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Shortage of declining and damaged sun-exposed trees in European mountain forests limits saproxylic beetles: a case study on the endangered longhorn beetle *Ropalopus ungaricus* (Coleoptera: Cerambycidae)

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Abstract

European mountain forests are unique ecosystems, and they harbour specific saproxylic beetle fauna, including relict species such as the longhorn beetle *Ropalopus ungaricus* (Herbst, 1784). This endangered species is endemic to European mountain forests and is considered to be monophagous on living sycamore trees (*Acer pseudoplatanus* L.). Insufficient knowledge of the species ecology limits its effective conservation. Hence, to investigate its habitat requirements, 175 sycamore trees (87 occupied and 88 unoccupied by the species) were surveyed in the Hrubý Jeseník Mts. and Moravskoslezské Beskydy Mts. in northern Moravia (Czech Republic) in 2016. The species strongly preferred trees with reduced vitality, including variously damaged trees. The species was also documented to be much more abundant on sun-exposed trees, and the parts of the trunk mantle (south- and east-facing quarters) with the warmest microclimates were preferred. Surprisingly, trunk diameter seems to be an unimportant characteristic for this species (the diameters of occupied trees varied between 5 and 72 cm). In conclusion, *R. ungaricus* is a specialised species whose survival depends upon a continuous supply of sun-exposed declining and damaged sycamores in mountain forests. Based on the results of the present study, we suggest concrete conservation measures to support the species, and these will benefit other saproxylic species associated with the same habitat.

Keywords Conservation · Czech Republic · Ecology · Endangered species · Forest management · Habitat requirement

Introduction

Saproxylic beetles represent one of the most species-rich and functionally diverse group of endangered organisms dwelling in forest ecosystems (Jonsell et al. 1998; Stokland et al. 2012). However, the forest area in Europe is currently increasing (FAO 2015). Forests have been degraded in many ways due to their intensive economic use (Dudley and Vallauri 2004; Lindenmayer et al. 2012). As a result, European forests consist mainly of uniform, even-aged, shady and species-poor stands (Kopecký et al. 2013; Miklín and Čížek 2014) with low numbers of over-mature trees and a shortage of dead wood (Siitonen et al. 2000; Lindenmayer et al. 2012). Among the main threat factors to saproxylic beetles in European forests is the greatly reduced abundance of dead wood and large over-mature damaged and declining trees (Stokland et al. 2012; Seibold et al. 2015). The abundance of declining and damaged trees regardless of their diameter and age is strongly limited in managed forests due to their systematic removal during thinning and salvage logging (Hibberd 1991; Wermelinger 2004). Furthermore, forest management has been preferring certain tree species, resulting in species-poor forest stands and overall rareness of some tree species (more than 70% of European forests consist of 1–3 tree species, FAO 2015). Additionally, current shady conditions in the majority of forests represent another well-documented threat to saproxylic beetles (Horák and Rébl 2013), because many endangered saproxylic beetles prefer sun-exposed habitats (Table 1).

There have been many attempts to define the requirements of saproxylic beetles on their habitat (Horák 2017).

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Table 1 Bibliographic compilation of studies addressing the habitat (tree, snag, log or site) sun exposure requirements of European endangered saproxylic beetles (Coleoptera)

Species	Association with habitat sun exposure	Study location	References
Ampedus cardinalis (Schiödte, 1865)	+	SE Sweden	Ranius et al. (2011)
Boros schneideri (Panzer, 1795)	−	NE Poland	Gutowski et al. (2014)
	+/−	Lithuania	Blažytė-Čereškienė and Karalius (2012)
Cerambyx cerdo Linnaeus, 1758	+	W Poland	Oleksa and Klejdysz (2017)
	+	Czech Republic	Albert et al. (2012)
	+	N, NW Germany	Buse et al. (2007)
Cerambyx welensii Küster, 1846	−	SW Spain	Torres-Vila et al. (2017)
Cucujus cinnaberinus (Scopoli, 1763)	+	SE Poland	Goczal and Rossa (2017)
	+	Czech Republic	Horák et al. (2012)
Elater ferrugineus Linnaeus, 1758	NS	SE Sweden	Ranius et al. (2011)
Limoniscus violaceus (P.W. & J. Müller, 1821)	NS	SW France	Gouix et al. (2009)
Lucanus cervus (Linnaeus, 1758)	NS	N Italy	Tini et al. (2017)
	+	Europe	Harvey et al. (2011)
	+	W Germany	Rink and Sinsch (2008)
Morimus asper[a] (Sulzer, 1776)	−	C Italy	de Gasperis et al. (2016)
Osmoderma barnabita Motschulsky, 1845	NS	S Finland	Landvik et al. (2016)
Osmoderma eremita (Scopoli, 1763)	NS	C Italy	Chiari et al. (2012)
	+	SE Sweden	Ranius et al. (2011)
	+	W France	Dubois et al. (2009)
	+	SE Sweden	Ranius and Nilsson (1997)
Pytho kolwensis C. Sahlberg, 1833	NS	C Finland	Siitonen and Saaristo (2000)
Rosalia alpina (Linnaeus, 1758)	+	N Spain	Castro and Fernandez (2016)
	+	Italy	Russo et al. (2015)
	+	C Italy	Russo et al. (2011)
Tragosoma depsarium (Linnaeus, 1767)	+	C Sweden	Wikars (2004)

