



Relict of primeval forests in an intensively farmed landscape: what affects the survival of the hermit beetle (*Osmoderma barnabita*) (Coleoptera: Scarabaeidae) in pollard willows?

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Abstract

Background The hermit beetle (*Osmoderma barnabita*) is an internationally protected specialist of tree hollows considered a relic of primeval forests. The backbone of its distribution in eastern Czechia, however, is a system of pollard willows in intensively farmed lowlands. Pollarding, a traditional agroforestry practice inducing formation of tree hollows, was partly abandoned in the area during the twentieth century.

Aim To assess the state of the system of pollard willows and to investigate parameters of pollards and their stands which affect the beetle's presence.

Methods We inventoried pollard trees and beetle distribution across ca 2000 km² of lowlands along the Dyje, Morava and Odra rivers and their tributaries in eastern Czechia and westernmost Slovakia.

Results We found 10 441 pollard willows in 324 stands: most stands contained trees of large diameters and poor health; young trees were rare. Probability of *O. barnabita* presence increased with number of trees in stand, decreased with distance to the nearest occupied stand, and was further affected by the health state of trees.

Discussion Our results show that high hollow density in pollards allows for the existence of specialized, dispersal limited forest organisms in virtually deforested landscapes. They suggest stands should contain at least 200–300 pollard willows to sustain the beetle population. Although the beetle is still widespread over the study area, the existing populations are isolated and subjected to extinction debt.

Implications for insect conservation Large-scale restoration of pollarding practice, planting and pollarding of numerous young trees, and increasing connectivity is vital to facilitate the survival of this hermit beetle population but also support other hollow associated organisms.

Keywords Biodiversity conservation · Extinction debt · Saproxyllic · Agroforestry · Patch size · Habitat connectivity

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Introduction

Agroforestry combines agricultural and forestry practices (Rigueiro-Rodriguez et al. 2009). It was among the traditional land uses in the European landscape and it created structurally and biologically highly diverse, open-wooded habitats such as pasture woodlands and orchards (Burgess 1999; Horak 2014; Kirby and Watkins 2015). Agriculture and forestry intensifications in last ca. 200 years, however, have led to abandonment of agroforestry practices in most of Europe (Eichhorn et al. 2006). As a result, the cover of open woodlands has heavily declined (Hartel et al. 2013). This process was particularly rapid in productive, intensively farmed lowlands (Bičík and Kupková 2002).

Pollard trees were an indispensable part of many European silvopastoral and agricultural landscapes. Pollarding, i.e. the periodical removal of the upper branches of a tree by pruning, allowed to combine grazing, hay or crop production on the ground with fodder and/or fire-wood production in the tree layer (Petit and Watkins 2003). Pollarding has surprisingly wide, positive effects on biodiversity associated with trees. Not only does it prolong the lifespan of trees, it is also a technique of tree veteranization. In young trees, pollarding induces formation of deadwood microhabitats mostly associated with old trees, such as tree hollows and bare deadwood (Read 1996; Sebek et al. 2013; Siitonen and Ranius 2015). Stands of pollard trees thus offer high density of otherwise rare deadwood microhabitats to a wide spectrum of saproxylic (deadwood dependent) organisms (Čížek et al. 2020). Typical inhabitants of pollard trees include specialists of tree hollows, such as the hermit beetle (*Osmoderma* spp.; Coleoptera: Scarabaeidae), but also the stag beetle *Lucanus cervus* (Linné, 1758) (Coleoptera: Lucanidae), and the Rosalia longicorn *Rosalia alpina* (Linné, 1758) (Coleoptera: Cerambycidae) that exploit other deadwood microhabitats (Sebek et al. 2012, 2013; Castro and Fernández 2016).

