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ORIGINAL PAPER

Habitat requirements of the endangered longhorn beetle *Aegosoma scabricorne* (Coleoptera: Cerambycidae): a possible umbrella species for saproxylic beetles in European lowland forests

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Abstract Detailed knowledge of habitat requirements is an essential prerequisite for efficient conservation of any endangered species. Despite the grain support beetle *Aegosoma scabricorne* (Cerambycidae) being one of the largest European beetles, and an endangered, disappearing, species in Central Europe, its bionomics remain relatively poorly known. *A. scabricorne* is known as a polyphagous species on broadleaved trees; thus, to investigate its habitat preferences 174 broadleaved trees (87 occupied and 87 unoccupied by the species) were surveyed in the area of southern Moravia (Czech Republic) in 2015. The species was found to be strongly associated with declining or freshly dead trees that are, preferably, further damaged (breakage of stem or primary branch, hollows, etc.) and it particularly thrives on large trees (diameter >50 cm). Surprisingly, stem exposure to the sun was shown to be an unimportant characteristic for this species. However, in this study the number of exit holes was significantly smaller on the shaded north-facing quarter of the stem. Our results suggest concrete conservation measures to support the species. We also suggest that this species may be used as an umbrella species for saproxylic beetles of European lowland forests.

Keywords Conservation · Czech Republic · Ecology · Endangered species · Surrogate species · Veteran trees

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Introduction

European forests host an amazing species richness and diversity of organisms associated with moribund trees and dead wood (i.e., saproxylic organisms) (Speight 1989; van Helsdingen et al. 1996; Nilsson et al. 2001). However, a decrease in forested area, along with forest degradation, has led to a significant loss in diversity of saproxylic organisms (Nieto and Alexander 2010; Stokland et al. 2012), with beetles representing one of the most species-rich and endangered groups of these organisms (Jonsell et al. 1998; Farkač et al. 2005). The current adverse state of most European forests for these organisms occurs mainly because of changes to the tree species composition, reduced age, and modified spatial structure of the forests and by the presence of relatively small amounts of dead wood (Siitonen et al. 2000; Vodka et al. 2009) and veteran trees (Lindenmayer et al. 2012).

In general, the most species-rich assemblages of saproxylic beetles are found in lowland forests (Brunet and Isacsson 2010). Because lowland forests are the forests most affected by humans over the long term (Whitehouse 2006), saproxylic beetles associated with them are among the most endangered (Seibold et al. 2015) but the ecological requirements of only a few have been studied sufficiently to enable efficient conservation. Such better-studied species are used as umbrella species (Lambeck 1997; Simberloff 1998) for the entire lowland forest community of saproxylic beetles. For example, *Cerambyx cerdo* Linnaeus 1758, *Cucujus cinnaberinus* (Scopoli 1763), *Limoniscus violaceus* (P.W. & J. Müller 1821) and *Osmoderma barnabita* (Motschulsky 1845) are used as umbrella species for conservation of saproxylic beetles associated with standing old broadleaved trees in European lowland forests. However, *C. cerdo* is associated with oaks (see Buse et al. 2007, 2008), and the remaining species listed are mostly bound to specific microhabitats such as newly dead trees (*C. cinnaberinus*—see Horák et al. 2012) or well developed hollows (*L. violaceus* and *O. barnabita*—see Gouix et al. 2015; Ranius 2002, respectively). Consequently, these species only partially cover the full saproxylic beetle diversity in European lowland forests as an array of endangered species is associated with various other microhabitats on trees such as elm (*Ulmus* spp.), lime (*Tilia* spp.), poplar (*Populus* spp.) and willow (*Salix* spp.) etc. (Sláma 1998; Bílý 2002). Our knowledge of the ecological requirements of the saproxylic beetle fauna of these tree species is insufficient, and there is a clear need to develop further umbrella species to represent them and facilitate their conservation.

