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Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles

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Abstract

Aim: Open woodlands are biologically highly diverse habitats, and veteran (i.e., old, senescent) trees are key structures supporting their biodiversity. Open canopy structure had been maintained by both natural- and human-induced disturbances. In the past two centuries, suppression of such disturbances, together with forestry intensification, has turned most lowland woodlands into closed-canopy forests. We investigated the effect of increased canopy closure on veteran trees and several threatened beetles associated with them.

Location: Floodplain woodlands along the lower Dyje and Morava rivers, Czech Republic.

Methods: We used an approach combining the study of aerial photographs with on-ground survey of veteran trees and associated endangered beetles. The aerial images were used to obtain the information on historical (1938) and recent (2009) canopy closure in the area of 146 km^2, where we mapped large oaks (d.b.h. >70 cm), hollow trees and three associated beetles including the hermit beetle (*Osmoderma barnabita*), the great capricorn beetle (*Cerambyx cerdo*) and the jewel beetle *Eurythyrea quercus*.

Results: The presence of large oaks, hollow trees and their associated beetle species are negatively related to recent high canopy closure, and the historical level of canopy closure matters, as in nowadays closed-canopy stands, the beetles and veteran trees are more common in places that were rather open in 1938 than in the places with closed canopy already in 1938. Moreover, the health state of veteran trees highly depends on the canopy closure.

Main conclusion: The negative effect of canopy closure on veteran trees and their endangered inhabitants is several decades delayed and may thus often go undetected. In the forests, however, large and hollow trees and their associated biodiversity are relics of the past, more open conditions. The restoration of open woodlands is therefore vital for preventing their further decline. Conservation management planning needs to take this into account wherever, veteran trees and associated biota are concerned.

KEYWORDS
conservation management, extinction debt, land cover changes, open woodlands, saproxylic beetles, veteran trees

1 | INTRODUCTION

Forest cover has increased considerably in Europe over the past two centuries (Agnoletti, 2007; Bičík, Jeleček, & Štěpánek, 2001; Devi et al., 2008; Piussi, 2000). At the same time, a substantial portion of woodland biodiversity has, however, declined severely across the continent (Bergman, 2001; Kopecký, Hédl, & Szabó, 2013; Nieto & Alexander, 2010; van Swaay, Warren, & Loïs, 2006). The decline in forest biodiversity is usually attributed to intensive practices of modern forestry (Agnoletti, 2007; Benes, Cizek, Dovala, & Konvicka, 2006; Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008). For that reason, increasingly large areas of forests are protected from intensive or any use in effort to alleviate the decline (Schultze, Gärtner, Bauhus, Meyer, & Reif, 2014; Winter, 2012).

The reason behind the recent decline in woodland biodiversity despite an increase in forest cover and conservation efforts, however, lies rather in an altered structure of forest habitats. Through most of the Holocene, temperate woodlands in Europe had a diverse spatial, species and age structure characterized by a low-contrast-border mosaic of patches with various levels of canopy closure from open to closed forests (Alexander, 1998; Rackham, 2003; Vera, 2000), which supported both light-demanding and shade-tolerant woodland organisms. The varied canopy closure was primarily maintained by natural factors such as fires, grazing of large herbivores and windthrows (Bengtsson, Nilsson, Franc, & Menozzi, 2000; Bradshaw & Hannon, 2004; Hultberg, Gaillard, Grundmann, & Lindbladh, 2015; Vera, 2000). Later, the natural disturbances were supplemented or gradually replaced by traditional forest management including, for example, pasture grazing, coppicing and burning (Jamrichová et al., 2013; Kirby & Watkins, 2015; Rackham, 2003; Szabó, Müllerová, Suchánková, & Kotačka, 2015). In the past two centuries, however, the remaining natural disturbance factors have largely been suppressed and the traditional management has been replaced by the practices of modern forestry (Bürgi, 1999; Brunet, Felton, & Lindbladh, 2012). This led to a substantial increase in canopy closure and formerly common open woodlands were replaced by closed-canopy forests in most of the temperate Europe, which led to a decline in light-demanding woodland species (Bugalho, Caldeira, Pereira, Aronson, & Pausas, 2011; Hartel et al., 2013; Lindbladh et al., 2007; Müllerová, Szabó, & Hédl, 2014; Szabó, 2010). The increased canopy closure affected commercial as well as protected forests across the continent (Bürgi, 1999; Miklín & Čížek, 2014; Saniga, Balanda, Kucbel, & Pittner, 2014).