Species listed in European Red List of saproxylic beetles (Nieto and Alexander 2010) and Annex II of The Habitats Directive 92/43/ECC were considered. Additionally, only studies based on statistical analyses, or at least quantification of primary data, were included in the compilation. Association with habitat sun exposure is coded as follows: preference for sun-exposed habitat (+); preference for habitat half-exposed to sun (+/−); preference for shady habitat (−); no significant association found (NS). Study location is expressed by country and, if appropriate, its part: *C* Central, *N* North, *E* East, *S* South, *W* West and combinations thereof

[a]According to Solano et al. (2013), *M. asper* is a morphologically variable species that contains all the European *Morimus* species, including *Morimus funereus* (Mulsant, 1863), the species listed in Annex II of The Habitats Directive 92/43/ECC

Such studies usually employ the umbrella species concept, wherein conservation of a certain species, including its habitat, may support many other species as well (Ranius 2002; Buse et al. 2008; Gouix et al. 2015; Foit et al. 2016). Mainly the ecological requirements of saproxylic beetles associated with lowland broadleaved forests have been studied so far (see citations above). The ecology of mountain species remains less well known, which limits conservation of these species and their habitat (i.e., mountain forests). Mountain forests are unique ecosystems that differ in many aspects from the lowland forests, and thus they harbour a specific saproxylic beetle fauna, including relict species (Sláma 1998; Weiss et al. 2016). Additionally, in many regions, the largest forest complexes were preserved in mountains, and these forests may serve as refugia for regional saproxylic beetle diversity.

Hence, the present study addresses the longhorn beetle *Ropalopus ungaricus* (Herbst, 1784), an endangered species that is associated with mountain forests of Europe (Horák et al. 2010). The species is one of the most endangered saproxylic beetles in Europe and is rated as endangered according to the IUCN. Currently, the species' remaining distributional range is estimated to be less than 500 km^2 (Horák et al. 2010; Nieto and Alexander 2010). The species is endemic to Europe and occurs locally in most of the countries of Central and Eastern Europe, reaching the Ukraine and Crimea in the East and central Italy and the Balkan peninsula in the South (Bense 1995). Our current knowledge of the species' ecology is mainly

based on summarised unsystematic observations, including some inconsistent information. To date, no systematic, statistically verified study has been carried out to define the species' habitat requirements.

Ropalopus ungaricus is widely considered monophagous on maples (*Acer* spp.) Its development in trees other than maples (genera *Alnus, Ficus, Fraxinus, Salix*, etc.) is doubtful (Sláma 1998) or at least considered to be rare (Rejzek and Hadulla 2000; Horák et al. 2010). In the Czech Republic, development of *R. ungaricus* was reliably documented only in sycamore (*Acer pseudoplatanus* L.) (Sabol 2014). Larvae develop under the bark and pupate in the sapwood of living trees (Sabol 2014). Larval development usually lasts two years. Prior to pupation deep in the sapwood, the larva bores a flat, wide gallery under the bark (up to the size of a human palm), which gives rise to a characteristic patch of naked wood with the larval entrance hole to the sapwood, and some extent of swelling of surrounding living tissues may be visible as well (Rejzek and Hadulla 2000; Sabol 2014). These traits enable the reliable identification of attacked trees.

Development of *R. ungaricus* occurs mainly in trunks, or in some cases also in branches. Most of the larval galleries are found in the base part of the trunk (to the height of 3 m). The species is known to develop in large old trees as well as small young trees (Sabol 2014). Data from available literature regarding the species' preference for the tree age and size are discrepant. Horák et al. (2010) and Sabol (2014) mention older and larger trees to be preferred, whereas Sláma (1998) and Rejzek and Hadulla (2000) consider the species to prefer young, thin trees. There are also some discrepancies regarding host tree vitality; Sláma (1998), Horák et al. (2010) and Sabol (2014) referred to the species as developing mainly in weakened, mechanically damaged or pruned trees, whereas Heyrovský and Sláma (1992) and Rejzek and Hadulla (2000) mention that its development occurs in vital, apparently healthy trees. According to some authors, sun-exposed trees are preferred by *R. ungaricus* (Sláma 1998; Horák et al. 2010; Sabol 2014). In the Czech Republic, the species occurs at elevations of 600–1200 m and it inhabits various habitats, such as near-natural and partly open mountain forests, forest edges, treelines along roads or solitary trees, etc. Adult beetles are active during the day from May to August (Sabol 2014).

The current insufficient knowledge of *R. ungaricus* ecology substantially limits any efforts towards the effective conservation of this species and its habitat (i.e., mountain forest). The goals of the present study are (a) to first define the parameters of the trees suitable for the development of *R. ungaricus* and (b) to propose conservation measures for the species and its habitat.