In Central Europe, an endangered longhorn beetle—the grain support beetle *Aegosoma scabricorne* (Scopoli 1763)—seems to be a suitable candidate for another umbrella species (Gobbi et al. 2012). Although *A. scabricorne* is one of the largest European beetles (reaching 5 cm in body length), its bionomics remains relatively poorly known. It is a highly polyphagous species that develops in the wood of a wide range of broadleaved host trees (documented from more than 20 genera of host trees). However, the most usual host trees are poplars (*Populus* spp.) and willows (*Salix* spp.). *A. scabricorne* develops mostly in the dead stem wood of living trees, less frequently in standing dead trees and only rarely in fallen trees and stumps. Larvae burrow mostly in sapwood and heartwood, and full development of the species lasts at least 3 years. Colonised trees can be easily identified by the typical oval exit holes that can reach up to 20 mm in their longer dimension. Adults are active at night from June to September with the highest abundance from July to mid-August. *A. scabricorne* ranges from the Caucasus and the Near East through the European portion of the Mediterranean area up to the southern part of Central Europe (Švácha and Danilevsky 1986; Heyrovský and Sláma 1992; Bense 1995; Sláma 1998), where it is mostly confined to lowland alluvial plains (Sláma 1998). The species occurs mainly in floodplain forests, pasture woodlands and old parks (Sláma 1998; Hardersen et al. 2012).

In Central Europe, *A. scabricorne* is a disappearing species; hence, it is legally protected in the Czech Republic, Germany and Slovakia and is listed among the most endangered species in the Red Lists of Austria (Adelbauer 2001), the Czech Republic (Farkač et al. 2005), Germany (Binot et al. 1998) and Switzerland (OFEV 2011). The species' decline is distinctive even in countries with relatively higher numbers of populations, e.g., Slovakia (Sláma 1998). Despite being listed in higher categories of threatened species at various country levels in Central Europe, *A. scabricorne* is listed in the category of Least Concern at the European level (Nieto and Alexander 2010).

In Central Europe, *A. scabricorne* is an endangered "Urwald relict species" inhabiting biologically rich forests (Müller et al. 2005). However, its habitat requirements have not yet been systematically studied, and in general, its bionomics are relatively poorly known. However, sufficient knowledge of its bionomics and habitat requirements is an essential prerequisite for conservation of this species as well as for its possible employment as an umbrella species (McGeoch 1998; Nieto and Alexander 2010). Hence, the main goals of the present study are (a) to define the characteristics of the trees favourable for the development of *A. scabricorne*, and (b) to suggest management approaches which will support both the species and its habitat.

Materials and methods

Study area

The study was conducted in the broader surroundings of the town of Lanžhot, which is located in the alluvium of the Dyje and Morava rivers in south Moravia, the Czech Republic. This area represents the main distribution area of *A. scabricorne* in the Czech Republic (Sláma 1998). The study area was defined as a circle with an approximately 10 km diameter (the centre coordinates are 48°44,05′N; 16°57,86′E). The elevation of the studied area is between 150 and 170 m a.s.l., and its climate is warm and characterised by mean annual temperatures of 9.5 °C and an average annual rainfall of approximately 530 mm. The study area is a part of the Lower Morava Biosphere Reserve (UNESCO), and it is a Central European hotspot of saproxylic beetle diversity (Rozkošný and Vaňhara 1995, 1996).

However, the main habitat of saproxylic beetles in the study area consists of floodplain forests; trees dispersed in open agricultural and urban land are also of substantial significance (Vodka et al. 2009). The main tree species are common ash (*Fraxinus excelsior*), penduculate oak (*Quercus robur*), European hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), small-leaved lime (*Tilia cordata*), elms (*Ulmus* spp.), poplars (*Populus* spp.) and willows (*Salix* spp.).

Field sampling

The field work was performed from May to September 2015. The study area was systematically scanned by foot for standing broadleaved trees with occurrences of *A. scabricorne*. The presence of the species was judged by the presence of the reliably distinguishable galleries and exit holes of the species. For each tree found with occurrence of *A. scabricorne* (i.e., an occupied tree), one control tree without exit holes from the studied species (i.e., an unoccupied tree) was also selected. The control tree was selected as the nearest broadleaved tree (excluding oaks as non-host trees) with a breast height diameter ≥20 cm. Subsequently, examinations of both the occupied and unoccupied trees were performed the same way.