Biota associated with dead wood (i.e., saproxylic organisms) was generally thought to profit from an increase in forest cover and especially increased amounts of dead wood in protected forests (Vandekerkhove, De Keersmaeker, Menke, Meyer, & Verschelde, 2009; but see the meta-analysis of Lassauce, Paillet, Jactel, & Bouget, 2011). While some saproxylic organisms are indeed favoured by such changes (e.g., Drag et al., 2015; Horák, Chumanová, & Hilszczański, 2012), others experience a severe decline similar to that of other biota associated with open woodlands such as plants or butterflies (Bergman, 2001; Hédl, Kopecký, & Komárek, 2010; Kopecký et al., 2013; van Swaay et al., 2006). For instance, saproxylic beetles requiring sun-exposed dead wood have higher red list status than species preferring shady forests (Seibold et al., 2015). Despite the increased forest cover and high dead wood volumes in many protected forests, the decline in saproxylics is especially true for the species associated with veteran trees and their specific microhabitats (Siitonen & Ranius, 2015).

Veteran trees are trees that have passed beyond maturity and often bear dead wood microhabitats such as cavities, bare wood and dead branches (Kraus et al., 2016). The term "veteran tree" may include even younger individuals that have developed similar characteristics as a result of adverse growing conditions or injury (Lonsdale, 2013; Siitonen & Ranius, 2015). Veteran trees are considered keystone ecological structures of woodlands (Lindenmayer, Laurance, & Franklin, 2012; Lindenmayer et al., 2014; Read, 2000). Interestingly, the populations of many veteran tree-associated organisms are often found in the last remains of open woodlands such as game reserves and chateau parks, rather than in strictly protected forests where trees are protected from cutting but where high canopy closure prevails (Ranius et al., 2005). The above suggests that biota associated with veteran trees is negatively affected by canopy closure. This assumption is supported not only by the preference for open conditions among numerous flagship species associated with veteran trees (Albert, Platek, & Cizek, 2012; Buse, Ranius, & Assmann, 2008; Ranius & Jansson, 2000) but also by generally better thriving of veteran trees in open conditions (Lonsdale, 2013; Read, 2000). The fact that canopy closure may compromise the survival and recruitment of veteran trees is, however, insufficiently documented and thus often ignored.

Moreover, open woodlands that have been affected by humans for centuries were often considered of limited value for nature conservation. Instead, management measures allowing for increasing canopy closure are widely advocated and practised in protected areas, presuming to restore "natural" conditions by minimizing human impact (Schultze et al., 2014; Winter, 2012). In the absence of natural disturbances, such approaches, unfortunately, do not lead to the desired "natural" stage and often have detrimental consequences to veteran trees and their associated biodiversity. The reason why we often fail to see the problem may also lie in a delayed response of veteran trees to canopy closure. Deteriorating health of tree veterans under closed-canopy conditions temporarily increases the amounts of dead wood and postpones the negative effects of canopy closure on saproxylic organisms, while it supports other species than those associated with veteran trees. Veteran tree-associated species may thus actually undergo the extinction debt (Jackson & Sax, 2010; Tilman, May, Lehman, & Nowak, 1994).

To address this important issue and provide background information for qualified management decisions, we investigated the survival and distribution patterns of veteran trees and their specialized beetle inhabitants under the changing conditions of increasing canopy closure. Using aerial photographs, we quantified the past and recent canopy closure over 146 km^2 of the lowland floodplain forests and meadows of Central Europe. We mapped trees that can be considered veteran, including oaks of large diameters, hollow trees and trees occupied by three beetle species typically associated with veteran trees, that is the great capricorn beetle (*Cerambyx cerdo* Linnaeus 1758), the hermit beetle (*Osmoderma*

FIGURE 1 The study area lies in the south-eastern part of Czechia, near the border with Austria and Slovakia

barnabita Motchulsky 1842) and the jewel beetle *Eurythyrea quercus* (Herbst 1784). This study specifically aims to (1) describe changes in woodland canopy closure using old and recent aerial photographs; (2) evaluate the effect of canopy closure on the presence and mortality of veteran trees; (3) assess the importance of present canopy closure for endangered model species of saproxylic beetles, (4) evaluate the influence of the past levels of canopy closure on the present distribution of veteran trees and model beetles, and (5) propose the principles of the conservation management of protected woodlands based on our findings.

2 | METHODS

2.1 | Study area

Our study covers 146 km^2 of the south-eastern part of the Czech Republic, namely along the lower Dyje and Morava rivers and their confluence (Figure 1). About 60% (*c*. 85 km^2) of the area is covered by forests and woodlands (Miklín & Hradecký, 2016). Prevailing trees are pedunculate oak (*Quercus robur*), narrow-leaf ash (*Fraxinus angustifolia*), hornbeam (*Carpinus betulus*) and field maple (*Acer campestre*). The area is an important biodiversity refuge (Miklín & Čížek, 2014). Minimum intervention management prevails in state reserves (*c*. 250 ha), while the rest of the area consists of commercial forests under clear-cut management system. Traditional forest managements such as pasture, coppicing and pollarding were abandoned 150–60 years ago, in favour of the cultivation of high forests with 90–150-year rotation (Altman et al., 2013; Sebek et al., 2015; Vrška et al., 2006). Today, the area comprises a mosaic of commercial oak/ash plantations, managed using c. 2 ha clear-cuts (Blaha, 2007), interspersed with fragments of open and formerly open woodlands and meadows with old (>150 years) trees, mainly oaks.

