

Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management

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Abstract Oaks host the richest fauna of saproxylic insect in Europe. We studied habitat preferences of two beetle families, Buprestidae and Cerambycidae, by rearing the beetles from standardised oak timber baits. Species density was higher in the understorey than in the canopy; and in sun-exposed baits if within the understorey. Insolation was the most important factor affecting the composition of reared assemblages (explaining ca. 30% of variation in the data), followed by vertical stratum (ca. 10%). Local dead wood volume had no effect. The high preference for sun-exposed wood located near the ground suggests that: (i) open-canopy woodlands had to be rather common in temperate Europe; (ii) oak-utilising xylophages would benefit from restoration of management practices such as coppicing or woodland pasture; (iii) the policy of increasing dead wood volume in commercial forests is principally correct, but its success will depend on dead wood location within the forests.

Keywords Biodiversity conservation · Forest management · Oak · Saproxylic · Xylophages

Introduction

The specialised invertebrates depending on dead wood are among the most rapidly declining parts of European biodiversity (Berg et al. 1994). The EU Habitat Directive explicitly protects 21 saproxylic species, representatives of this guild stand in prominent positions on national insect red lists (e.g. Farkac et al. 2005; Jedicke 1997). It is understood that thus listed species represent only a small portion of declining saproxylic biodiversity. The declines are occurring despite a steady increase of forest cover across Europe, increase of average stand age, and genuine effort of foresters to grow forests with a more natural tree species composition (Zanchi et al. 2007). Given that European saproxylic fauna comprises thousands of species, often with highly specific requirements for substrate type and quality, the decline warrants serious concern (Jonsell et al. 1998; Schiegg 2000; Kappes and Topp 2004; Gibb et al. 2006).

The declines are usually attributed to the low supply of dead wood in managed forests. It is hence advised to increase dead wood supply, either via establishment of non-intervention reserves, or, in commercially managed stands, via such management modifications as prolonging harvest cycle or retaining harvest remnants in the woods (e.g., Hodge and Peterken 1998; Martikainen et al. 2000; Chandler 1991; Økland et al. 1996). Only few works take into account possible differences in habitat preferences of saproxylic species depending on different species of trees, woodland types and regions (but see Jonsell et al. 1998).

Much of the current research on substrate and habitat requirements of saproxylic insect has been carried out in boreal or sub-boreal forests of Fennoscandia (Siitonen 1994; Kaila et al. 1997; Martikainen et al. 2000; Sverdrup-Thygeson and Ims 2002; Jonsell and Weslien 2003; Wikars

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et al. 2005; Selonen et al. 2005; Schroeder et al. 2006), although these regions are on the margin of the area of many European saproxylic beetles (Komonen 2007). The bulk of saproxylic insect diversity, in terms of species richness, occurs in more southerly regions (Baselga 2008).

An aspect that is often not taken into account is the potential importance of such structural features of woodland habitat as tree density and sun-exposure. European lowland woods have become considerably denser during the last ca. 150 years due to the policy of increasing timber supply, concurrent with abandonment of such traditional management techniques as coppicing and woodland pasture (Warren and Key 1991; Rackham 1998). The non-intervention strategy, often recommended for reserves, also increases canopy closure (Vera 2000), which is the exact opposite to habitat requirements of such flagships of saproxylic diversity as the *Osmoderma eremita* (s.l.), *Cerambyx cerdo* and *Rosalia alpina* (Ranius and Nilsson 1997; Binner and Bussler 2006; Buse et al. 2007), as well as many other red-listed saproxylic organisms requiring sun-exposed substrates (Jonsell et al. 1998; Lindhe and Lindelöw 2004). There are strong reasons to assume that temperate lowland woods would had been rather open even in the absence of human intervention due to various disturbance factors (e.g., Attiwill 1994; Vera 2000; Lindblad et al. 2003; Bakker et al. 2004; Bouget and Duelli 2004; Moretti and Barbalat 2004). References to requirements of rare species for sun-exposed substrates are frequent in life history descriptions (e.g., Bily 2002; Sláma 1998) and it is the shared knowledge of beetle enthusiasts that many rarities are best encountered at sunny sites, such as in parks or at woodland edges.