Central European lowlands are a typical example of highly productive, agricultural landscapes. The lowlands of eastern Czech Republic and western Slovakia have been intensively farmed and nearly devoid of forests since the Middle Ages (Bičák and Kupková 2002). Today, their landscape grain is extremely coarse; land cover consists mainly of large blocks of arable land (Skokanová et al. 2009; Šálek et al. 2018). Forests cover a small proportion of the area. Most stands are commercial, plantation-like forests managed by clearcutting with an 70–120 year rotation cycle. The hermit beetle (*Osmoderma barnabita* Motschulsky, 1845), considered a relic of primeval forests (Eckelt et al. 2018) and an umbrella species for tree hollow fauna (Ranius 2002a; Ranius et al. 2005), is, nevertheless, present in the area (e.g. Hauck 2006). Agriculture intensification, mechanization and forced land collectivization took a heavy toll on the landscape in the last century. The process culminated in the late 1950s. The average size of landscape grain increased more than ten times; most grasslands, hedgerows and other non-forest wooded habitats were converted into arable fields, and watercourses were channelized (Skokanová et al. 2009). This, of course, caused a drastic disruption to the network of grasslands with pollard trees. As a result, the hermit beetle population is likely to be severely fragmented and threatened (Čížek et al. 2020).

In order to assess the importance of pollard trees for the survival of the hermit beetle and to contribute to the conservation of the beetle and fauna locally associated with pollard trees, we inventoried the pollard trees and mapped the presence of the hermit beetle in area of ca. 2000 km² of lowlands along the Dyje, Morava and Odra rivers and their tributaries

in eastern Czech Republic and western Slovakia. We then tested how patch size (number of pollard trees in a group), connectivity between them, and characteristics of pollard trees affect the probability of the hermit beetle presence.

Materials and methods

Study area and data collection

We surveyed pollard willows and assessed the occurrence of *O. barnabita* in the floodplains of south and east Moravia (along the Morava and Dyje rivers and their tributaries), and north Moravia (along the Odra river in the Poodri Protected Landscape Area), Czech Republic, and in the floodplains of the Zahorie Protected Landscape Area (W of the town of Senica), Slovakia. Altogether, an area of about 2000 km² of lowlands between Znojmo, Brno, Lanžhot, Senica, and Ostrava was inspected for the presence of pollard trees from 2016 to 2019 (Fig. 1).

Potential stands of pollard willows were identified using historical (1952–53) and current aerial photographs (provided by Cenía 2019). On the historical photographs, we searched for wooded meadows and other open wooded habitats in the floodplains and along watercourses. Each area with open wooded habitats in the 1950s was surveyed in the field if actual aerial photographs indicated the presence of woody vegetation today. In the field, we searched for trees with branches growing from the top of a short trunk (2–5 m), which is the typical habitus of traditionally pollarded trees in the area (Fig. 1).

For each stand of pollard willows encountered during the field survey, we recorded the position (GPS coordinates) and number of trees; we also assessed the presence of *O. barnabita* based on the presence of adults, their remains, larvae or typical larval frass in hollows. As “stands”, we considered spatially distinct groups (separated by at least 150 m) of pollards or even single trees. Altogether 324 stands were recorded. For pollard stands in south and east Moravia (258 stands, covering 80% of all recorded stands), we further assessed the mean characteristics of the trees in the stand; these were: tree health state and conditions of surroundings (Fig. S1 of Supplementary Material), diameter class, hollow size and approximate time since last pollarding (see Table 1 for characteristics descriptions).

In order to assess the effect of individual tree characteristics on the presence of *O. barnabita* at tree level, for part of the pollard willows (mainly in heterogeneous stands) we recorded GPS coordinates and recorded values of the above-mentioned characteristics for each tree (Table 1). Altogether, the characteristics were measured for 3 010 individual willows.