2.2 | Land use/land cover data

Changes in the woodland structure (canopy closure) and cover were quantified using aerial photographs from the years 1938, 1953, 1976 and 2009 with 1:5,000 scale of vectorization. Based on the canopy closure (Figure 2a) and with high precision and minimal spatial generalization, we distinguished by visual photo-interpretation patches of the following *woodland types*: (1) *closed unstructured forests* (homogenous closed-canopy stands), (2) *closed structured forests* (stands with heterogeneous closed canopy with visible differences in tree heights), (3) *semi-open woodland* (visible ground among trees, with average distance between trees <10 m), (4) *open woodland* (average distance between trees 11–40 m), (5) *wooded meadows* (grasslands with scattered trees, average distance between trees >40 m) and (6) *clear-cuts*. The photo-interpretation was made by a single, experienced person (JM) to avoid bias caused by a subjective view. Land cover data thus consisted of patches as basic units; for each patch, we had the information on the woodland type in 1938, 1953, 1976 and 2009.

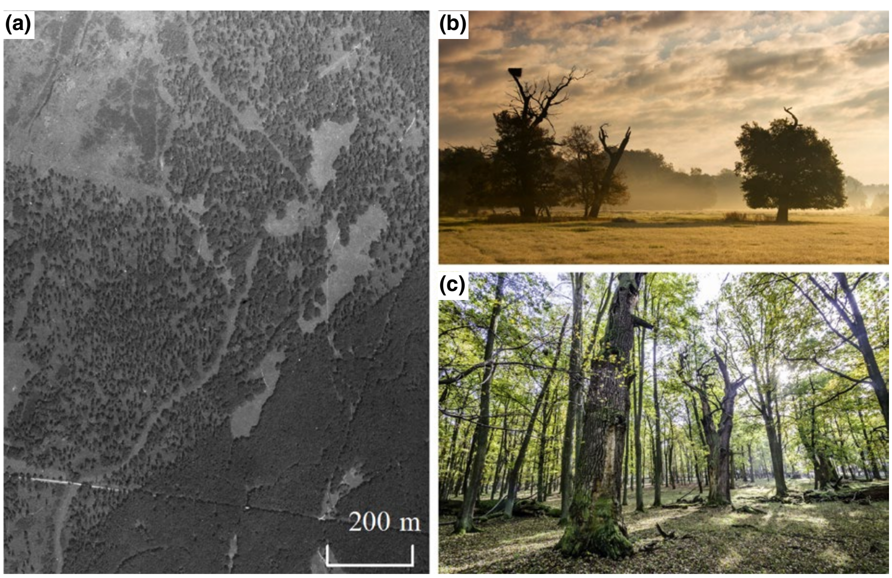

FIGURE 2 (a) Large areas of open woodlands in 1938; (b) old oaks grown in open conditions; (c) a veteran tree grown in a closed forest

2.3 | Tree and beetle data

The data on the presence of trees that can be considered as veterans (*see below*) as well as data on the presence of trees inhabited by three saproxylic beetles associated with veteran trees, *C. cerdo*, *O. barnabita* and *E. quercus*, were recorded during an intensive survey of the whole study area between 2006 and 2015 (Miklín, Hauck, Konvička, & Cizek, 2017).

The first two beetle species represent flagship saproxylic species listed in EU Habitats Directive (CEC, 1992), and the last one is among the most threatened European beetles (Bílý, 2002). All three species prefer sun-exposed veteran trees. While *C. cerdo* is associated with live oaks, *O. barnabita* inhabits hollows of trees, and *E. quercus* develops in dry dead wood of old, both live and dead oaks (Bílý, 2002; Buse et al., 2008; Ranius et al., 2005). All three species are relatively common in the area, but only *C. cerdo* is ubiquitous; the presence of *O. barnabita* and *E. quercus* is rather clumped.

There is not a single definition of a veteran tree (Lonsdale, 2013). Veterans can be trees with distinct features of ageing, trees with deadwood microhabitats or trees apparently older than others. To minimize bias caused by a single point of view, for the purpose of this study, we used several clearly delineated categories of trees that can be considered veterans:

1. Large oaks with d.b.h. >70 cm. The threshold was chosen to only include trees with apparently larger d.b.h. than the surrounding stands (i.e., large solitary trees, former open-grown trees and standards),
2. Hollow trees, that is, trees with cavities detectable from the ground,
3. Trees inhabited by *C. cerdo*, identified by the presence of typically sized and shaped exit holes on a tree (Buse et al., 2008),
4. Trees inhabited by *O. barnabita*, identified by the presence of typical larval frass in tree hollows (Dubois et al., 2009),
5. Trees inhabited by *E. quercus*, identified by the presence of typically sized and shaped exit holes on a tree (Bílý, 2002).

For each tree, we recorded tree species, GPS coordinates, diameter at breast height (d.b.h.), situation (closed forest, edge/semi-open and solitary), health state and the presence of target beetles.