Furthermore, the vertical aspects of saproxylic beetles' habitat selection have rarely been studied in temperate regions (but see Ranius and Nilsson 1997, Jukes et al. 2002, Ranius 2002, Wermelinger et al. 2007, Ulyshen and Hanula 2007), although the importance of vertical stratification, relative to sun exposure, may be crucial for conservation management. If species requiring sun-exposed substrates breed high in the canopy, non-intervention strategies might safeguard their populations. If they, in contrast, prefer the understorey, then more active management measures would be necessary. However, the few quantitative studies that considered vertical requirements of saproxylic beetles have relied on patterns of adult activity (i.e. trapping of adults: Martikainen et al. 2000; Similä et al. 2002; Bouget 2005; Gibb et al. 2006; Hjältén et al. 2007; Wermelinger et al. 2007) rather than on selection of breeding substrate (but see Ranius and Nilsson 1997).

To contribute to the debate, we studied effects of dead wood insolation and vertical position on the composition of assemblages of two large xylophagous families, long-horned

(Cerambycidae) and jewel (Buprestidae) beetles. We use a novel method of rearing beetles from standard oviposition baits, thus overcoming possible problems with not recognising true breeding habitats.

Methods

Study area

The study was conducted in alluvial woodlands of Southern Moravia, Czech Republic (alt. 160–170 m., 16°45'–16°55' E, 48°45'–48°50' N), within a landscape of managed hardwood forests and meadows with old solitary trees. The prevailing trees are pedunculate oak (*Quercus robur*), hornbeam (*Carpinus betulus*), limes (*Tilia cordata*, *T. platyphyllos*), narrowleaf ash (*Fraxinus angustifolia*), elms (*Ulmus laevis*, *U. minor*), white poplar (*Populus alba*), and field maple (*Acer campestre*). The solitary trees in meadows are mainly pedunculate oaks more than 150 years old.

Historically, the forests were managed as coppice with standards or pasture woodland. These practices were abandoned 100–150 years ago in favour of growing high forest with 90–150 year rotation. The entire area is rich in saproxylic insects, forming their hot-spot within the Czech Republic and Central Europe (Rozkosny and Vanhara 1995–1996).

Baiting procedure

We reared the beetles using standardised baits, exposed to ovipositing females. The baits were made of freshly cut oak (*Quercus robur*), each weighting 15–20 kg (mean: 17.4 kg). The wood originated from healthy small trees (DBH 15–20 cm). Each bait was 1 m long, consisting of 2–3 pieces of stem (diameter 8–12 cm), 2–3 thicker branches (3–8 cm), 4–8 thinner branches (1–3 cm) and a bunch of twigs (<1 cm).

The baits were prepared in mid-April 2004 and immediately exposed to attract ovipositing beetle females. We collected them in October of the same year, and enclosed them in fly-wire cages. Baits originally exposed in shady positions (see below) were placed into shade, while those from sunny positions were exposed to the sun. Baits were fully exposed to rain during exposition as well as when enclosed in cages. Emerging beetles were collected 2–3 times a week for 2 years (2005–2006), mounted, and identified.

Metallic fly-wire with square openings 1.2 × 1.2 mm was used for the caging, allowing small insects (e.g., bark beetles, Diptera, parasitic Hymenoptera) to escape, but keeping larger insects inside. Cerambycidae and Buprestidae

were analysed, as even the smallest members of these families were unable to pass through the openings in fly-wire used for caging. These taxa also formed more than 98% of individuals of reared xylophagous beetles; other families such as Anobiidae, and Bostrichidae were represented mostly by singletons. Note that the baits offer dead wood in quality and diameter similar to broken branches and tree-tops commonly found in all forest strata as a result of such events as wind-storms or tree-falls; baits did not attract beetles depending on wood of large diameters, living wood and wood in advanced stages of decay.

