly with increasing distance to the protected areas and increasing level of light pollution, which is a proxy of human activity (Fig. 3). The probability of occurrence of suitable habitats was the highest in forest stands characterized by a sparse and moderate density but dropped sharply where there was no density (e.g.,

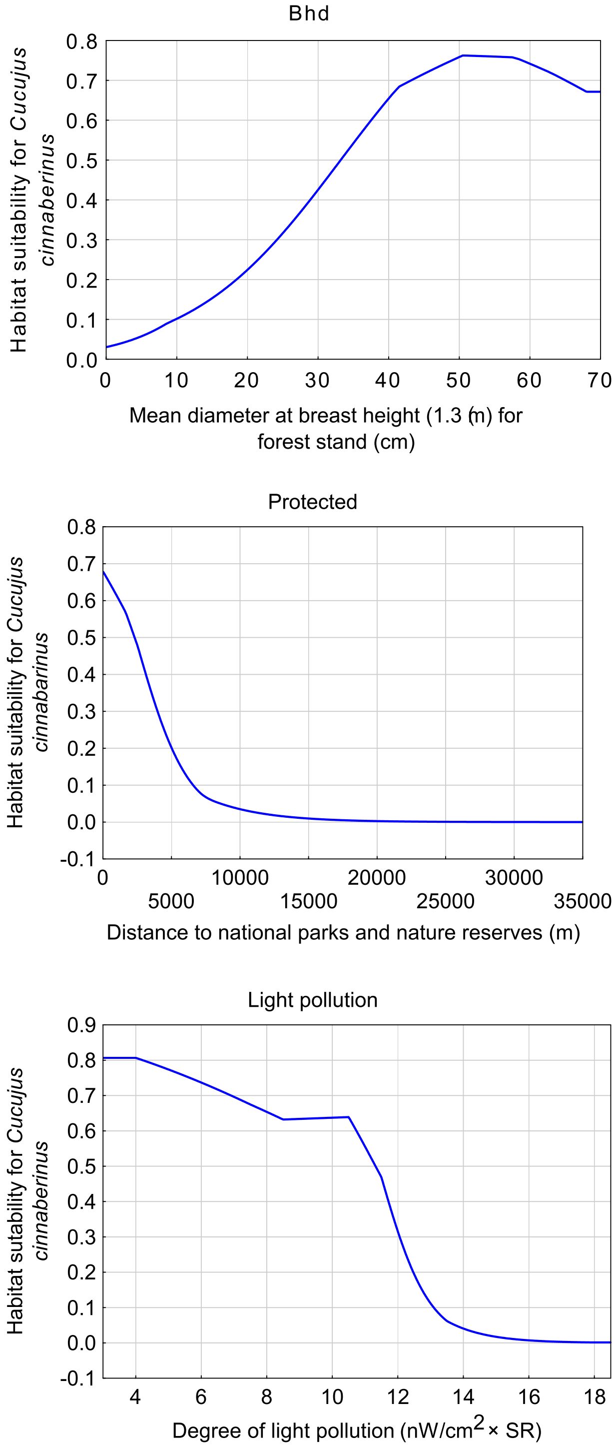

Fig. 3 Effect of the mean diameter at breast height (1.3 m) for the forest stand, distance to protected areas and amount of light pollution on the habitat suitability for *Cucujus cinnaberinus*