The woodlands of the whole study area were thus divided into patches characterized by their woodland type (i.e., canopy closure) in the past and at present and for each of these patches we had information on the number of large oaks, hollow trees and trees inhabited by the three above-mentioned beetle species.

2.4 | Analyses

Firstly, we analysed the percentage cover of woodland types in the past and at present using the information on the woodland structure and its changes from aerial photographs.

Secondly, we analysed two phenomena: (1) the effect of the present woodland type on the densities of the large oaks, hollow trees and trees inhabited by the three beetle species, and (2) the effect of the past woodland type on the densities of focal trees in present *closed unstructured forests* (woodland type category 1). For (1), we used the data on the patches with known woodland type in 2009 together with the data on the trees growing in such patches (5,224 oaks with d.b.h. >70 cm, 1,136 hollow trees, 2,601 trees with *C. cerdo*, 80 trees with *O. barnabita* and 273 trees with *E. quercus*). For (2), we used the data on the patches covered by *closed unstructured forests* in 2009 for which we knew the woodland type in 1938, together with the data on the trees growing in such patches (4,164 oaks with d.b.h. >70 cm, 891 hollow trees, 1935 trees with *C. cerdo*, 60 trees with *O. barnabita* and 191 trees with *E. quercus*). The numbers of large oaks, hollow trees and trees inhabited by the three beetle species acted as a response variable, while the woodland type in 2009 for (1) and the woodland type in 1938 for (2) were explanatory variables. Due to a high number of zeros in the response variables, we analysed the effect of woodland type on the number of trees by fitting zero-inflated regression models with Poisson distribution, separately for each focal tree type. In every single analysis, we selected the best model from three possible models by log-likelihood ratio tests. Firstly, assuming no differences among the woodland types, we fitted a null model with a patch area (in ha, ln-transformed) as an offset variable accounting for differences in the patch size (and thus effectively analysing the density of trees per ha). Secondly, we added a woodland type as an explanatory variable to the model but let the zero-inflation parameter be constant among all the woodland types. We compared this model with the null model. Thirdly, we added a woodland type to the zero-inflation process to allow for differences in the generation of absences (zeros) among the woodland types. We compared the third model with the second one. The regression models were fitted using “PSCL” package (Zeileis, Kleiber, & Jackman, 2008) in R 2.14.2. (R Development Core Team, 2012). Only, the oldest (1938) and most recent (2009) data of the cover of individual woodland types were used because the main changes in the canopy structure in the study area occurred between 1938 and 1953 (*see below*).

To reduce the possibility that the changes in the veteran tree density could fully be explained by factors not included in this study such as the changes in forest management, we investigated the relation between canopy closure and veteran tree health. Using the data obtained during the intensive survey, we analysed the probability of tree death in relation to its d.b.h. and the growth situation, that is the canopy closure in its immediate surroundings: forest interior (closed-canopy conditions), forest edge (semi-open conditions) and solitary trees (open-grown conditions). For this, we used a generalized linear regression model with binomial distribution (logit link), where tree health state (alive = 0, dead = 1) was a dependent variable, d.b.h. was an explanatory variable, and the growth situation (canopy closure) was a factor variable. An interaction between the d.b.h. and the situation (d.b.h.:situation) was added to the model in order to assess the differences in the slope shape among trees growing in different canopy closure situations.

3 | RESULTS

3.1 | Changes in the canopy closure and woodland cover

While the woodland cover was stable (ranging from 8,412.4 to 8,538.7 ha), the cover of individual woodland types changed