Sampling design

We exposed the baits on old solitary trees in meadows (i), and in four situations in forests: (ii) canopy-shade, (iii) canopy-sun, (iv) understorey-shade, and (v) understorey-sun.

For the canopy treatments, the baits were suspended in the upper tree layer, 17–22 m above the ground in crowns of larger trees, either protected from the sun by dense foliage (ii), or exposed near tree tops at forest edge (iii). The understorey treatments were suspended 1 m above the ground, either in a shady understorey (iv), or at sunlit edges (v).

There were a total of three trapping sites, located 1–6 km apart. At each site, each of the five treatments was sampled by one bait, except for site 1, where two additional baits were exposed, one in understorey-shade, one in understorey-sun. We thus had three replicates for each of the positions (i), (ii), (iii), and four replicates for (iv) and (v), with seventeen baits in total.

Explanatory variables

Two variables of primary interest, both coded as factors, were *stratum* (canopy, understorey, solitary tree) and *insolation* (sun, shade). In addition, we considered three potentially confounding variables.

Site. Factorially coded site identity, used as a covariable.

Bait weight. Fresh weight (in kg), used as a covariable.

Dead wood volume (DWV). As the baiting targeted beetles developing in fresh wood, we considered only non-disintegrating woody matter. The DWV was estimated as the amount of dead wood (in m³ per 1 ha) surrounding a bait and situated in conditions corresponding to the exposition conditions of the bait. For a solitary tree, it was merely the dead wood found within a circle of 50 m diameter with the bait in its centre. For shade treatments, it was dead wood within the 50 m circle; for sun treatments, we considered dead wood within a rectangle of 10 × 50 m situated along the forest edge with the bait in its centre. For canopy treatments, we considered dead wood situated in

the section of canopy from 5 m below the bait to the tree tops; and for understorey, we considered dead wood up to 5 m above the ground within the above-defined sections of the forest.

Analyses

In order to compare diversity between sun-exposed and shaded wood, forest strata and among the five treatments, species accumulation curves with confidence intervals were computed using sample-based rarefaction (Mao Tau function) in the EstimateS 8,00 software (Colwell 2006). Species density (Colwell et al. 2004) was thus used as diversity measure.

To test for relationship between the composition of samples and environmental variables, we used redundancy analysis (RDA), a linear constrained ordination method that relates the species composition of samples to external predictors, in CANOCO v. 4.51 (ter Braak and Smilauer 2002). We focused scaling on inter-sample distances; species scores were divided by standard deviations, species counts were log-transformed and centered, samples were neither centered nor standardised.

We performed two separate RDA analyses, one on full dataset and one on reduced dataset. The full dataset included all sampled situations, the reduced dataset excluded solitary tree samples. This exclusion facilitated determining the effect of each of the examined variables in the forest via the variance partitioning procedure (Leps and Smilauer 2003). The statistical significance of the contribution of each variable was assessed using the Monte Carlo permutation test (9,999 permutations). The effects of site, bait weight and DWV were considered as covariables.

RDA was also applied to distinguish insolation and stratum preference of individual species. We run separate analysis for each of the two explanatory variables (coded as factors with two levels). Full dataset was used for insolation and reduced dataset for stratum. Resulting species scores on the first ordination axes quantify the strengths of the association between individual species and stratum/insolation predictors. We used a deliberate value of 10.31 as indicating a strong relationship.

Results

We reared a total of 2,605 beetle individuals in 22 species (Buprestidae: 374/5; Cerambycidae: 2,231/17) (Table 1). These numbers correspond to 8.8 individuals per 1 kg of wood.