Selected characteristics of the trees known to affect occurrence of saproxylic beetles were recorded for the purpose of the present study (Stokland et al. 2012). The positions of the sampled trees were assessed by GPS. The tree species and type of surrounding habitat was recorded (three types of habitat were distinguished: forest, forest edge and forest free area). The tree diameter was recorded at breast height with a precision of 1 cm. The circumference of the tree stem was divided by lines into quarters, each facing a different cardinal direction (i.e., North, East, South and West). The number of exit holes of *A. scabricorne* was counted separately for each quarter of the stem circumference up to a height of 3 m above the ground. Furthermore, any decline in the tree's vitality/degree of decay (henceforth "tree vitality") was evaluated by distinguishing among 6°: (i) highly vital tree; (ii) tree with slightly reduced vitality (growth stagnation, dieback of peripheral branches); (iii) tree with significantly reduced vitality (tree crown recession, dieback of terminal part of crown); (iv) tree with residual vitality (most of crown dead); (v) freshly dead tree (trees that died approximately <3 years ago, bark and twigs still present); and (vi) long-dead tree (trees that died approximately ≥3 years ago, bark and twigs mostly fallen off). Sun exposure at the basal part of the tree stem (0–3 m above the ground) was evaluated on a 4-point scale according to the estimated percentage of stem circumference exposed to sun as follows: (i) completely in shade (0–25 %); (ii) mostly in shade (25–50 %); (iii) half-exposed to sun (50–75 %); or (iv) completely exposed to sun (75–100 %). Furthermore, several additional tree characteristics were recorded: (i) presence of breakage of the stem or primary branch with diameter ≥15 cm ("breakage"); (ii) presence of a hollow in the stem with a volume ≥1 dm^3 ("hollow"); (iii) presence of fruiting bodies of wood-decaying fungi on the stem ("fungi"); and (iv) presence of stem blaze (the part of the trunk without bark) with an area ≥40 cm^2 ("stem blaze").

Statistical analysis

To evaluate the effects of tree characteristics on the recorded number of exit holes of *A. scabricorne*, generalized linear mixed models (GLMM) with a Poisson distribution and a logarithmic link function were computed using the R 3.0.2 statistical package lme4. The number of exit holes was treated as the response variable, tree characteristics were treated as fixed effect factors, whereas the locality (six localities within the study area were identified) and type of surrounding habitat were treated as random effect factors. All the fixed effect factors except tree diameter (i.e., tree species, tree vitality, sun exposure, breakage, hollow, fungi and stem blaze) were considered as categorical variables. The statistical significance of fixed factors was evaluated by means of χ^2-based likelihood ratio tests comparing the full model involving fixed as well as random effect factors with the reduced model involving only random effect factors. The effect sizes of selected fixed effect factors were quantified as the percentage of model deviance explained by each factor. This was calculated as the decrease in model residual deviance after adding the given fixed effect factor to the reduced model (see above) multiplied by 100 and divided by the deviance of the intercept-only model.

To test the significance of differences in the number of exit holes among the four quarters of the stem circumference facing different cardinal directions, GLMM was used in the same way as described above. The cardinal direction was treated as a fixed effect factor, whereas tree identity was treated as a random effect factor.

To identify the thresholds of tree diameter, we used the conditional inference tree method from the family of recursive partitioning, which is based on maximally selected rank statistics (Hothorn and Zeileis 2008) through the R package "party."

Results

In total, 87 trees occupied by *A. scabricorne* supplemented by another 87 unoccupied (control) trees were surveyed. *A. scabricorne* was found to develop in various tree species including willows (36 occupied trees/60 surveyed trees), poplars (19/25), ashes (12/49), European hornbeams (7/11), horse chestnuts (*Aesculus hippocastanum*) (4/7), elms (4/9), field maples (2/5), sweet chestnuts (*Castanea sativa*) (2/2) and limes (1/3). In total, 1066 exit holes of *A. scabricorne* were recorded on the surveyed trees.