Materials and methods

Study area

The study was carried out in the Hrubý Jeseník Mts. and Moravskoslezské Beskydy Mts., the main distribution area of the species in the Czech Republic (Sláma 1998; Sabol 2014). The elevation of the studied area is between 760 and 1175 m a. s. l., and the climate is generally cold and wet, characterised by mean annual temperatures of 3–5 °C and an average annual rainfall of approximately 1000–1400 mm (Tolasz 2007). Eight localities with sufficient numbers of trees with occurrence of the species were selected based on the previous faunal survey by Sabol (2014). Six localities were situated in the Hrubý Jeseník Mts. (village Vidly, Střední Opava river—end of valley, Kamzičí vrch Mt., Sokol Mt., Tupý Vrch Mt.—north and Tupý Vrch Mt.—west), and the remaining two localities were located in the Moravskoslezské Beskydy Mts. (Smrk Mt.—cottage Hubertka, Smrk Mt.—south). Particular study sites were at least 500 m apart from each other. All the studied localities represent patches of near-natural mountain mixed forest (mostly scree forest) dominated by European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.) and sycamore. In the case of one locality (Vidly), also trees in non-forest surroundings of the village (treelines along roads and forest edges) were sampled. The studied localities are mostly surrounded by managed even-aged Norway spruce stands (Norway spruce forms more than 70% of the tree composition in the study area). The study area is situated in protected landscape areas (Jeseníky and Beskydy, respectively).

Field sampling

The field work was performed from September to October 2016. All the sycamore trees at each locality were scanned for occurrence of *R. ungaricus*. The presence of the species was judged by the presence of the reliably distinguishable galleries and exit holes of the species (Fig. 1). As the present study aimed to reveal associations between species occurrence and tree characteristics (see below), a dataset largely covering variability of characteristics of available host trees at the study localities was needed. Hence, for each tree found with an occurrence of *R. ungaricus* (i.e., an occupied tree), one control tree without galleries of *R. ungaricus* (i.e., an unoccupied tree) was also selected. The control tree was selected as the nearest sycamore tree with a diameter at breast height ≥ 5 cm. Subsequently, examinations of both the occupied and unoccupied trees were performed in the same way. At least ten (five occupied and five unoccupied) trees were sampled at each locality.
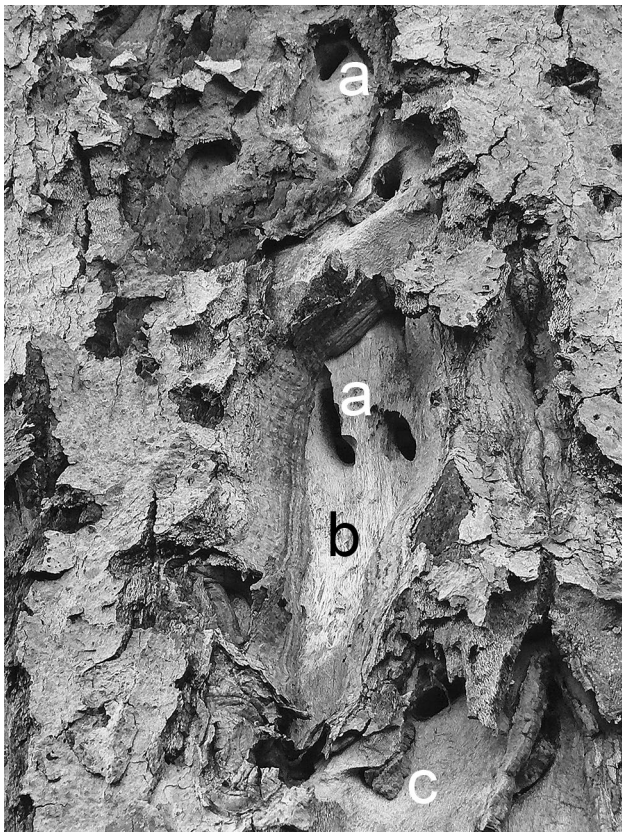
Fig. 1 Galleries of *R. ungaricus* on the trunk of a sycamore tree (*A. pseudoplatanus*). Several exit holes (*a*), with associated typical blaze area (*b*) and pieces of fine, but tightly compressed, frass in dismantled larval tunnels (*c*), are shown. Photo was taken at the Sokol Mt. locality, Hrubý Jeseník Mts., in the Czech Republic

The tree diameter was recorded at breast height with a precision of 1 cm. The circumference of the tree trunk 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 *R. ungaricus* was counted separately for each quarter of the trunk circumference up to a height of 4 m above the ground. Furthermore, any decline in the tree's vitality (henceforth "tree vitality") was evaluated by distinguishing among 4 degrees: (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 the crown dead). Additionally, the social status of the tree was recorded in terms of its dominance in the stand: (i) dominant tree; (ii) co-dominant tree; (iii) suppressed tree. For each tree, we recorded the presence of breakage of the trunk or primary branch with diameter ≥ 1/3 of the tree's breast height diameter ("breakage"), presence of fruiting bodies of wood-decaying fungi on the trunk ("fungi") and

the presence of a hollow in the trunk with an estimated volume ≥ 1 dm³ ("hollow").