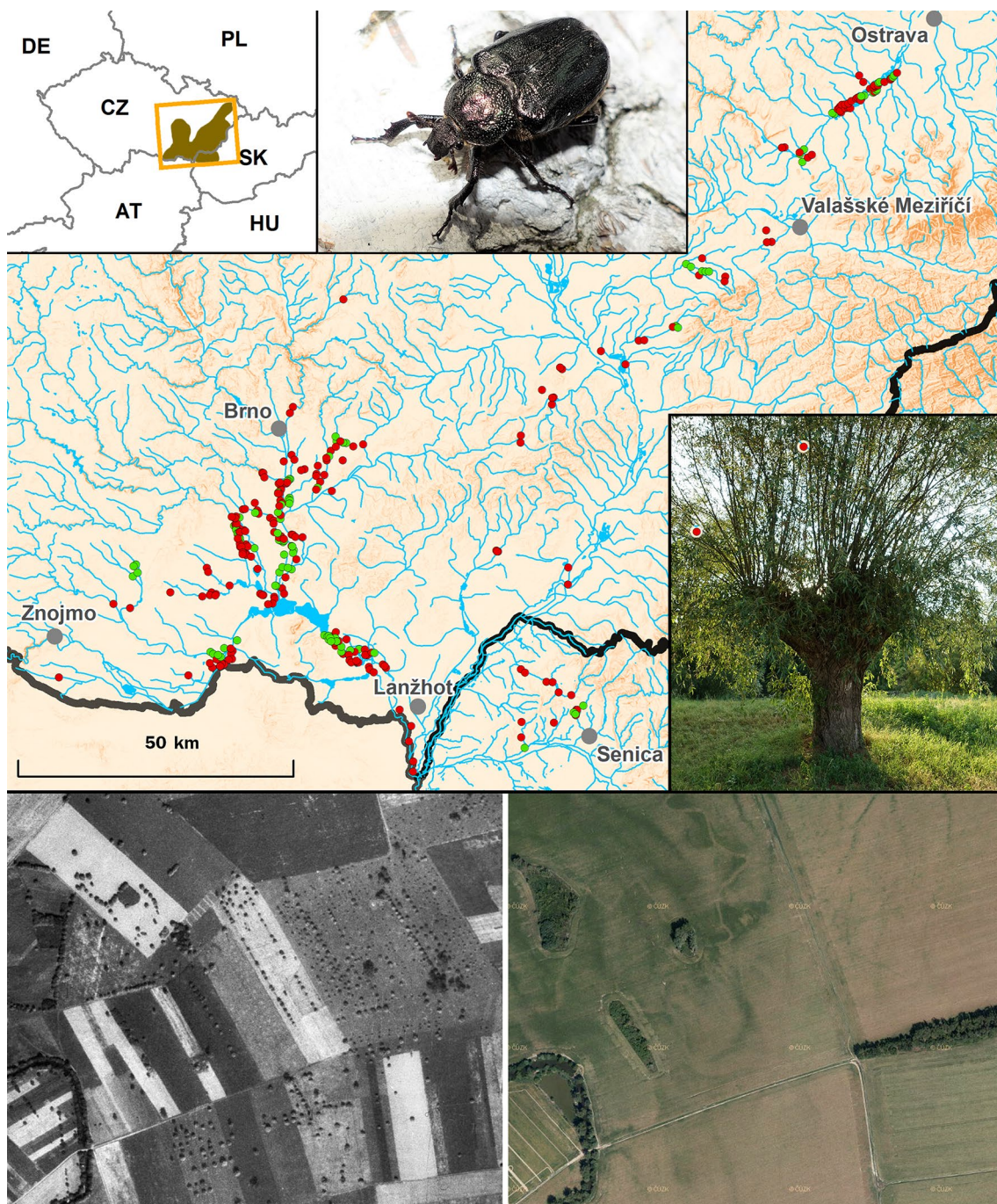


Fig. 1 Map of the study area with stands of pollard willows where *Osmoderma barnabita* was present (green points) and absent (red points) with indication of its position, the beetle, and typical pollard

willow. Bellow: Historical (1953, left) and recent (2018, right) aerial photos showing the decline of solitary trees, mostly pollard willows, in an agricultural landscape

We then created a distance matrix of all stands and trees with their spatial position marked (324 stands, 3 010 trees). For each stand/tree we created variables representing distance to the nearest occupied stand/tree (they are referred to as *distStand* and *distTree*, respectively; see Table 1 for details). Due to skewed distribution, these variables were log-transformed before use in statistical analysis (see below).

Statistical analysis

We first tested the effect of the number of pollard willows in a stand and the distance to the nearest occupied stand, and mean tree characteristics in a stand on the probability of occurrence of *O. barnabita* in stands. Then, we used the data at tree level to test the effect of distance to the nearest

Table 1 List of explanatory variables measured at tree and stand level with their description and range