All the habitat factors studied (i.e., tree species, tree diameter, tree vitality, sun exposure, breakage, hollow, fungi and stem blaze) significantly affected the number of *A. scabricorne* exit holes on the tree (Table 1) and, combined, were able to explain a high portion of the model's deviance (52.4 %) (Fig. 1). Tree vitality was by far the most important explanatory factor, followed by the presence of breakage of stem or primary branch. The tree species and diameter as well as the presence of stem hollows also exhibited substantial explanatory power. The effect sizes of the remaining factors tested were markedly lower and—in the case of sun exposure-negligible.

A. scabricorne exit holes were found almost exclusively on trees whose vitality had significantly declined. The highest numbers of exit holes were found on dead trees (Fig. 2). However, the number of exit holes accumulates throughout

Table 1 Results of generalized linear mixed model analysis

Factor	df	χ2	P	Explained deviance (%)
Tree species	10	366.4	<0.001	12.8
Tree diameter	1	291.2	<0.001	10.1
Tree vitality	5	921.4	<0.001	32.1
Breakage	1	560.8	<0.001	19.5
Hollow	1	300.9	<0.001	10.5
Fungi	1	312.2	<0.001	5.9
Stem blaze	1	140.2	<0.001	3.0
Sun exposure	3	4.7	0.018	0.2

The number of *A. scabricornis* exit holes is the response variable, while locality and habitat type were treated as random effect factors. The significance of the effect of individual fixed effect factors is demonstrated by the χ^2-based likelihood ratio tests results, while the size of factors' effects is illustrated using the percentage share of model deviance explained by each factor (see Methods)

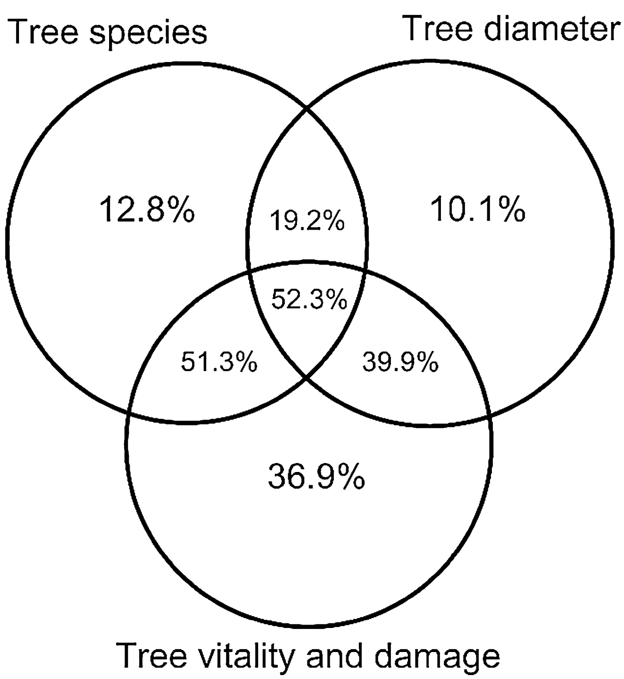

Fig. 1 Venn diagram of the percentage share of the model deviance explained by the tree characteristics individually and jointly (overlapped portions of *circles*) based on the generalized linear mixed model analysis (see Table 1). Tree vitality and damage represent the combined effects of five factors (i.e., tree vitality, presence of: breakage, hollow, fungi and stem blaze). The negligible effect of sun exposure is not shown

the life history of a tree occupied by *A. scabricorne*; therefore, this result does not suggest that dead trees are the most preferred or the most suitable (see Discussion).

Larger numbers of exit holes were found on trees with various types of damage (Fig. 3) with the greatest difference documented between trees with breakage and unbroken trees (Fig. 3a). However, a distinct increase in the number of exit holes was also recorded on trees with hollows (Fig. 3b), fungi (Fig. 3c) or stem blaze (Fig. 3d). The number of exit holes rose significantly as the tree diameter increased. Two significant diameter threshold values were found: a marked increase in the number of exit holes was observed on trees with diameters >50 and 102 cm (Fig. 4).