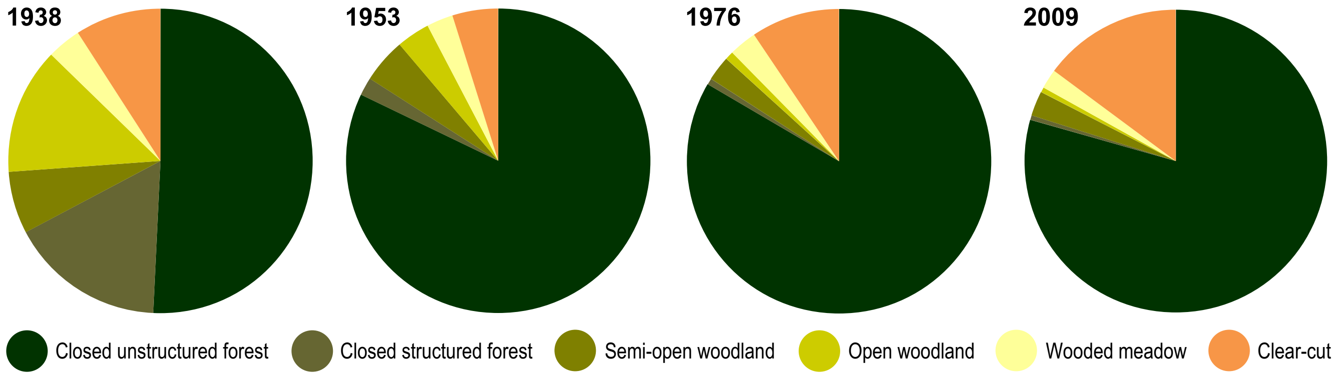

FIGURE 3 Woodland cover in the studied years

TABLE 1 Woodland cover and its changes

	1938		1953		1976		2009	
Woodland types	[ha]	[%]	[ha]	[%]	[ha]	[%]	[ha]	[%]
Closed unstructured	4,290.4	50.8	6,907.7	82.1	7,108.8	83.4	6,779.9	79.4
Closed structured	1,394.9	16.5	162.1	1.9	56.2	0.7	41.3	0.5
Semi-open	557.5	6.6	399.2	4.7	225.1	2.6	226.3	2.7
Open	1,134.8	13.4	297.6	3.5	75.1	0.9	45.2	0.5
Wooded meadow	305.1	3.6	236.3	2.8	252.8	3.0	177.6	2.1
Open and structured woodlands total	3,392.3	40.1	1,095.1	13.0	609.3	7.2	490.4	5.7
Clear-cut	769.7	9.1	409.6	4.9	802.1	9.4	1,268.3	14.9
Total	8,452.4	100	8,412.4	100	8,520.1	100	8,538.7	100
Processes of change	**1938–1953**		**1953–1976**		**1976–2009**		**1938–2009**	
Canopy closure	2,283.3	26.1	594.7	6.7	240.3	2.7	2,456.9	27.0
Canopy opening	222.7	2.5	136.1	1.5	136.3	1.6	124.0	1.4
Clear-cutting	335.8	3.8	779.3	8.8	1,216.6	13.8	1,226.4	13.5
Reforesting	675.2	7.7	373.6	4.2	728.6	8.3	685.7	7.5
Afforesting	152.3	1.7	392.4	4.4	240.5	2.7	579.7	6.4
Deforesting	209.0	2.4	307.5	3.5	193.8	2.2	426.1	4.7
Disappearance of solitary trees	120.6	1.4	35.9	0.4	57.1	0.6	139.2	1.5
No change	4,741.9	54.3	6,240.9	70.4	5,976.3	68.0	3,465.9	38.1

substantially between 1938 and 2009 (Figure 3, Table 1). A rapid increase in the canopy closure is the main feature of the changes as the unstructured closed-canopy forest replaced most of other woodland types. The highest rate of canopy closure occurred between 1938 and 1953, when 2,283.3 ha (or 67.3%) of open and structured woodlands were replaced by a closed forest. Later, the rate of the loss of open habitats was still rapid, though decreasing (54.3% between 1953 and 1976, and 39.4% between 1976 and 2009, respectively). Over the whole studied period, 3,025.9 ha (89.2%) of open and structured woodlands were lost, while only 124.0 ha appeared *de novo*.

3.2 | Effect of the present woodland type

The woodland type in 2009 was found to be a significant predictor of veteran tree density and beetles associated with them (Figure 4) (see Appendix S1 for the results of model selection procedure and Appendix S2 for estimated parameter coefficients). Oaks with d.b.h. >70 cm were most abundant in open woodlands and least abundant in clear-cuts ($\chi^2_{(10)} = 728.3$, $p < .0001$). The density of hollow trees and those occupied by *C. cerdo* was highest in open woodlands and wooded meadows and lowest in clear-cuts ($\chi^2_{(10)} = 306.3$, $p < .0001$; $\chi^2_{(10)} = 617.3$, $p < .0001$). The

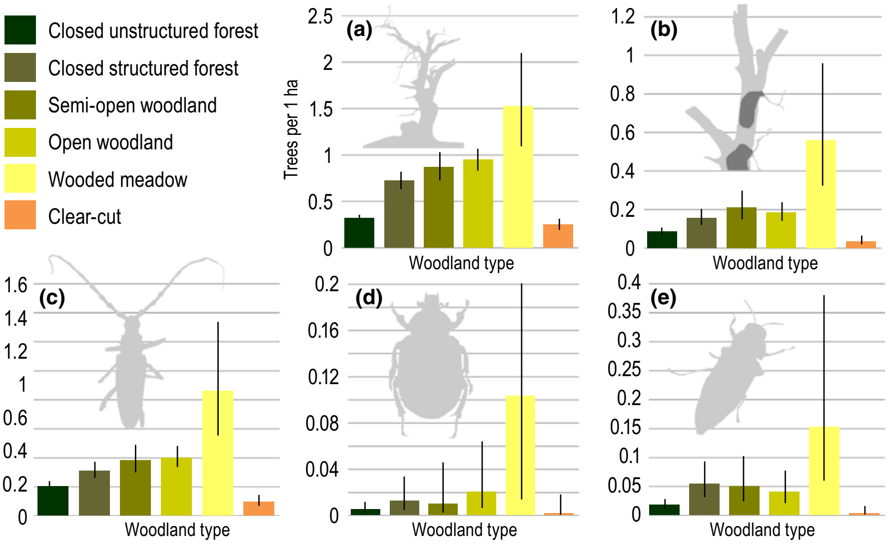

FIGURE 4 Average numbers (with CI) of (a) large oaks, (b) trees with hollows, (c) trees with *Cerambyx cerdo*, (d) trees with *Osmoderma barnabita* and (e) trees with *Eurythyrea quercus* per hectare in present-day (2009) woodland types