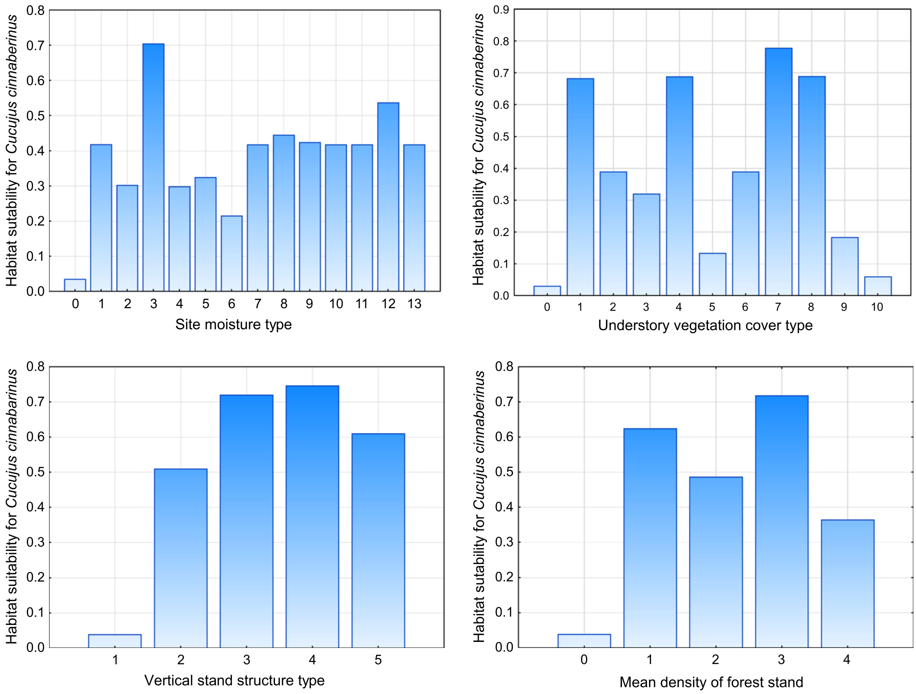

Fig. 4 Effect of the environmental variables on *Cucujus cinnaberinus* on habitat suitability. Site moisture (0—No forest cover; 1—Moist; 2—Drained wet; 3—very moist; 4—wet swamps; 5—wet; 6—drained swamps; 7—dry; 8—flooded wet; 9—riparian flooded; 10—riparian non-flooded; 11—heavily drained swamps; 12—heavily wet swamps; and 13—riparian heavily flooded), understory vegetation cover type (0—no forest cover; 1—noxious plants; 3—heavy turf; 4—turf; 5—herbaceous; litter 6—naked; 7—light vegetation cover; 8—disturbed; 9—moss carpet; and 10—moss and blueberries), vertical stand structure type (1—no forest cover; 2—normal stand; 3—harvested and regenerated stand; 4—multi-storey stand; and 5—harvested stand) and mean density of a forest stand (0—no forest cover; 1—sparse density (30% of forest floor covered by a canopy shadow); 2—patchy density (50% of forest floor covered by a canopy shadow); 3—moderate density (70% of forest floor covered by a canopy shadow); and 4—full density (100% of forest floor covered by a canopy shadow)

clearcuts) or a high density (e.g., dense plantations, Fig. 4). The species inhabited forest stands of a wide array of vegetation cover types (including herbs and low and high shrubs) but was less frequent in areas with bare litter or mossy ground cover (Fig. 4). Furthermore, the species tended to prefer multi-storey stands characterized by high moisture (e.g., very moist sites, Fig. 4).

Discussion

Our large-scale study revealed that the optimal habitats for the flagship saproxylic specialist *C. cinnaberinus* included large forest complexes located mostly in the southeastern and northeastern parts of Poland (Fig. 2). These areas are characterized by the occurrence of forests with long-lasting ecological continuity, with Białowieża Forest and certain

Table 2 Percent contribution of environmental variables used to develop the *Cucujus cinnaberinus* habitat distribution model

Variable	Percent contribution	Permutation importance
Diameter at breast height	37.4	13.6
Distance to protected areas	18.3	42.2
Light pollution	12.3	34.4
Forest site moisture	10.0	1.2
Type of understory vegetation cover	8.2	4.5
Vertical stand structure	5.7	0.1
Mean density of forest stand	3.8	0.0
Forest stand height	2.0	0.1
Distance to roads	1.1	1.9
Stand density code for forest site	0.5	0.0
Distance to inhabited areas	0.5	1.8
Number of trees per 1 ha	0.2	0.1
Perimeter–area ratio of forest stand	0.0	0.1

Carpathian forests representing examples of areas with permanent natural forest coverage since the last glaciation and encompassing the largest and best preserved forests in all of Europe (Bernadzki et al. 1998; Mitchell and Cole 1998; Jaworski et al. 2002; Kucharzyk 2008; Zimny et al. 2017). Moreover, our analyses indicated that suitable habitats are currently overlapped with areas of high conservation priority that are protected as national parks (Białowieża, Bieszczady and Magura national parks; Fig. 1). Other potentially suitable habitats were highly scattered across the country, although they coincided with the distribution of well-preserved forest remnants, including forests of the Świętokrzyskie Mts National Park (see Fig. 1), which are currently known for hosting isolated populations of *C. cinnaberinus*.