The distribution of exit holes among the quarters of stem circumference facing in different cardinal directions was significantly uneven (GLMM: df = 3, $\chi^2 = 45.5$, $P < 0.001$); substantially smaller numbers of exit holes were recorded on the north facing quarter (Fig. 5).

Discussion

Our results showed that tree vitality and tree damage were the most important tree characteristics. These factors explain a substantial portion of the habitat preferences of *A. scabricorne* (Table 1; Fig. 1). The number of *A. scabricorne* exit holes increased as tree vitality declined. As a cumulative variable, the number of exit holes reached its highest values on the long-dead trees—the last stage of our tree vitality decline scale (Fig. 2). At the time when a tree dies, an increased amount of freshly dead wood (an optimal substrate for *A. scabricorne* development) becomes available, thus enabling the development of more individuals. With respect to the distribution of *A. scabricorne* exit holes among the degrees of decline of tree vitality (Fig. 2) and its developmental time (Bense 1995; Sláma 1998) it is probable that colonisation of trees commences when tree vitality is slightly to significantly reduced and that *A. scabricorne* thrives the best when the tree exhibits only residual vitality or is freshly dead. In accordance with this finding, *A. scabricorne* has been reported to develop primarily in the dead wood of living trees (Švácha and Danilevsky 1986; Sláma 1998); less often in standing dead trees and its development in fallen trees or stumps is rare (Sláma 1998).

However, estimated tree vitality exhibited by far the biggest explanatory power. Tree vitality is a complex characteristic that only partly encompasses the presence of tree damage (there is a large overlap of explained model deviance—see Table 1; Fig. 1) and does not provide much real insight into the detailed habitat preferences of the studied species. A substantial part of the *A. scabricorne* habitat preference explained by tree vitality may be attributed to tree damage because the species strongly preferred trees with various types of damage (Fig. 3). Accordingly, Sláma (1998) and Berger (2012) mention that the species preferentially occupies hollow and damaged trees, e.g., trees stripped by fast water flow during floods.

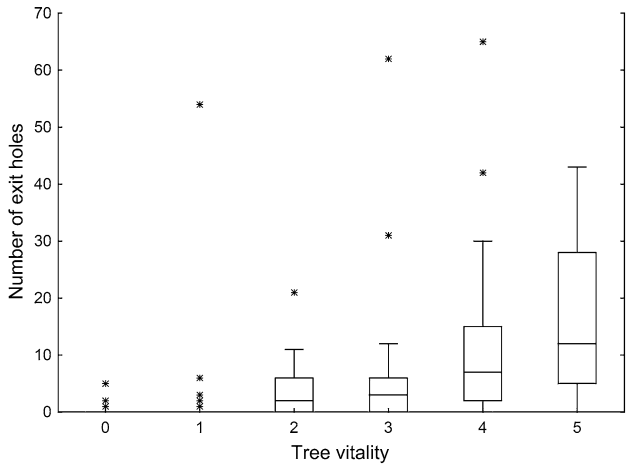

Fig. 2 *Box*-and-*whisker plots* showing the distribution of the number of *A. scabricorne* exit holes among trees characterised by different stages of decline of tree vitality/tree decay. Six degrees of tree vitality are distinguished: *0* highly vital trees, *1* trees with slightly reduced vitality, *2* trees with significantly reduced vitality, *3* trees with residual vitality, *4* freshly dead trees, *5* long-dead trees (see Methods). The *box*-and *whisker plots* are composed of outliers (*asterisks*), non-outlier ranges (*whiskers*), lower and higher quartiles (*boxes*) and medians (*middle lines*)