Tree level	Description	Range (mean)	Abbrev.
Distance to the nearest occupied tree	Distance of a tree to the nearest tree with <i>O. barnabita</i> present. Calculated as Euclidean distances of GPS coordinates. Log-transformed before analysis	0.0000086–0.43 (0.047) (approx. 0.0008–42 km)	<i>distTree</i>
Diameter	Diameter class of a tree: 1 = 1–10 cm, 2 = 10–30 cm, 3 = 30–60 cm, 4 = 60–100 cm, 5 = 100+ cm	1–5 (3.9)	<i>diameter</i>
Health state	Health state class of a tree; from 1 = pollard in a good state with a small or no visible hollow, to 4 = pollard in an advanced stage with disintegrated or collapsed trunk and little or no wood mold; see Fig. S2 for details	1–4 (2.8)	<i>state</i>
Hollow size	Tree's hollow size class: 1 = none or small hollow with little wood mold, 2 = larger hollow in upper parts of tree trunk filled with wood mold, 3 = large hollow mostly in whole trunk with wood mold, 4 = large hollow in whole trunk, mostly open with no or little wood mold left	1–4 (2.9)	<i>hollow</i>
Surroundings	Conditions in close surroundings of a tree; from 1 = tree in open conditions, to 4 = tree in shady conditions, fully overgrown by other trees or shrubs. See Fig. S2 for details	1–4 (2.3)	<i>surroundings</i>
Pollarding	Approximate time since pollarding, in classes of: 1 = no or short sprouts of max. 2 m long (1–2 years), 2 = branches max. 10–15 cm thick (2–5 years), 3 = branches from 15 to 25 cm thick (5–15 years), 4 = branches > 25 cm thick (15 and more years since last pollarding)	1–4 (2.5)	<i>pollarding</i>
Stand level	Description	Range (mean)	Abbrev.
Distance to the nearest occupied stand	Distance of a stand to the nearest stand with <i>O. barnabita</i> present. Calculated as Euclidean distances of GPS coordinates. Log-transformed before analysis	0.0017–0.43 (0.04) (approx. 0.17–42 km)	<i>distStand</i>
Number of trees in stand	Number of pollard trees in stand, the tree was a part of a stand if it was closer than 100 m from the closest pollard tree. Log-transformed before analysis	1–1000 (32)	<i>Trees</i>
Diameter (mean)	Mean diameter class of trees in stand	1–5 (4.1)	<i>diameterM</i>
Health state (mean)	Mean health state class of trees in stand	1–4 (2.7)	<i>stateM</i>
Hollow size (mean)	Mean hollow size class of trees in stand	1–4 (2.8)	<i>hollowM</i>
Surroundings (mean)	Mean surrounding conditions of trees in stand	1–4 (2.4)	<i>surroundingsM</i>
Pollarding (mean)	Mean time since pollarding of trees in stand	1–4 (2.6)	<i>pollardingM</i>

occupied tree and tree characteristics on the probability of occurrence of *O. barnabita* in trees. We fitted generalized linear models using a binomial distribution (*logit* link function) with presence/absence of *O. barnabita* in stands/trees acting as dependent variables. At stand level, we found strong correlations between a tree's health state and its diameter (Pearson's correlation coefficient $r=0.64$), between the health state and hollow size ($r=0.94$), and between pollarding and surroundings ($r=0.67$). Very similar strong correlations were found at tree level: $r=0.60$, $r=0.91$, and $r=0.64$, respectively for the above-mentioned pairs. Therefore, we decided to use only tree health state and surroundings as explanatory variables associated with tree characteristics.

At stand level, we first tested the number of trees in a stand and distance to the nearest occupied stand (both as continuous explanatory variables) using the full dataset on stands (324 stands of pollard trees). To provide information for conservation managers, we looked for threshold

values in the relationship between the response variable (presence/absence of *O. barnabita*) and the explanatory variables of the model. We used the inference trees, from the family of recursive partitioning methods combined with bootstrapping, to get threshold confidence bands (Hothorn et al. 2006). Values of the response variable over the threshold of the explanatory variable signify suitable habitat for *O. barnabita*, whereas values below the threshold signify unsuitable habitat.

Further, we used forward selection to test the effect of mean tree characteristics (continuous explanatory variables) together with the number of trees in stand and distance to the nearest occupied stand using a restricted dataset of 258 pollard stands for which we had mean tree characteristics recorded. For each mean tree characteristic (i.e. *health stateM*, *surroundingsM*, see Table 1), we included also the second polynomial function in the model, as there was a presumption that the characteristics could have a hump-shaped

effect on the probability of *O. barnabita* occurrence, i.e. the probability would reach maximum/minimum in middle values of the characteristics' range. The final model contained only significant variables.

Finally, at tree level (3010 trees), we tested the effect of the distance to the nearest occupied tree and the tree characteristics *health state* and *surroundings* on *O. barnabita* occurrence probability. Again, forward selection was used to build a final model and second polynomial functions of tree characteristics were added to the models to test for hump-shaped relationships.