Sample-based rarefaction showed that species density was higher in the understorey samples than in the canopy samples (Fig. 1a), and in the understorey-sun samples than

Table 1 List of long-horned and jewel beetles reared from baits of oak wood in the five investigated situations of the woodland

	Abbr.	Solitary tree	Understorey sun	Canopy sun	Understorey shade	Canopy shade	Total
Buprestidae							
<i>Agrilus angustulus</i> (Illiger, 1803)	Agan	88	102	40	3	4	237
<i>Agrilus obscuricollis</i> Kiesenwetter, 1857	Agob	78	13	5	–	–	96
<i>Agrilus olivicolor</i> Kiesenwetter, 1857	Agol	–	–	–	1	1	2
<i>Agrilus sulcicollis</i> Lacordaire, 1835	Agsu	2	17	10	3	1	33
<i>Chrysobothris affinis</i> (Fabricius, 1794)	Chraf	2	4	–	–	–	6
Cerambycidae							
<i>Anaesthetis testacea</i> (Fabricius, 1791)	Ante	–	–	–	–	1	1
<i>Cerambyx scopolii</i> Füsslins, 1775	Cesc	10	3	–	–	–	13
<i>Clytus arietis</i> (Linnaeus, 1758)	Clar	–	11	–	–	–	11
<i>Exocentrus adspersus</i> Mulsant, 1846	Exad	180	6	71	48	21	326
<i>Exocentrus lusitanus</i> (Linnaeus, 1767)	Exlu	–	2	–	–	–	2
<i>Leiopus nebulosus</i> (Linnaeus, 1758)	Lene	62	109	14	315	254	754
<i>Mesosa curculionoides</i> (Linnaeus, 1761)	Mecu	23	39	56	–	57	175
<i>Mesosa nebulosa</i> (Fabricius, 1781)	Mene	1	–	–	–	–	1
<i>Poecilium alni</i> (Linnaeus, 1767)	Phal	152	198	418	2	85	855
<i>Phymatodes testaceus</i> (Linnaeus, 1758)	Phte	5	–	33	5	24	67
<i>Plagionotus arcuatus</i> (Linnaeus, 1758)	Plar	–	8	–	–	–	8
<i>Pogonocherus hispidulus</i> (Pill. et Mitt., 1783)	Pohi	–	–	–	2	1	3
<i>Pyrrhidium sanguineum</i> (Linnaeus, 1758)	Pysa	1	–	–	–	–	1
<i>Ropalopus macropus</i> (Germar, 1824)	Rhma	–	1	–	–	–	1
<i>Saperda scalaris</i> (Linnaeus, 1758)	Sasc	–	4	–	4	4	12
<i>Stenostola ferrea</i> (Schrank, 1776)	Stfe	–	1	–	–	–	1
<i>Xylotrechus antilope</i> (Schönherr, 1817)	Xyan	1	–	–	–	–	1
Total species/individuals		13/607	15/515	8/647	9/383	11/453	22/2605

Abbreviations are used in ordination graph (Fig. 3)

in the understorey-shade samples (Fig. 1b). It was probably also higher for the sun-exposed than the shaded samples; the confidence intervals, however, marginally overlapped (Fig. 1c). Individual-based rarefaction showed that the species richness of understorey samples was higher than richness of the canopy samples (not shown). Confidence intervals overlapped among other treatments as well as between sun-exposed and shaded samples. Majority of species reached highest abundances in understorey-sun or solitary tree situations, while only single species was most abundant in the understorey-shade (Fig. 2).

In the RDA ordination, local DWV explained only a low percentage of variation in species composition of samples, with no significant effect (full dataset: eigenvalue = 0.113, $F = 1.53$, $P = 0.17$; reduced dataset: eigenvalue = 0.123, $F = 1.27$, $P = 0.26$; the results are after entering bait weight and site as covariables). This justified ignoring DWV in further analyses.

In the RDA of the full dataset, with stratum and insolation as explanatory variables, the first axis (eigenvalue = 0.278,

$F = 6.18$, $P = 0.002$) represented a gradient from sunny to shady treatments, whereas the second axis (eigenvalue = 0.084) represented the vertical stratification (Fig. 3). All canonical axes together explained 39.3% of total variation in species data ($F = 3.91$; $P = 0.001$), or 53.9% of residual variation after considering the site and weight effects. A majority of species displayed an affiliation towards sun. Only four species were associated with shade, two of them reared just in a few individuals (*Agrilus olivicolor*, *Pogonocherus hispidulus*), and no species displayed an affiliation towards understorey-shade. Visualising the effect of DWV revealed that it was independent of the two major gradients.