Sun exposure of the basal part of the tree trunk (0–4 m above the ground) ("sun exposure") was evaluated on a 4-point scale according to the estimated percentage of trunk circumference exposed to the 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%). Further recorded characteristics related to the basal part of the trunk were as follows: (i) measured total surface area of the trunk parts without bark (with a precision of 25 cm²); (ii) estimated total percent coverage of mosses and lichens ("mosses") with a precision of 5%; (iii) evaluated roughness of the bark ("bark roughness") according to the degree it was cracked (smooth bark, medium-rough bark and rough bark).

Data analysis

To evaluate the effects of tree characteristics on the recorded number of exit holes of *R. ungaricus*, generalised linear mixed models (GLMM) with a Poisson distribution and a logarithmic link function were computed using the R 3.0.2 statistical package lme4 (function glmer). The number of exit holes was treated as the response variable, tree characteristics were treated as fixed effect factors, and the locality was treated as a random effect factor. Most of the fixed effect factors (tree vitality, social status, hollow, fungi, sun exposure, breakage and bark roughness) were considered as categorical variables, whereas tree diameter, trunk blaze area and coverage of mosses and lichens were treated as continuous variables. Prior to analysis, the measured trunk blaze area was reduced by the area debarked due to feeding of *R. ungaricus* larvae; the area was computed as the number of exit holes counted on the particular tree multiplied by the average blaze area associated with one exit hole (based on a measurement of 30 exit holes). Subsequently, the obtained reduced blaze area was log10 transformed, and coverage of mosses and lichens was arcsine square root transformed. The statistical significance of fixed effect factors was evaluated by means of Chi square-based likelihood ratio tests comparing the full model involving fixed as well as random effect factors with the reduced model involving only the random effect factor. 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. Subsequently, for significant categorical fixed effect factors, the pairs of their categories that differed significantly were found using post hoc tests in the R 3.0.2 statistical package multcomp (function glht).

To test the significance of differences in the number of exit holes among the four quarters of the trunk 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 illustrate mean direction of the *R. ungaricus* exit holes, a vector of mean directions was computed using the R 3.0.2 statistical package circular (function mean).

Results

In total, 87 trees occupied by *R. ungaricus* with 701 counted exit holes supplemented by another 88 unoccupied (control) trees were surveyed. The number of exit holes found on individual trunks ranged from 0 to 89 (mean = 8.1, median = 4.0 for the occupied trees). Most of the habitat factors studied (i.e., tree vitality, sun exposure, trunk blaze, breakage, bark roughness, mosses, hollow and trunk diameter) significantly affected the number of *R. ungaricus* exit holes on the tree (Table 2). Factors combined, were able to explain a high proportion of the model's deviance (44.5%) (Table 3). Tree vitality was by far the most important explanatory factor, followed by trunk sun exposure, trunk blaze and the presence of breakage of trunk or primary branches. The bark roughness, coverage of mosses and lichens and, in part, presence of trunk hollows also exhibited substantial explanatory power. Although the trunk diameters of the trees sampled varied between 5 and 95 cm (5–72 cm for the occupied trees), the

Table 2 Results of generalised linear mixed model analysis

Factor	df	X^2	P	Explained deviance [%]
Tree vitality	3	803.3	< 0.001	34.1
Sun exposure	3	510.2	< 0.001	21.6
Trunk blaze	1	500.0	< 0.001	21.2
Breakage	1	423.6	< 0.001	18.0
Bark roughness	2	267.9	< 0.001	11.4
Mosses	1	219.9	< 0.001	9.3
Hollow	1	136.5	< 0.001	5.8
Trunk diameter	1	16.3	< 0.001	0.7
Fungi	1	2.4	0.1192	0.1
Social status	2	1.8	0.4091	0.1
Tree vitality X social status	11	918.33	< 0.001	38.9

The number of *R. ungaricus* exit holes is the response variable, while locality was treated as a random effect factor. The significance of the effect of individual fixed effect factors is demonstrated by results of the Chi square-based likelihood ratio tests, while the size of factors' effects is illustrated using the percentage share of model deviance explained by each factor (see the "Materials and Methods" section)

Table 3 Percentage of deviance explained by generalised linear mixed models fitted during the forward selection process

		Factors already included in the model					
		–	Tree vitality	Tree vitality; sun exposure	Tree vitality; sun exposure; trunk blaze	Tree vitality; Sun exposure; trunk blaze; Bark roughness	Tree vitality; sun exposure; trunk blaze; bark roughness; mosses
Factors added stepwise to the model	Tree vitality	**34.1*****					
	Sun exposure	21.6***	**40.3*****				
	Trunk blaze	19.1***	37.0***	**42.4*****			
	Breakage	18.0***	34.2[n]				
	Bark roughness	11.4***	38.5***	41.2***	**43.9*****		
	Mosses	9.3***	36.2***	41.7***	42.9***	**44.5****	
	Hollow	5.8***	34.1[n]				
	Trunk diameter	0.7***	34.2*	40.3[n]			
	Fungi	0.1[n]					
	Social status	0.1[n]					
	Tree vitality X social status	38.9***	38.9***	43.4***	45.3***	46.4***	47.0***