All analyses were performed in R 3.5.1 (R Core Team 2018). We used the *party* package for recursive partitioning (Hothorn et al. 2010) and the *boot* package for calculations of confidence intervals with the bootstrap method (Canty and Ripley 2017).

Results

The survey included 324 stands of pollard willows with 10 441 trees. The hermit beetle was found in 99 stands; i.e. in 31% of them. The restricted dataset from south Moravia contained 258 pollard stands with information on tree characteristics; *O. barnabita* was found in 79 of them. Most stands consisted of trees of relatively large diameters, very few stands consisted of or contained also young trees (Table 1, Figure S2 of Supplementary Material; see also Živě břehy 2020). Similarly, the health state of trees in most stands was rather poor. The dataset at tree level contained 3 010 trees; *O. barnabita* was found in 152 of them (5%), indicating that even within an occupied stand, many trees are not inhabited by the beetle.

Stand level

Both the number of trees in a stand and the distance to the nearest occupied stand affected the probability of *O. barnabita* occurrence. It increased with the number of trees and decreased with increasing distance from the nearest occupied stand (Fig. 2). Thresholds identified by recursive partitioning showed that the suitable stands should consist of more than 28 trees (CI: 10–62 trees) and should be less than 1.33 km (CI: 0.82–1.55 km) from the nearest occupied stand (Fig. 3. See Table 2 for details).

Using the restricted dataset with stands from south Moravia for which tree characteristics were available, the final model, in addition to a significant effect of the number of trees in a stand ($\chi^2_{(1)} = 95.6$, $P < 0.0001$) and distance to the nearest occupied tree ($\chi^2_{(1)} = 41.0$, $P < 0.0001$), further revealed a significant effect of tree health state ($\chi^2_{(1)} = 8.94$, $P = 0.003$) and its polynomial ($\chi^2_{(1)} = 21.6$, $P < 0.0001$) on the occurrence probability. The effect of health state was

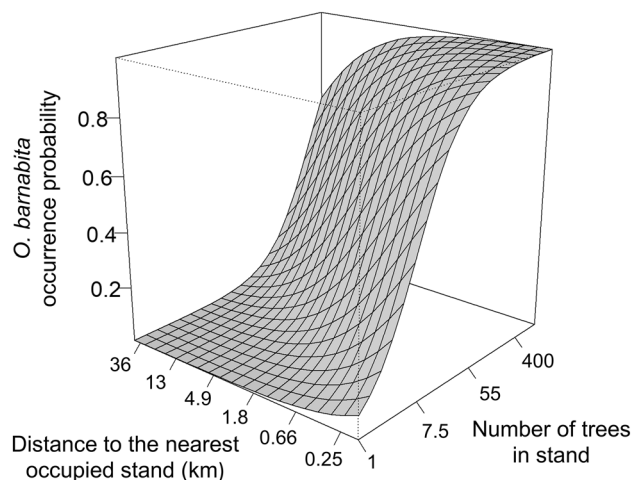


Fig. 2 Occurrence probability of *O. barnabita* in pollard stands predicted by generalized linear model with binomial distribution based on two major significant explanatory variables: number of trees in stand (*Trees*; log-scale) and distance to the nearest occupied stand (*distStand*; log-scale). Tick labels give values recalculated to reflect the original variable meaning, number of trees and distance in km, respectively