The pattern returned by RDA on the reduced dataset (solitary tree excluded) was practically identical to that of the full data set (diagram not shown). The first axis (eigenvalue = 0.326, $F = 5.67$, $P = 0.001$) again corresponded with sun exposure, the second axis (eigenvalue = 0.101) with vertical stratification. All axes together explained 42.7% of total variation ($F = 4.75$, $P = 0.001$),

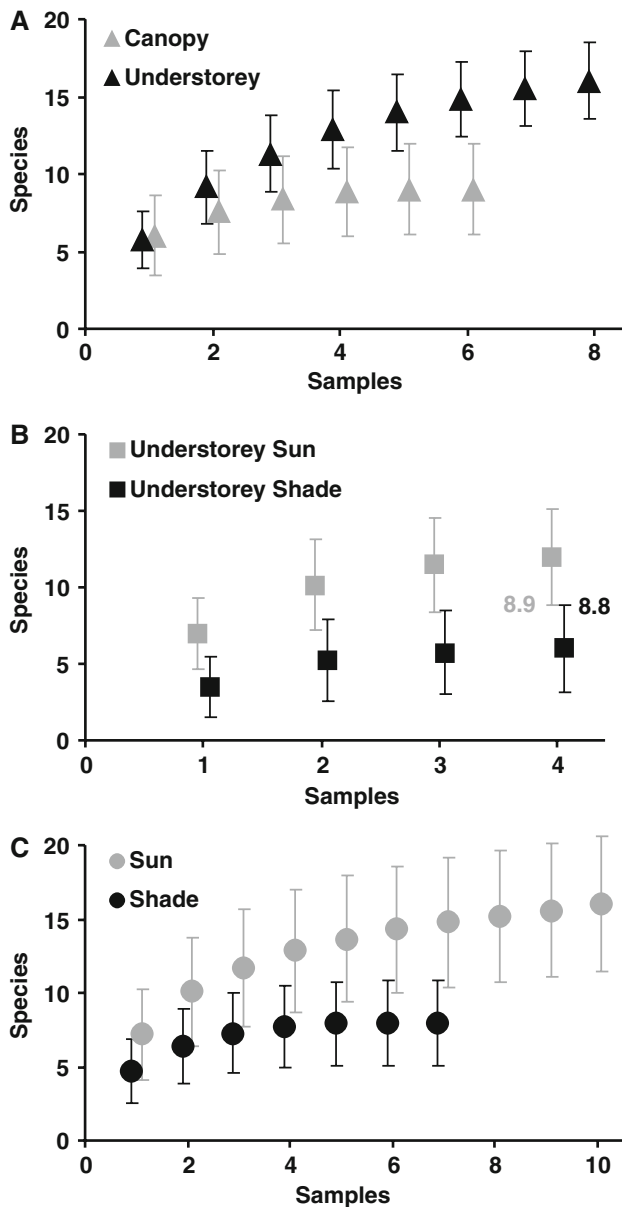


Fig. 1 Diversity of xylophagous beetles (Buprestidae, Cerambycidae) assemblages reared from oak-wood baits in a temperate woodland. Sample based rarefaction (Mao Tau with 95% confidence intervals) of assemblages: **a** reared from baits exposed in the canopy vs. the understorey; **b** understorey assemblages reared from sun-exposed vs. shaded wood; **c** all assemblages from sun-exposed vs. shaded wood

or 54.3% of residual variation. The variance partitioning procedure on reduced dataset revealed that insolation alone explained 29.3% of variation in species data not explicable by vertical stratification, whereas vertical stratification explained 14.0% of variation in species data.