The number of *R. ungaricus* exit holes is the response variable, while locality was treated as a random effect factor. The goodness of fit of each model is illustrated using the percentage share of model deviance explained. The significance of the model improvement in each step (fixed-effect factor addition) was tested by the Chi square-based likelihood ratio tests (see the "Materials and Methods" section) and denoted as follows: ***P < 0.001, **P < 0.01, *P < 0.05, [n]P ≥ 0.05. Each step of the forward selection procedure is represented by individual columns. The best-fit model in each step that was subsequently used in the next step is highlighted by its value of explained deviance being written in bold. However, the values of explained model deviance for interaction between factors tree vitality and social position of the tree are shown in the table; this complex factor was set aside from the forward selection procedure to keep results more demonstrative

size of its effect on the number of *R. ungaricus* exit holes was negligible. The presence of fungi and the social status of the tree did not significantly affect the number of *R. ungaricus* exit holes. Due to correlations among some of the factors studied, the model's deviance explained by particular factors overlapped remarkably in some cases, which came to light during the forward selection process within the model fitting (Table 3). A significant interaction was found between tree vitality and social status of the tree; if this interaction was included in the model among other significant fixed effect factors, the explained portion of the model's deviance reached 47% (Table 3).

Ropalopus ungaricus exit holes were found almost exclusively on trees whose vitality had declined. The highest numbers of exit holes were found on trees with residual vitality (Fig. 2a). The number of the studied species' exit holes increased significantly with the sun exposure of the

trunk (Fig. 2b). A great difference in the number of *R. ungaricus* exit holes was documented between trees with breakage and unbroken trees with the higher values pertaining to broken trees (Fig. 2c). Significant differences in the number of exit holes were associated also with the bark roughness. The highest values were found on the trees with medium-rough bark (Fig. 2d). Further, the number of *R. ungaricus* exit holes significantly increased with greater area of the trunk blaze (Fig. 3a), whereas the number decreased with increment of coverage of mosses and lichens (Fig. 3b).

The distribution of exit holes among the quarters of trunk circumference facing in different cardinal directions was significantly uneven (GLMM: df = 3, X^2 = 164.5, P < 0.001); the highest numbers of exit holes were recorded on the east-facing quarter, slightly fewer on the south-facing quarter and substantially fewer on the north- and west-facing quarters
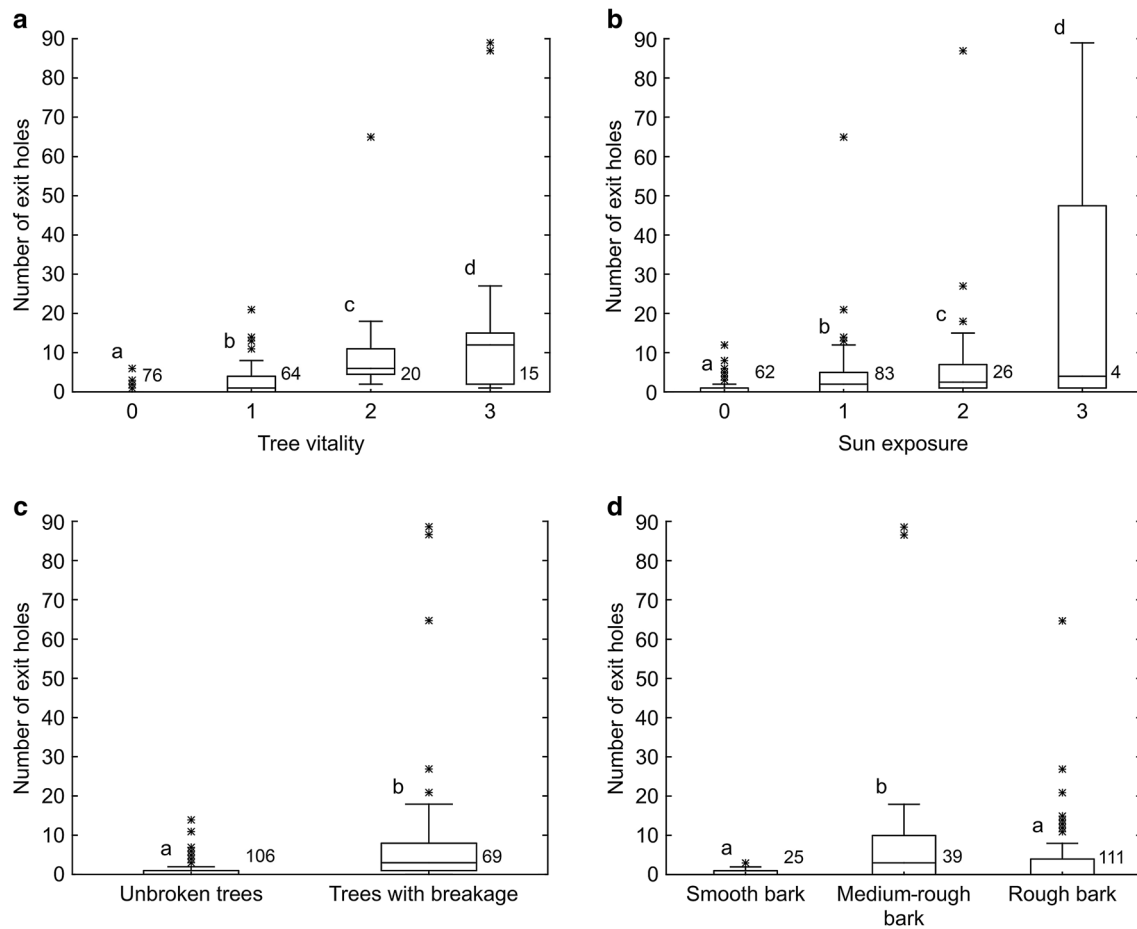