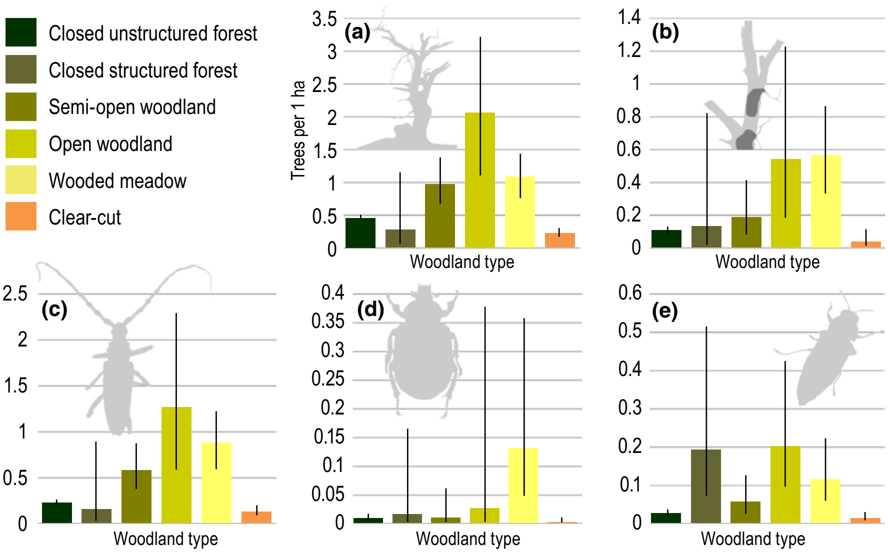

FIGURE 5 Average number of (a) large oaks, (b) trees with hollows, (c) trees with *Cerambyx cerdo*, (d) trees with *Osmoderma barnabita* and (e) trees with *Eurythyrea quercus* per hectare in present-day (2009) closed unstructured forest according to their woodland type in 1938

density of trees occupied by *O. barnabita* was highest in wooded meadows and lowest in clear-cuts and closed unstructured forests ($\chi^2_{(5)}$ = 52.9, p < .0001). The density of trees occupied by *E. quercus* was highest in wooded meadows, open woodlands and closed structured forests but lowest in clear-cuts and closed unstructured forests ($\chi^2_{(5)}$ = 85.2, p < .0001).

3.3 | Situation in closed forests: effect of the woodland type in 1938

In the stands classified as closed unstructured forests in 2009, the woodland type in 1938 had a significant effect on the density of veteran trees and beetles associated with them (Figure 5, or see Appendix S2 for estimated parameter coefficients). The density of large oaks, hollow trees and trees occupied by *C. cerdo* was highest in former open woodlands and wooded meadows, but lowest in clear-cuts, followed by closed unstructured forests ($\chi^2_{(5)}$ = 1,051, p < .0001; $\chi^2_{(5)}$ = 174, p < .0001; and $\chi^2_{(5)}$ = 232.2, p < .0001, respectively). The density of trees occupied by *O. barnabita* was highest in former wooded meadows ($\chi^2_{(5)}$ = 25.1, p = .0001). The number of trees occupied by *E. quercus* was highest in former open woodlands and closed structured forests, but lowest in former clear-cuts and closed unstructured forests ($\chi^2_{(5)}$ = 74.4, p < .0001). In general, the current closed-canopy forests had a higher number of focal trees if their canopy was open or structured (wooded meadows, semi-open woodlands, open woodlands and closed structured forests) in 1938 than if it was already closed at that time.

3.4 | Effect of canopy closure on tree health

Data of 4,823 veteran trees were analysed, including 924 solitary trees, 2,197 trees at the forest edge or semi-open stands and 1,702 trees in the forest interior. The probability of tree death increased with d.b.h., and it was affected by the growth situation (Table 2). All three parameters in the model were significant, d.b.h.: $\chi^2_{(1)}$ = 326.9, p < .0001; situation: $\chi^2_{(2)}$ = 83.9, p < .0001; and their

TABLE 2 Tree mortality model parameters. Coefficient estimates (on *logit* scale) for parameters of generalized regression model with binomial distribution testing the effect of d.b.h., growth situation (*solitary/edge/interior*) and their interaction on the probability of tree death (See also Figure 6)