Testing for preferences of individual species (Table 2) revealed that seven species were distinctly sun preferring, while only two appeared to prefer shade. Results for

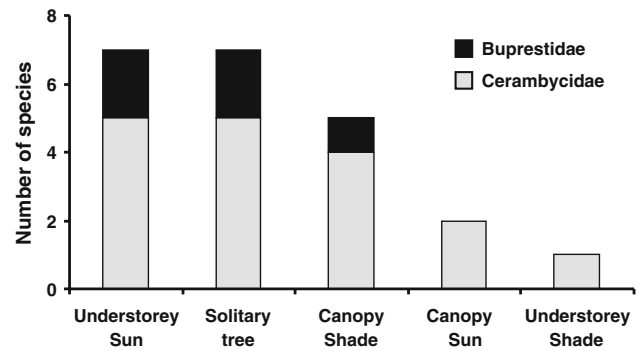


Fig. 2 Habitats preferred by xylophagous beetles (Buprestidae, Cerambycidae) reared from oak-wood baits. Numbers of species that reached the highest abundance in samples from the five treatments

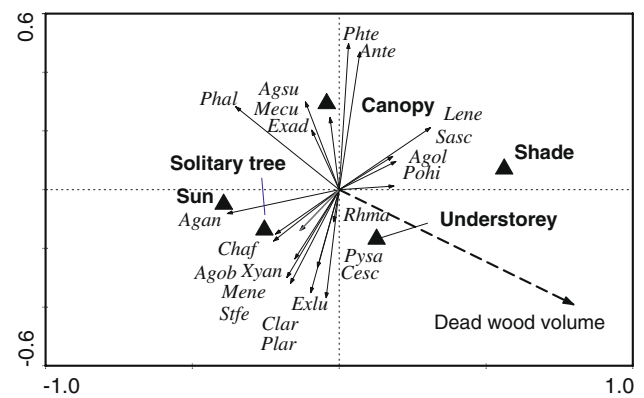


Fig. 3 RDA ordination biplot relating the species composition of xylophagous beetles (Buprestidae, Cerambycidae) reared from oviposition baits related to exposition of the baits, i.e., insolation (sun, shade), and bait position (canopy, understorey, solitary tree). Dead wood volume (a quantitative variable) did not enter the analysis, and is visualised as a “supplementary” explanatory variable here

stratification were less clear, suggesting that preference for both canopy or understorey stratum was rather minor factor influencing the beetles preference, especially if compared with preference for insolation.

Discussion

We showed that exposure to the sun and vertical position of dead wood affects the composition of assemblages of oak-utilising xylophagous beetles in a lowland forest of Central Europe. Species richness was higher near the ground than in the canopy. Within the near-ground level, it was higher for sun-exposed wood than for the shaded wood.

Exposition to the sun positively affects distribution of majority of individual species. Shade-preferring species also commonly occurred in sun-exposed wood, but some species common in the sun were rare or missing from shaded samples (e.g. *Agrilus angustulus*, *A. obscuricollis*,

Table 2 Individual species of long-horned and jewel beetles reared from baits of oak wood, whose RDA-scores indicated a preference for respective strata and insolation categories

Insolation		Stratification	
1st RDA axis eigenvalue: 0.292, $F = 6.27$, $P < 0.001$		1st RDA axis eigenvalue: 0.215, $F = 6.27$, $P = 0.06$	
Sun	Shade	Canopy	Understorey
<i>Agrilus angustulus</i> (−0.80)	<i>Leiopus nebulosus</i> (0.70)	<i>Mesosa curculionoides</i> (0.53)	<i>Clytus arietis</i> (−0.41)
<i>Phymatodes alni</i> (−0.68)	<i>Saperda scalaris</i> (0.34)	<i>Exocentrus adspersus</i> (0.53)	<i>Plagionotus arcuatus</i> (−0.39)
<i>Agrilus obscuricollis</i> (−0.65)		<i>Phymatodes alni</i> (0.51)	
<i>Cerambyx scopoli</i> (−0.39)		<i>Phymatodes testaceus</i> (0.44)	
<i>Chrysobothris affinis</i> (−0.39)			
<i>Clytus arietis</i> (−0.35)			
<i>Plagionotus arcuatus</i> (−0.33)			