Fig. 2 Box-and-whisker plots showing the distribution of the number of *R. ungaricus* exit holes among trees characterised by **a** different stages of decline of tree vitality: 0—highly vital trees, 1—trees with slightly reduced vitality, 2—trees with significantly reduced vitality, 3—trees with residual vitality; **b** different sun exposure of the trunk: 0—completely in shade, 1—mostly in shade, 2—half-exposed to sun, 3—completely exposed to sun; **c** presence/absence of breakage of the trunk or primary branch; **d** different roughness of the bark. The box-and whisker plots are composed of outliers (asterisks), non-outlier ranges (whiskers), lower and higher quartiles (boxes) and medians (middle lines). In each plot, categories labelled with the same letter did not differ significantly. The number of cases in particular categories is mentioned on the right next to the pertinent box
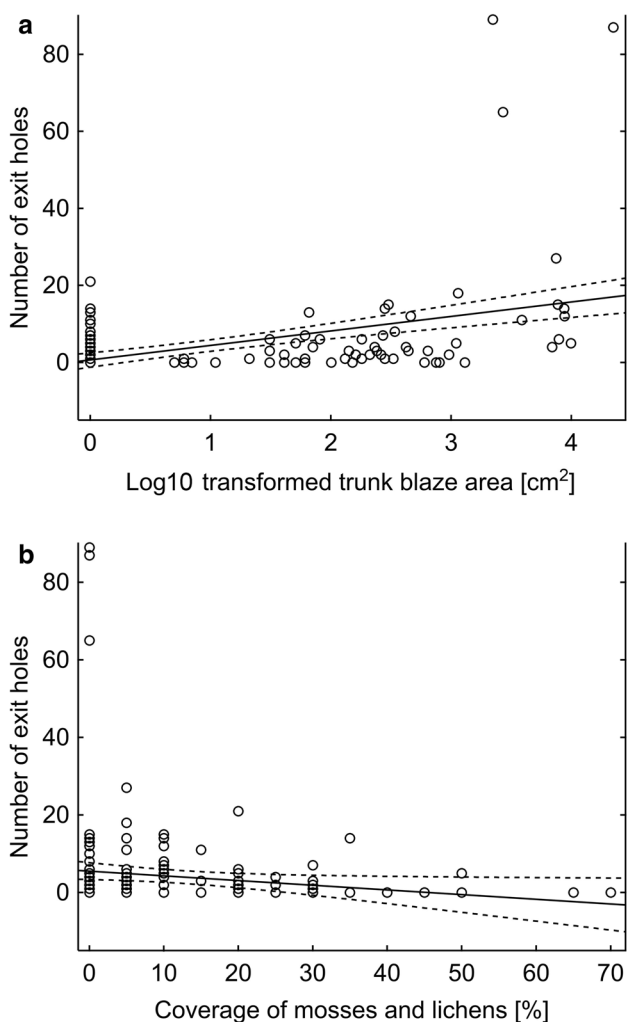
Fig. 4 Vector of mean direction of *R. ungaricus* exit holes (bold arrow positioned in solid line cross of cardinal directions) and percentage share of exit holes recorded on each quarter of tree trunk circumference facing different cardinal directions (pie chart depicted with dashed line, 100% = 701 exit holes). Cardinal directions labelled with the same letter did not differ significantly in occurrence of *R. ungaricus* exit holes

Fig. 3 Scatter plots showing the association between the number of *R. ungaricus* exit holes and **a** trunk blaze area [cm²] that has been logarithmically transformed; **b** coverage of mosses and lichens on the surface of the trunk [%]. Individual observations are shown as empty circles, the solid line represents the trend as fitted to the points using the linear least squares method, and the dashed lines show the 95% confidence interval of the fitted line

(Fig. 4). Thus, the mean direction of *R. ungaricus* exit holes was approximately southeast.