Model parameter	Estimate	*SE*	*z* value	*p*
Intercept (Edge)	−3.368	0.218	−15.44	<.0001
d.b.h.	0.019	0.002	10.38	<.0001
Situation interior	−0.073	0.323	−0.23	.82
Situation solitary	0.319	0.356	0.90	.37
d.b.h.: Situation interior	0.006	0.003	2.12	.03
d.b.h.: Situation solitary	−0.003	0.003	−1.15	.25

interaction d.b.h.:situation: $\chi^2_{(2)}$ = 10.1, *p* = .006. The trees growing in closed-canopy conditions of the forest interior had significantly higher mortality than the trees growing at the edge or the solitary trees (semi-open and open conditions). For instance, at the d.b.h. of 150 cm, the probability of death was .6 for the trees in the forest interior, whereas for the solitary trees and the trees at the edge, it was .35 and .4, respectively. The negative effect of closed canopy increased with diameter of a tree (Figure 6).

4 | DISCUSSION

Our study relates historical levels of canopy closure to the presence of veteran trees and organisms associated with them. We quantify changes in the canopy closure and demonstrate their negative effect on the occurrence of flagship saproxylic beetles and their habitats. We also show the relationship between the canopy closure and veteran tree mortality. Our results indicate that the disappearance of veteran trees from closed-canopy stands is a gradual process lasting for at least several decades. The study thus offers a unique perspective on the changes in the structure of European lowland woodlands and may serve as a case study of their effect on biodiversity.

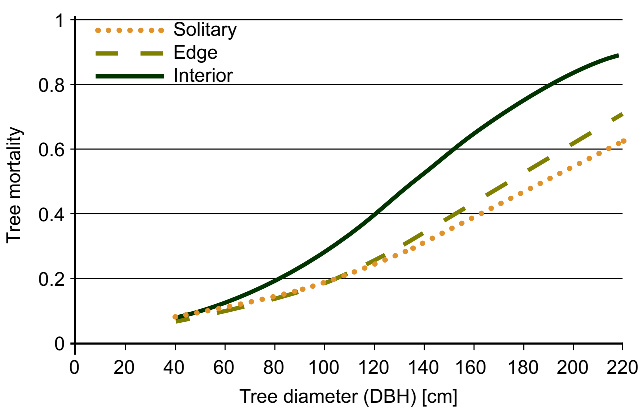

FIGURE 6 Tree mortality. Probability of tree death in relation to the tree diameter (d.b.h.) and the growth situation. Solitary trees and trees at the forest edges had significantly lower probability of death than trees in the forest interior. Estimated values predicted from the regression model with binomial distribution are displayed

4.1 | European lowland woodlands in transition

The decline in open woodlands reflects socio-economic changes in the past two centuries that have affected other forests in the region and also most lowland woodlands in temperate Europe (Bércesné Mocskonyi, 2011; Brunet, Felton, & Lindbladh, 2012; Bürgi, 1999; Drag et al., 2015; Hédl et al., 2010; Saniga et al., 2014; Szabó et al., 2015; Varga, Ódor, Molnár, & Bölöni, 2015). Formerly open, mainly oak-dominated woodlands managed by traditional silvicultural practices such as wood–pasture, burning or coppicing have been largely transformed into high forests with closed canopies. In the absence of most natural disturbances, these closed forests lack the formerly common open and semi-open habitats. While the timing of the management change might differ locally, the pressure on open woodlands, its causes and outcomes are likely universal across the continent. Its negative effect on biodiversity is substantial and documented in literature (Chudomelová, Hédl, Zouhar, & Szabó, 2017; Hartel et al., 2013; Horak et al., 2014; Plieninger et al., 2015). It is, however, still rarely perceived as a problem that needs to be addressed by nature conservation.

4.2 | Effect of increased canopy closure on veteran trees and beetles

Higher canopy closure investigated in our study was found to have led to higher mortality of veteran trees. Further, we found that closed-canopy stands had more veteran trees if they were open in the 1930s. Our results thus point to the fact that the occurrence of veteran trees in a stand is largely conditioned not only by the current canopy closure of the stand but also by the closure decades ago.

Forestry activities have certainly had a direct effect on the presence of veteran trees by their active removal (Doerfler, Müller, Gossner, Hofner, & Weisser, 2017). On the other hand, large veteran trees are locally valued for aesthetic reasons as important landmarks in the study area and the quality of their timber is low. The trees were thus often retained even in the commercial stands. Although we lack the data on the trees removed by forest management, our analysis of veteran tree mortality suggests that canopy openness is a key factor affecting the survival as well as the presence of veteran trees in forests.

The existing veteran trees grew up in more open conditions with no or little competition from other trees. This is well illustrated by our results as the occurrence of veteran trees in closed-canopy forests was mostly conditioned by their open structure in the past. Such formerly open-grown trees are lower than their younger, closed-canopy grown neighbours, and they are unable to compete with them for light (Rackham, 1998). Forest-grown trees are taller and thinner, and their increment growth is slower (Altman et al., 2013); they are thus unlikely to gain the form of tree veterans. Further, under the highly competitive conditions of closed canopy, any decrease in tree vitality likely results in the tree death. This is the most likely explanation why closed-canopy conditions increase the mortality of existing veteran trees and block the recruitment of new veteran tree candidates. Relatively, rapid death of weakened trees under closed-canopy conditions means that potential veterans die before acquiring veteran features such as dead wood microhabitats as these usually need long time to develop (Doerfler, Müller, Gossner, Hofner, & Weisser, 2017).