Our analyses indicated that secondary forests located mainly in the western part of Poland seem to be unsuitable for *C. cinnaberinus* despite the high total forest coverage and the presence of large forest complexes in this part of the country (Fig. 2). One explanation is that secondary forests still do not have features characteristic of natural habitats and the period of nearly 70 years since their reforestation is not sufficient to reproduce the characteristic features of natural ecosystems. Managed and protected forests of Poland differ significantly in dead wood resources, with the average volume of dead wood at 5.5 m^3/ha and 37.4 m^3/ha in managed forests and national parks, respectively (Bureau for Forest Management and Geodesy 2015). Moreover, human-induced deforestation has likely led to the interruption of the forest's continuity and total extinction of local populations of the studied species. A lack of source population caused by the large-scale habitat fragmentation and limited mobility of *C. cinnaberinus* may prevent population recovery. In the case of saproxylic organisms, even a temporary gap in availability of suitable dead wood hosts could lead to rapid population collapses (Speight 1989; Ranius and Fahrig 2006; Seibold et al. 2015), especially for habitat specialists that are only able to inhabit specific microhabitats.

Limited dispersal ability is a crucial feature for all living organisms that influences the population dynamics, gene flow and extinction risk of local populations (Ranius 2006). This ability is particular important in the case of saproxylic organisms, which usually occupy small and heavily fragmented habitat patches (Brouwers and Newton 2009; Zauli 2014). A large number of saproxylic insects have declining populations and are considered endangered due to low habitat availability in heavily transformed landscapes (Ranius 2006). Unfortunately, direct data on the dispersal abilities of saproxylic insects are extremely rare. Nevertheless, some indirect methods for estimating a species' dispersal potential are available. Given that occurrence of a given species is usually shaped by colonization and extinction processes, it may serve as an indirect measure of a species' colonization potential (Ranius 2006). The results of our study based on the distribution pattern of the saproxylic specialist *C. cinnaberinus* showed that the occupied and potentially suitable forest patches do not differ in size and that the clustering of the latter group is even higher. However, the majority of suitable habitat patches were located far from the occupied areas and beyond the potential movement reach of the species, which might indicate that the biggest obstacle in the dispersal of *C. cinnaberinus* throughout the country is the lack of suitable patches between optimal habitats, which are needed to realize long-distance colonization. One possible solution to this problem is to create, within the species migration reach, stepping stone habitats located between larger conservation structures, such as national parks or forest reserves. Such habitats may be realized by increasing the retention of dead wood of preferable properties in managed forests along the designed dispersal routes. Another possible solution is to conduct species introductions in forested areas that are characterized by high predicted suitability and located beyond the range of the potential spontaneous dispersion of *C. cinnaberinus*. The latter solution might potentially bring faster results, although the stepping stone approach will certainly provide benefits for other dead wood-dependent organisms, which potentially co-occur with *C. cinnaberinus*, a proper umbrella species.

In some parts of Europe, *C. cinnaberinus* may temporarily benefit from some secondary habitats where the recent abandonment of forest fragments (e.g., poplar plantations) contain a high accumulation of dead wood resources. However, based on a long-term perspective, this approach may form an ecological trap that does not ensure the continuity of some key processes related to tree mortality and decomposition, which are essential for the long-term survival of saproxylic organisms (Hunter 1990; Grove 2002). Our study provides evidence that the conservation of old-growth forests, occurrence of natural disturbances, and creation of small sun-exposed gaps in the forest canopy are integral components of the lifecycle of temperate forests (Rademacher et al. 2004; Mitchell 2005; Senf and Seidl 2017) and may ensure the long-term survival of *C. cinnaberinus* populations.