Discussion

According to our results, the preference of *R. ungaricus* for particular trees is mostly driven by vitality and sun exposure of the tree. In the present study, these two tree characteristics together were able to explain a substantial part of the species' habitat preference (40.3% of model deviance) (Table 3). Other tree characteristics tested were either insignificant or strongly correlated with the aforementioned factors, and therefore they did not exhibit considerable explanatory
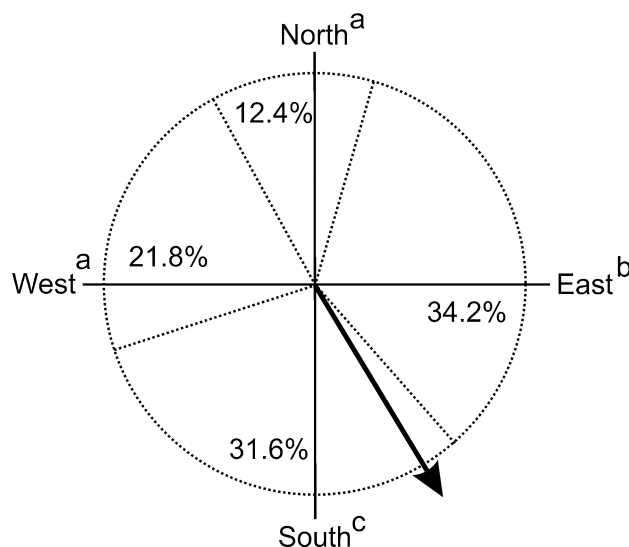
power if tree vitality and sun exposure had already been involved in the model (Tables 2, 3).

The tree vitality was the most important tree characteristic studied (Table 2), similarly to the case of other longhorn beetles developing in living trees (Buse et al. 2008; Foit et al. 2016). The number of *R. ungaricus* exit holes increased as tree vitality declined. As a cumulative variable, the number of exit holes reached its highest values on the trees with only residual vitality—the last stage of our tree vitality decline scale (Fig. 2a). From the distribution of *R. ungaricus* exit holes among the degrees of decline of tree vitality (Fig. 2a), it can be inferred that trees start to be attractive when their vitality is slightly reduced and that *R. ungaricus* thrives most when the tree exhibits only residual vitality.

Unfortunately, the methods used for assessing tree vitality did not fully reflect the competitive stress on the trees; therefore social status of the trees was recorded in addition. Although the social status of the tree alone was an insignificant factor (Table 2), its interaction with the tree vitality had highly significant, and the effect size of this combined factor was considerably higher than that of the tree vitality itself (Table 3). The most probable explanation is that social status of the tree took effect mostly within trees with high vitality. Thus, highly vital trees that were attacked by *R. ungaricus* in the present study were mostly supressed, competitively stressed trees. This might be an explanation for observations of the species attacking apparently healthy trees, which was reported by Heyrovský and Sláma (1992) and Rejzek

and Hadulla (2000). Similarly, some other phloeoxylophagous insect species such as *Pissodes* weevils or wood wasps (Siricidae) are known to develop in both damaged trees and supressed understory trees (Schwenke 1974; Dodds et al. 2010).

In many cases, the decline of the tree vitality was associated with (or caused by) breakage of the trunk or primary branch and with the presence of large trunk blaze; hence, tree vitality encompassed most of the *R. ungaricus* habitat preferences explained by these factors. However, *R. ungaricus* strongly preferred trees with breakage (Fig. 2c); this factor emerged as insignificant if tree vitality had already been included in the model (Table 3). Similarly, the number of *R. ungaricus* exit holes significantly increased with the greater area of trunk blaze, although most of the habitat preference explained by this factor overlapped with those explained by the tree vitality (Table 3). On the other hand, according to some reports (Sláma 1998; Sabol 2014), females of *R. ungaricus* prefer trunk blaze margins for egg laying; thus, we can hypothesise that the presence of a larger trunk blaze might enhance the occurrence of *R. ungaricus* in this way.

In addition to tree vitality, the occurrence of *R. ungaricus* was mostly affected by the sun exposure of the trunk (Tables 2, 3). The number of species' exit holes significantly increased with higher trunk sun exposure (Fig. 2b). However, an insufficient number of completely sun-exposed trees had been sampled in the present study; from Fig. 2b. We can infer that the species thrives the best on the trees that are completely or at least half exposed to the sun, whereas completely shaded trees represent undoubtedly suboptimal habitats. Additionally, the fact that only four completely sun-exposed trees were present in our dataset reflects the rareness of such trees in the studied forest habitats. Further, the observed higher abundance of *R. ungaricus* exit holes on the east- and south-facing quarters of the trunk mantle as well as the mean direction of the species' exit hole being southeast (Fig. 4) represents another piece of evidence that the species is heliophilous. In general, the south-facing quarter is the most sun-exposed, the east-facing quarter is relatively sun-exposed and the least exposed to the wind [prevailing wind direction in the studied localities is approximately west (Tolasz 2007)]. These findings are in accordance with species' preference for sun-exposed trees previously mentioned by Sláma (1998), Horák et al. (2010) or Sabol (2014). Thus, exposure of the tree trunk and its parts to the sun is a key factor determining the occurrence of *R. ungaricus*, similarly to the case of some other saproxylic beetles (Buse et al. 2007; Russo et al. 2011; Horák et al. 2012).