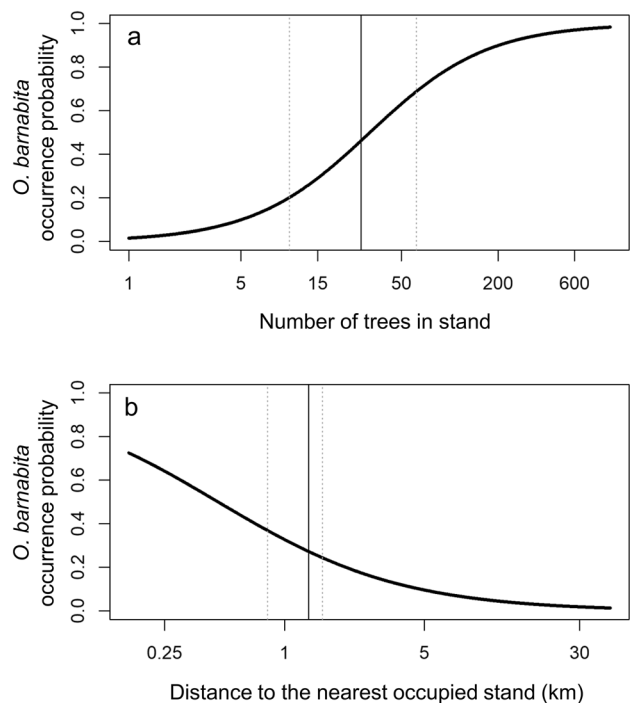
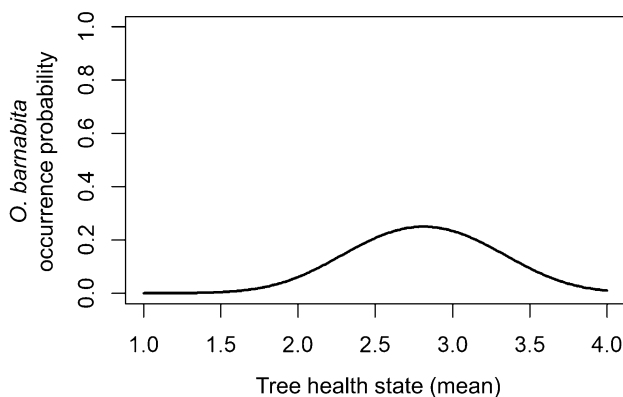


Fig. 3 Threshold values for explanatory variables, **a** number of trees in stand and **b** distance to the nearest occupied stand. Thresholds are denoted by full vertical lines (with confidence limits denoted by dashed grey lines). The x-axis values were recalculated to reflect the original variable meaning

Table 2 Threshold values (and their confidence limits) for the distance to the nearest occupied stand (*distStand*) and number of trees in stand (*Trees*) identified by recursive partitioning method combined with bootstrapping

Variable	Threshold	Value	Confidence limits	
			Lower	Upper
Distance to the nearest occupied stand (<i>distStand</i>)	Model (log) meaning (km)	- 4.31 1.33	- 4.78 0.82	- 4.15 1.55
Number of trees in stand (<i>Trees</i>)	Model (log) meaning (trees)	3.33 28	2.30 10	4.13 62

Threshold values give the value of the explanatory variable where response variable (occurrence probability of *O. barnabita*) reaches significantly higher probabilities, therefore indicate suitable habitats (see also Fig. 3). Bold print gives values recalculated to reflect the original variable meaning

**Fig. 4** The effect of health state (as mean characteristic of trees in stand) on the occurrence probability of *O. barnabita* in willow stands as predicted by final model (see model parameters in Table 3; GLM with binomial distribution). The prediction displayed is based on mean values for the number of pollards in a stand and distance to the nearest occupied stand

hump-shaped (Fig. 4) with maximum occurrence probability between 2.4 and 3.3 and very low probabilities in healthy trees and in advanced stages/disintegrated trees (Fig. S1a of Supplementary Material, categories 1 and 4). The effect of surroundings was not significant. See Table 3 for coefficient estimates of the final model.

Tree level

At tree level, the final model revealed a negative effect of the distance to the nearest occupied tree ($\chi^2_{(1)} = 127.6$, $P < 0.0001$), a slight hump-shaped effect of health state ($\chi^2_{(1)} = 7.9$, $P = 0.005$; 2nd polynomial: $\chi^2_{(1)} = 72.3$, $P < 0.0001$), and a slight positive effect of surroundings ($\chi^2_{(1)} = 14.3$, $P = 0.0002$). See Table 4 for coefficient

Table 3 Final model at stand level

Parameter	Coefficient estimate	Standard error	z value	P level
(Intercept)	- 28.90	5.25	- 5.51	< 0.0001
<i>Trees</i>	1.47	0.23	6.49	< 0.0001
<i>distStand</i>	- 1.14	0.21	- 5.50	< 0.0001
<i>stateM</i>	13.83	3.57	3.88	0.0001
$I(\text{stateM}^2)$	- 2.46	0.67	- 3.68	0.0002