However, the host tree species was also found to be a significant variable affecting the occurrence of *A. scabricorne*. In accordance to literature (Švácha and Danilevsky 1986; Bense 1995; Sláma 1998), the species was widely polyphagous in our study, exhibiting only limited preferences for any particular tree species. Among the sufficiently represented tree species (i.e., 20 trees sampled), a slightly increased rate of occupation was observed for poplars (76 % of the sampled trees occupied) and willows (60 %), whereas ashes were occupied least often (24 %). A certain level of preference for specific tree species is probable as such preferences have been documented for some other polyphagous saproxylic species that display regionally conditioned preferences for host tree species (Cizek et al. 2009). Aside from direct attraction to certain tree species (e.g., chemical attraction), the observed preferences for soft-wooded tree species such as poplars and willows might arise from the increased susceptibility of these trees to damage of various types (e.g., breakage, hollow) compared to hard-wooded species such as ashes (Lonsdale 1999). Thus, these soft-wooded tree species may offer more suitable wood microhabitats. Because there was a substantial interaction between tree species and

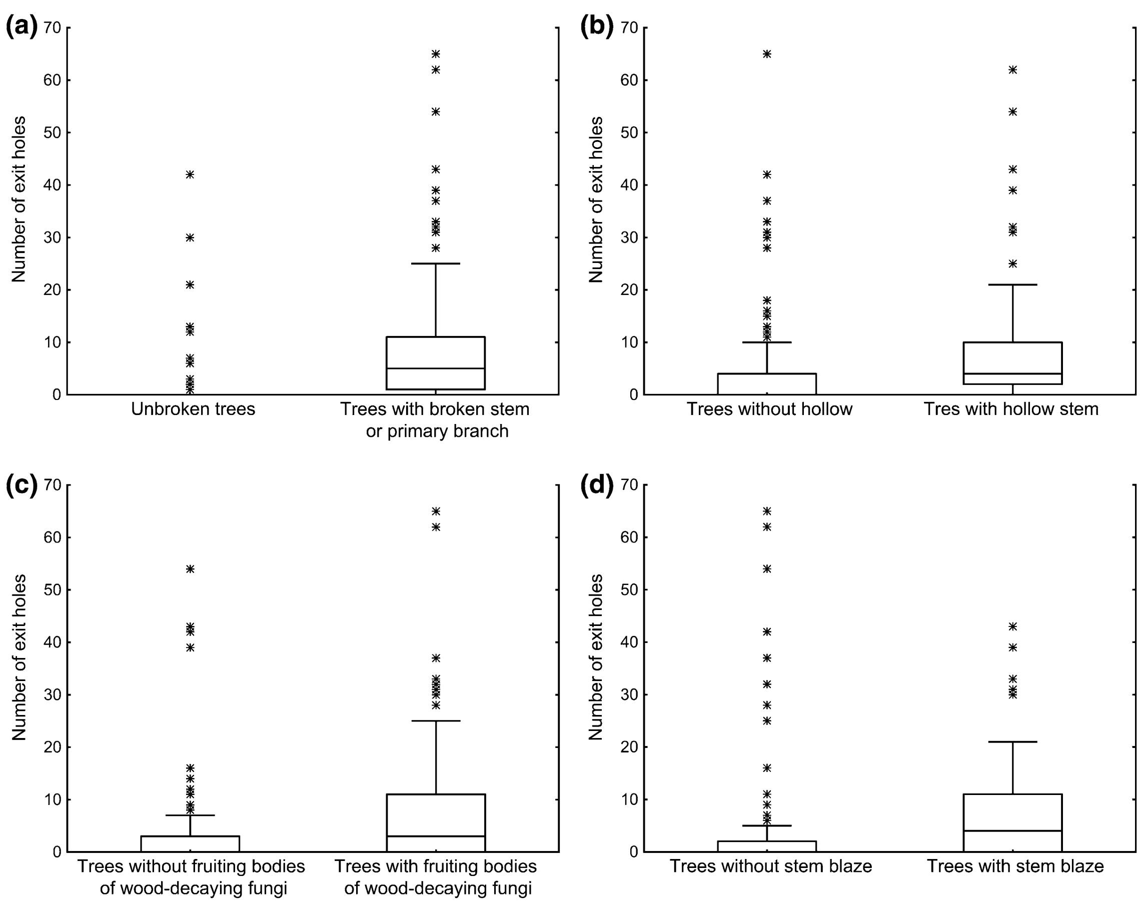

Fig. 3 *Box*-and-*whisker plots* showing the distribution of the number of *A. scabricorne* exit holes between damaged and undamaged trees. *Box*-and *whisker plots* are composed of outliers (*asterisks*), non-outlier ranges (*whiskers*), lower and higher quartiles (*boxes*) and medians (*middle line*)