To a certain degree, the occurrence of *R. ungaricus* was influenced by bark roughness and coverage of mosses and lichens (Tables 2, 3). The decreasing numbers of species' exit holes with increasing coverage of mosses and lichens on the trunk were probably associated with microclimatic conditions. As epiphytic mosses and lichens require a certain level of humidity, they reached higher coverage on shaded trees (Friedel et al. 2006), and therefore the observed explanatory power of mosses and lichens coverage might be in fact largely attributed to differences in sun exposure of the trees. On the other hand, the presence of large amounts of mosses and lichens on the trunk might adversely change microclimatic conditions of the bark or might mechanically obstruct *R. ungaricus* females while laying eggs. The observed effect of bark roughness on number of *R. ungaricus* exit holes in the present study corresponds to the fact that bark thickness and structure were previously documented to affect the occurrence of some saproxylic beetles in other studies (Foit 2010; Åström et al. 2013). Surprisingly, the response of the species to bark roughness in the present study seems to be unimodal, with the highest numbers of exit holes being counted on the trees with medium-rough bark. As bark roughness correlates with tree diameter and age (Sonmez et al. 2007), and older trees tend to be more damaged (Dudley and Vallauri 2004), *R. ungaricus* might be expected to prefer more damaged older and larger trees with rough bark, which does not correspond to our results. The observed highest numbers of *R. ungaricus* exit holes on the trees with medium-rough bark might be attributed to the occasional removal of the damaged and declining trees from the study stands within forest management practice, resulting in reduced numbers of such trees, particularly among largest older trees.

Tree diameter is an important parameter for occurrence of many longhorn beetles (e.g., Albert et al. 2012; Foit et al. 2016). The effect of trunk diameter on the number of *R. ungaricus* exit holes was found to be statistically significant, although its size was not biologically relevant. Even though this result could be partly caused by the fact that the biggest trees tended to be the most vital ones in our dataset, trunk diameter is not of considerable importance for this species. For instance, we recorded the occurrence of the species in six trees with trunk diameters < 10 cm (5 cm in the case of the smallest tree) as well as in trees with diameters > 70 cm. These findings correspond with previous observations of *R. ungaricus* development in thin young trees as well as large old trees (Sláma 1998; Rejzek and Hadulla 2000; Sabol 2014).

Management implications and conclusions

Fragments of European natural and near-natural mountain forests represent valuable ecosystems harbouring an array of unique organisms including *R. ungaricus*, one of the most endangered saproxylic beetles in Europe (see Horák et al. 2010). Based on the results of the present study and information from the literature (Sláma 1998; Rejzek and Hadulla

2000; Horák et al. 2010; Sabol 2014), a conclusion can be made, i.e., that *R. ungaricus* is a specialised species whose survival depends mostly upon a continuous supply of sun-exposed, declining and damaged sycamores (Fig. 5).

Based on the situation of *R. ungaricus* and its habitats in the study, we can state that survival of the species is mainly threatened by (a) the current adverse conditions of the most mountain forests in the species' range (changed tree species composition with low abundance of the host tree species, mostly even-aged shady stands, etc.); (b) ongoing intense forest management in most of the mountain forests (clear cutting, removing damaged and declining trees, etc.). To the best of our knowledge, this statement is more or less valid throughout the species range.

Hence, we propose conservational measures for the species: (a) do not remove any damaged or declining sycamores, particularly those that are sun-exposed; (b) near-natural and spatially differentiated open stands with considerable abundance of sycamores should be left unmanaged; (c) other stands with considerable abundance of sycamores should be thinned to reduce canopy closure and enhance spatially differentiation; (d) artificial damage to the trees (veteranisation) could be employed (such as cutting large branches, removing bark, pollarding, etc.) to increase the abundance of suitable trees, which might be effective because the species is often reported from regularly pruned trees (Sláma 1998; Horák et al. 2010); (e) in the long term, increase the abundance of sycamores in the forests; (f) plant and maintain secondary biotopes such as solitary sycamore trees, treelines along roads, trees in field hedgerows or in forest edges, etc. that already serve as refugia for some populations of *R. ungaricus* (see Horák et al. 2010; Sabol 2014).

Some of the proposed measures might be in conflict with forest management; in such cases, conservation efforts should be focused on less economically productive stands in extreme sites (e.g., steep slopes, scree, rock outcrops, spring areas, etc.). The aforementioned measures are primarily suited to promote *R. ungaricus* populations, but their application would generally increase the habitat quality within European mountain forests, it might be beneficial for many other saproxylic organism as well.

Compliance with ethical standards

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

Informed consent Informed consent was obtained from all individual participants included in the study.

Research involving human and animal participants This chapter does not contain any studies with human participants or animals performed by any of the authors.

Fig. 5 Sun-exposed, declining and damaged sycamores (*A. pseudoplatanus*) represent a favourable habitat of *R. ungaricus*. Photo was taken at the Střední Opava river—end of valley locality, Hrubý Jeseník Mts, in the Czech Republic. Photo by O. Sabol

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