Coefficient estimates for parameters of the generalized linear model with binomial distribution testing the effect of explanatory variables on the occurrence probability of *O. barnabita* in pollard stands. Only significant model parameters were included in the final model. See Results section for parameter tests (*Trees*=log-transformed number of trees in stand, *distStand*=log-transformed distance to the nearest occupied stand, *stateM*=health-state of the tree)

Table 4 Final model at tree level

Parameter	Coefficient estimate	Standard error	z value	P value
(Intercept)	- 10.24	0.82	- 12.57	< 0.0001
<i>distTree</i>	- 0.43	0.04	- 9.74	< 0.0001
<i>state</i>	3.98	0.60	6.68	< 0.0001
$I(\text{state}^2)$	- 0.87	0.12	- 7.47	< 0.0001
<i>surroundings</i>	0.33	0.09	3.75	0.0002

Coefficient estimates for parameters of the generalized linear model with binomial distribution testing the effect of explanatory variables on the occurrence probability of *O. barnabita* in trees. Only significant model parameters were included in the final model. See Results section for parameter tests (*distTree*=log-transformed distance to the nearest occupied tree, *state*=health state class of a tree, *surroundings*=conditions in surroundings of a tree)

estimates of the final model and Fig. S3 of the Supplementary Material for prediction curves.

Discussion

The survey of the pollard willows and *Osmoderma barnabita* showed that the beetle is still widespread in the intensively farmed landscape of southern and eastern Moravia and adjoining farmland areas of Poodří (N Moravia) and Záhorie (W Slovakia). It shows that the formerly common and rather intensive agroforestry practice created and sustained habitats allowing for survival of highly specialized, dispersal limited organisms. The network of pollards and the beetle distribution are, however, severely fragmented, and most pollards are old and of poor health. The probability of *O. barnabita* presence was affected mainly by the number of pollard trees in a stand, by the distance between stands, and tree health state. The latter was closely related to tree

diameter and hollow size. Parameters of surroundings exhibited weaker effect. Below, we discuss the results of the study in relation to the biology and conservation of the beetle.

Stand size

The probability of *O. barnabita* presence depended mainly on the number of trees in a stand, which represents the size of a habitat patch. Confidence interval of the threshold value indicated that the probability was very low for stands containing less than ten pollard trees. However, it increased rapidly with the increasing number of trees and was high in stands with more than 62 trees. Around 200 trees, the probability was higher than 0.8. Low occupancy at tree level as well as historical circumstances that have led to the current state of pollard stands, however, raise the suspicion that the effective number of pollards needed for survival of *O. barnabita* population in a stand is probably higher.

The network of pollard trees along watercourses was nearly continuous until the mid-1950s (Čížek et al. 2020). We may thus expect also virtually continuous distribution of *O. barnabita* within the network at that time. Major land use changes in the second half of the 1950s (Skokanová et al. 2009) inflicted a great decline of pollard trees by their active removal mainly due to ploughing of alluvial meadows and hedges, or channelization of watercourses (Jech 2001). After that period, we may expect that the numbers of pollards gradually declined at a slower pace, attributable to abandonment of pollarding practice rather than active removal of the trees. Therefore, using current stand size may lead to underestimation of the beetle's extinction risk. Some small stands might still be occupied at present because they were connected to substantially larger ones in the past.

A further study, testing the relationship between historical decline of pollard trees and current occurrence of the beetles, is needed in this context. For instance, the hermit beetle populations in French hedgerows persisted in areas where only few changes in habitat density occurred over time (Dubois et al. 2009; Dodelin et al. 2017). Our findings somewhat contrast the findings of Kadej et al. (2016), who found that *Osmoderma* presence in rural avenues increases with proximity to forests. Our results, though, are in accord with Oleksa and Gawronski (2006), where the proximity of forests had no effect. In the studied system, the pollards are found mainly in areas with very low or no forest cover. This is due to their role as source of firewood in the places where other sources (i.e. forest) were limited. Moreover, those few forests present in the area are managed as productive high forest stands and do not provide enough hollow trees to host the beetle.