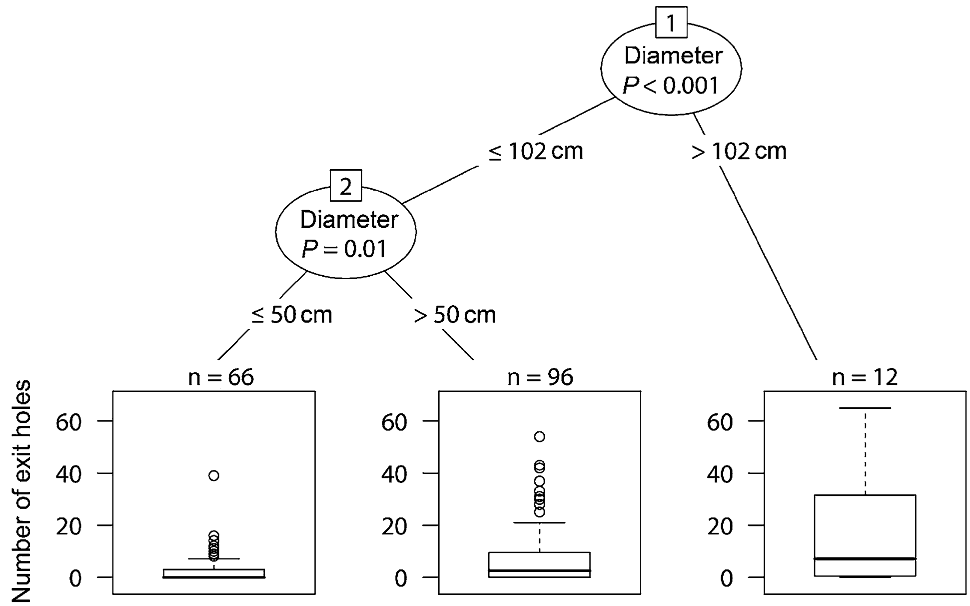

Fig. 4 Threshold analysis of the number of *A. scabricorne* exit holes as a function of tree diameter using the conditional inference tree method

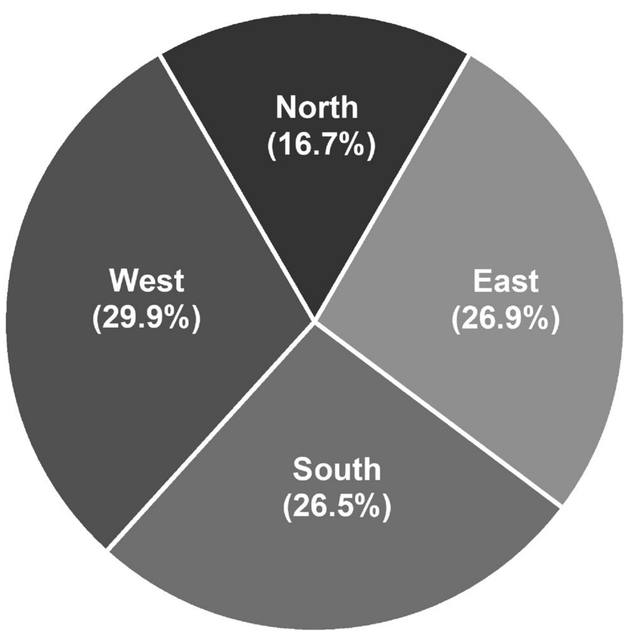

Fig. 5 Percentage share of *A. scabricorne* exit holes recorded on particular quarters of tree stem circumference facing different cardinal directions (100 % = 1066 exit holes)

its vitality and damage (the larger portion of model deviance could be explained by the variables jointly than by a simple sum of deviance explained by each individually—see Fig. 1), it is possible that state of tree vitality and damage preferred by the species differs somewhat among individual tree species.