A preferred association between old-growth forests and *C. cinnaberinus* distributions is also highlighted by the contribution of the most important environmental variables to its habitat model. The obtained model indicated that old forests characterized by the occurrence of large trees (based on the mean diameter at breast height in our model) located inside (or near) protected areas (based on the distance to protected areas in our model) are potentially optimal habitats for *C. cinnaberinus*. Other factors associated with high habitat suitability were tree density and stand structure. Our study indicates that species preferred multi-storey stands with moderate density but avoided clear-cut areas as well as high-density stands. Complex vertical structures with open-canopy patches are typical of old-growth natural forests, where the gap dynamic ensures the proper insolation of the stand interior below the canopy (Schelhaas et al. 2003). Although roads and inhabited areas had a weak effect, light pollution had a clear negative impact. This feature is widely used as a measure of anthropopressure (Longcore and Rich 2004; Gaston et al. 2013). Our results suggest that when modelling saproxylic insect distributions, light pollution may be a reliable indicator of human pressure on forest habitats if a better proxy is not available.

The forests of Europe have been subject to long-term anthropogenic modifications that have resulted in the extensive retreat of forest coverage across the continent and structural alterations of remaining forests by forest management practices (Grove 2002; Paillet et al. 2010). Poland is no exception. Despite the successful conservation of old-growth forests in eastern regions of the country, the woodlands of western Poland have experienced heavy anthropogenic transformations, which have deeply simplified their structure and interrupted the ecological continuity. Although habitat restoration, including the implementation of reforestation, reconstruction of natural species compositions and application of more nature-friendly management practices, has been performed for approximately 70 years, the secondary forests of western Poland are still unsuitable habitats for flagship saproxylic habitat specialists. These findings provoke questions about the results of reforestation and the ecological value of secondary forests. Certain evidence has shown the positive effect of habitat restoration in Poland for several threatened animal species, such as the recolonization of western Poland of the grey wolf *Canis lupus* (Nowak et al. 2017) and European Beaver *Castor fiber* (Dzięciołowski and Gozdziewski 1999). However, none of the saproxylic forest relict species have colonized western Poland thus far. Populations of old-growth relicts, such as *Rhysodes sulcatus* or *Boros schneideri*, remain restricted to a few localities in eastern Poland, and their distribution pattern resembles the actual distribution of *C. cinnaberinus* (Polish Biodiversity Information Network 2018). Therefore, we suggest that the initial widespread optimism for rewilding as an effective method of nature conservation (Helmer et al. 2015) should be verified by considering the presence of habitat specialists. Unfortunately, few comprehensive studies have clearly showed the actual value of restored forest habitats for such organisms. Therefore, we strongly encourage further comprehensive studies on the effectiveness of reforestation and rewilding in the conservation of highly specialized forest species.

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Appendix

See Table 3.

Table 3 Values for the categorical stand variables used to develop the *Cucujus cinnaberinus* habitat distribution model

Variable	Value	Description
Forest site moisture	0	No forest cover
Forest site moisture	1	Moisture
Forest site moisture	2	Drained wet
Forest site moisture	3	Very moisture
Forest site moisture	4	Wet swamps
Forest site moisture	5	Wet
Forest site moisture	6	Drained swamps
Forest site moisture	7	Dry
Forest site moisture	8	Flooded wet
Forest site moisture	9	Riparian flooded
Forest site moisture	10	Riparian non-flooded
Forest site moisture	11	Heavily drained swamps
Forest site moisture	12	Heavily wet swamps
Forest site moisture	13	Riparian heavily flooded
Vertical stand structure	1	No forest cover
Vertical stand structure	2	Normal stand
Vertical stand structure	3	Harvested and regenerated stand
Vertical stand structure	4	Multi-storey stand
Vertical stand structure	5	Harvested stand
Understory vegetation cover	0	No forest cover
Understory vegetation cover	1	Noxious plants
Understory vegetation cover	2	Heavy turf
Understory vegetation cover	3	Turf
Understory vegetation cover	4	Herbaceous
Understory vegetation cover	5	Litter
Understory vegetation cover	6	Naked
Understory vegetation cover	7	Light vegetation cover
Understory vegetation cover	8	Degenerated
Understory vegetation cover	9	Moss carpet
Understory vegetation cover	10	Moss and blueberries
Density	0	No forest cover
Density	1	Sparse density (30% of forest floor covered by a canopy shadow)
Density	2	Patchy density (50% of forest floor covered by a canopy shadow)
Density	3	Moderate density (70% of forest floor covered by a canopy shadow)
Density	4	Full density (100% of forest floor covered by a canopy shadow)

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