The changes in the historical vs. current state of the pollard stands have to be considered when justifying the minimum number of pollard trees needed to sustain *O. barnabita*

population in the long term. Minimum stand size is likely to be higher than the 62 pollard trees identified by the recursive partitioning method in our study (Table 2). The target number of pollard willows (or other softwood trees) for an *Osmoderma* population should probably range between at least 200 and 300. The recommended number of pollard willows is higher than that of veteran oaks recommended for *O. eremita* (Ranius 2000). This is because oaks live much longer than willows and also because the number of beetles in a tree depends on its size (Ranius 2001, 2002b). Small trees offer small habitat patches for the associated organisms. When there are only small trees available, there is a need to ensure the presence of greater numbers of trees in stands (Platek et al. 2019). In Sweden, the average inhabited oak (with DBH of 130 cm) hosted ~ 11 beetles (Ranius 2000), but numbers tend to vary among years (Ranius 2001; Lindman et al. 2020). In Italy, where the inhabited trees were smaller (mean DBH of 65 cm), the average tree hosted only 0.5–2 individuals (Chiari et al. 2013). Similarly, pollard willows generally host only a few individuals of the hermit beetle (Šebek 2011). The low occupancy of trees in our study (only 5% hosted the beetle) also suggests the need for larger stands in order to avoid extinction due to stochastic events (Ranius 2001; Lindman et al. 2020).

Connectivity, health state and surroundings

The probability of *O. barnabita* presence decreases with distance from the nearest occupied stand or tree. This is due to well documented dispersal limits described for the hermit beetle as well as other saproxylic beetles (e.g. Ranius and Hedin 2001; Buse et al. 2007). Distances that individuals of *Osmoderma* may cover by flying range from 200 to 700 m based on radio-tracking methods (Dubois and Vignon 2008; Hedin et al. 2008). Despite that genetic studies suggest higher mobility of *Osmoderma* (Oleksa et al. 2013), habitat connectivity still plays a crucial role in its survival, with short distance among trees increasing the probability that suitable trees are colonised (Lindman et al. 2020). Increasing connectivity of pollard stands is thus another measure to increase the probability of survival of local *Osmoderma* populations (Dubois et al. 2009). The threshold identified in our analysis shows that the beetle may have problems surviving in stands that are more than 1300 m away from another occupied one (an even shorter distance, 800 m, was revealed by confidence interval). At least partial restoration of the former network of pollards along watercourses in the study area would thus be necessary to ensure the survival of local populations.

The health state of trees affected the presence of *O. barnabita* at both stand and tree level. The hump-shaped curve of the relation as well as the strong correlation between health state and hollow size (see Material and Methods) indicate

that too healthy trees lack suitable hollows and are thus unsuitable for the hermit beetle. Trees of poor health, on the other hand, are usually old and their large, open hollows rarely contain enough wood mould for successful development of the beetle's larvae. The fact that most existing pollards are old and their health is poor is another source of great concern. The number of available trees will decrease in the future, inevitably threatening not only most of the *Osmoderma* populations recorded today, but also other hollow associated organisms.

In tree surroundings, increased closure of woody vegetation had a positive effect on the beetle presence. This is rather surprising as *Osmoderma* prefers insulated trees and trunks and free space near hollow entrances (Ranius 2002b; Miklín et al. 2018). It, however, might be an artifact of the fact that most trees growing in the open are young and recently planted. The young pollards often lack suitable hollows, but are usually well cared for, whereas older trees that host the bulk of the population are often forgotten and overgrown by surrounding vegetation. However, dense surrounding vegetation may compromise survival of shade-intolerant willows. It may also present a barrier for dispersing individuals. Flying beetles may have problems to navigate in dense and shady vegetation and thus get lost without reaching a potentially suitable hollow tree (Dubois and Vignon 2008).

Conclusions

Our study shows that pollard willows act as an important refuge of tree hollow specialist. The hermit beetle is still widespread in the study area. Its distribution is, however, severely fragmented. Existing populations of *Osmoderma* and other hollow specialists are thus isolated and subjected to extinction debt. This, together with the mostly poor health of remaining pollards and low numbers of younger ones, are the main threats to the survival of the hollow associated organisms.

Substantial effort is needed to ensure the existence of hollow trees which represent crucial structures for fauna of old trees in the area. Proper care should consist of re-pollarding old trees and clearing their surroundings to make the stands more open, park-like habitats; livestock grazing can be used to maintain the openness. In order to increase stand size, planting new willows within stands and in the proximity of existing trees is needed. To restore connectivity between patches, new willows should be planted along watercourses or roads to serve as stepping stones between distant stands. In both cases, when planting new trees, pollarding must be practiced from early age of trees to ensure development of hollows in them.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-021-00309-8>.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Animal care permitting was not required for this work.

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