Given the negative effect of closed-canopy conditions on veteran trees and the expansion of closed forests in the study area, a substantial decline in the availability of veteran trees seems to be an inevitable scenario in the near future. Biota associated with veteran trees is thus most likely subject to the extinction debt in the study area (Jackson & Sax, 2010; Tilman et al., 1994). The veteran trees which such biota occupies today have formed thanks to the past managements and its long-term existence is unlikely if the closed-canopy conditions prevail.

The effect of closed canopy on veteran trees may depend on various factors including, for example, light requirements of the tree species. Shade-tolerant trees are likely to be less affected than shade-intolerant ones. Many saproxylic beetles including the three studied species though require open canopy conditions or depend on shade-intolerant trees (Albert et al., 2012; Dubois & Vignon, 2008; Dubois et al., 2009; Ranius, 2002). Even if some veterans occur in shady forests, they are thus unlikely to harbour numerous species associated with veteran trees from more open conditions (Parmain & Bouget, 2017).

4.3 | Implications for conservation

Open-grown, large and hollow trees are keystone ecological structures sustaining woodland biodiversity (Lindenmayer et al., 2012, 2014; Manning, Fischer, & Lindenmayer, 2006; Müller, Jarzabek-Müller, Bussler, & Gossner, 2014; Siitonen & Ranius, 2015). Recently, more studies have revealed that trees in open conditions are especially important for saproxylic beetles as they host diverse communities with more red-listed species than trees in closed-canopy conditions (Horak et al., 2014; Parmain & Bouget, 2017; Sebek et al., 2016). Although even veterans in closed-canopy conditions may harbour rich saproxylic communities (Parmain & Bouget, 2017), these communities are usually characterized by diverse species composition containing rather generalist species and fewer red-listed individuals (Sebek et al., 2016).

Our study provides the evidence of gradual, long-lasting and detrimental effect of increased canopy closure on the occurrence of veteran trees and their associated biodiversity. We do not claim that there will be no veteran trees in closed-canopy forests. Yet, our data show that there will be substantially fewer veteran trees, especially if the closed-canopy conditions remain established for a long time.

A recent dramatic increase in canopy closure is a problem affecting lowland woodlands in Europe (*see above*). It needs to be addressed adequately by the conservation management as sustaining the current high canopy closure would inherently lead to a further decline in veteran trees and loss of associated biodiversity. This problem, however, is rarely considered by conservation practice and even science. Numerous studies, for example, compared the biodiversity of managed and unmanaged forests mostly concluding that minimal intervention management is important to sustain forest biodiversity (Lassauce, Larrieu, Paillet, Lieutier, & Bouget, 2013; Martikainen, Siitonen, Punttila, Kaila, & Rauh, 2000; Paillet et al., 2010). In fact, most of the "unmanaged" forests in Europe have now been unmanaged for only a few decades. Therefore, their species composition, spatial structure and biodiversity have at least partly resulted from the past traditional management rather than from the current absence of any management. Modern forestry measures as well as application of strict "hands-off" approach generally result in closed-canopy forests if natural disturbances creating open woodlands are missing. Neither approach is thus likely to conserve the biodiversity associated with veteran trees and open woodlands. Conservation approaches in most of the European temperate woodlands strongly contrast with the approaches applied in similar ecosystems of North America (e.g., oak woodlands). While in the latter, grazing, prescribed burning and thinning are among the most often employed measures (applied as they are supposed to mimic natural disturbances creating open woodlands) to maintain or restore open woodlands (Abella et al., 2017; Abrams, 2005; Harrington & Kathol, 2009); these are extremely rarely practised in Europe.

Responsible management of protected forests must take into account local history of the site (Foster et al., 2003; Jamrichová et al., 2013). Whenever there is a need to ensure continuous presence of veteran trees, the maintenance of existing veterans must go together with the recruitment of new cohorts of trees that could replace the old ones in the future. Conservation measures maintaining the open canopy of the forests, for example coppicing, wood–pasture, burning and/or significant thinning, are needed in such situations. Furthermore, the studies comparing the effects of various management approaches on woodland biota have to consider relevant temporal scales for correct interpretation of observed patterns. Studies concerning organisms associated with habitats that came into existence about a century ago, such as insects and lichens inhabiting veteran trees, need to consider the management practised centuries ago as it may be crucial for the explanation of today's distribution patterns of the studied organisms.

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Authors' contributions: J.M. and L.C. conceived the ideas; D.H. and O.K. collected the field data; J.M. and P.S. analysed the data; and J.M., P.S. and L.C. wrote the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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