In addition, stem diameter affected the occurrence of *A. scabricorne*: the number of exit holes increased with larger tree diameters. If this increment were continuous, this result might be explainable simply because larger trees offer an increased volume of wood available for the species' development (Albert et al. 2012). Simultaneously, larger trees are assumed to be older and to have had more time to be wounded, broken and colonised by saproxylic beetles (Speight 1989). However, the increment was not continuous; two threshold values of tree diameter (50 and 102 cm) were found that corresponded with sudden increases in the number of exit hole numbers (Fig. 4). Hence, the species thrives best on large trees with diameters >50 cm (the threshold of 102 cm, although statistically significant, is unreliable because it is based on a sample of only 12 trees with diameters >102 cm). This result corresponds to the fact that bigger species usually need larger diameter trees in which to develop (Stokland et al. 2012). In terms of metapopulation dynamics, large trees occupied by numerous populations of the species may be of the great importance for the species survival because bigger populations exhibit a lower risk of extinction (Hanski 1998).

Exposure of a wood habitat to sunlight is an important environmental variable that affects saproxylic beetles (Jonsell et al. 1998). Surprisingly, sun exposure of the tree stem was found to have almost no effect on the occurrence of *A. scabricorne* (the effect was statistically significant but negligible—Table 1). This finding contrasts with the common opinion that the highest diversity and most endangered saproxylic species thrive in sun-exposed wood microhabitats (Stokland et al. 2012). However, although the overall effect of sun exposure was negligible, our study documented that the exit holes of *A. scabricorne* were not distributed evenly around the stem with respect to cardinal directions (Fig. 5). Because the species' exit holes were significantly less abundant on the north-facing quarter of the stem in comparison with other directions, we can hypothesize that the species, even though it does not have a preference for the more sun-exposed trees, does preferentially lay eggs in the sun-exposed parts of the stem. A similar distribution of exit holes is exhibited by the longhorn beetle *C. cerdo*, whose adults are also nocturnal and lay eggs, preferably, on warmer south and west facing side of stems (Albert et al. 2012).

Management implications and conclusions

Due to the limited dispersal capacity of *A. scabricorne* (Holec and Kašák 2012), efforts to increase habitat availability and improve habitat quality should first and foremost be conducted within or nearby areas where the species is already known to exist (Huxel and Hastings 1999). Based on results of the present study, *A. scabricorne* is strongly associated with declining broadleaved trees that are preferentially further damaged (e.g., breakage of stem or primary branch, presence of hollows) and it particularly thrives on large trees (>50 cm). Thus, a fundamental prerequisite for *A. scabricorne* conservation in forests as well as in other woody habitats is to prevent the removal of such trees. Even though *A. scabricorne* mainly utilizes large trees, trees with different ages and sizes should be represented at any conservation locality because it is important to consider the continuity of habitat availability in the future (in general, sufficient heterogeneity of habitats is essential). Furthermore, in localities where conservation of *A. scabricorne* is of special importance, artificial damage to the larger trees (veteranisation) could be employed (such as cutting large branches, removing bark, pollarding, etc.) to increase the abundance of suitable habitats.

According to our results, *A. scabricorne* is a saproxylic species with high-quality habitat demands and thus, as a relic species, prefers biologically rich forests (Müller et al. 2005). Management intended to conserve *A. scabricorne* and the physical impact of the development of an abundant population of the species itself will also help support many other saproxylic species. Hence, we suggest that *A. scabricorne* can be effectively used as an umbrella species (sensu Lambeck 1997) for saproxylic beetles in European lowland forests, which has the following advantages: (i) the occurrence of *A. scabricorne* is easily and non-destructively detectable based on the presence of its typical exit holes; (ii) changes in its population abundance can be easily monitored at low cost according to changes in the number of occupied trees or the number of exit holes; and (iii) due to its polyphagy, conservation of *A. scabricorne* may also shield a wide range of other saproxylic species.

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