The RDA results Number in brackets indicates the species score on the first ordination axe (insolation, or stratification gradient) as returned by RDA. Only species represented by >5 individuals are considered

A. sulcicollis). Whereas the preference for sun among saproxylic beetles was repeatedly detected by other authors (Lindhe et al. 2005; Moretti et al. 2004; Ranius and Jansson 2000), the disclosed effect of vertical stratification is rather unexpected, and rarely reported (but see Ozanne et al. 1997; Wermelinger et al. 2007). The understorey was species-richer despite the fact that more tested species preferred the canopy. This is due to the fact that species preferring canopy were also common in the understorey, whereas species preferring understorey were absent in the canopy and several rare species occurred only in the understorey.

Temperature requirements are probably the main reason behind the high preference for sun-exposed wood. Also humidity affects larval survival and adult oviposition choice, as too dry or too wet substrates do not offer suitable conditions for xylophagous larvae (Hanks et al. 1999; Ueda and Shibata 2007). Further, wind may negatively affect selection of oviposition sites, as insects often avoid windy conditions (e.g. Bonsignore and Bellamy 2007). Fluctuations of humidity, temperature and wind speed are notably higher in the canopy, than in the understorey (Parker 1995). We thus consider it likely that unstable conditions in the canopy drive the insects towards the more protected understorey; whereas the lack of sunshine in the understorey of closed forests drives the insects towards gaps and edges.

Our results are based on rearing from oviposition baits, rather than on trapping of flying adults. This allows for a high confidence that our results indeed reflect the beetles' preferences for breeding substrates. Despite the rather low number of samples, the individual/species ratio is high (>100), and number of samples was sufficient to demonstrate important patterns of xylophagous insect distribution among the microhabitats studied. The earlier studies based on rearing sampled understorey, and mostly originated

from northern range edges of oak woodlands (Kappes and Topp 2004; Lindhe and Lindelöw 2004; Lindhe et al. 2005). Given that insects in harsher climates often utilise exceptionally warm microclimates (Shreeve et al. 1996; Bridle and Vines 2007), the preference for sun-exposed wood in the earlier studies could have been attributed to peculiar conditions near species' range edges. This cannot be the case in this study, and the beetles' preferences for sun-exposed wood apply for the latitudinal centre of Europe.

Note that our sampling targeted extremes of an insolation and height gradient, while insects likely respond to this gradient continuously, rather than abruptly. This does not disqualify the utility of our results for conservation. For a majority of species, shady conditions within closed forests understorey mean lower population sizes per dead wood volume and also per area unit. In the fragmented lowland woods of central Europe, a population size within a forest patch is likely crucial for survival of local populations.

No effect of dead wood volume

We did not detect any relationship between the composition of beetle assemblages and local DWV. Several other studies also found only weak relationship between local DWV and species richness of saproxylic beetles (Økland et al. 1996; Siitonen 1994). Franc et al. (2007) argued that what matters is overall supply of dead wood in wider landscapes, rather than its local amounts. We worked within a single contiguous wood with rather high overall DWV. Whereas we estimated DWV in immediate vicinity of the baits, the studied beetles are relatively mobile. Any inference regarding the importance of DWV for woodland saproxylic biodiversity hence should be viewed with caution.

Our results indicate that locally, dead wood placement and quality exhibits a stronger impact on xylophagous assemblages than mere volume. We found the highest DWV in the shaded understorey, an inferior habitat in terms of beetle diversity. Similarly, Wermelinger et al. (2007) compared the diversity of saproxylic beetles in forest interior and along forest edges in Switzerland, concluding that sun-exposed structures such as edges were responsible for maintenance of high species diversity. These observations do not refute the necessity to maintain or increase overall dead wood supply, but they issue a warning that it matters where precisely the dead wood is retained.

Another potentially important aspect is the temporal continuity of dead wood supply, critical for long-term persistence of individual species (Jonsell and Nordlander 2002). Continuity seems to explain the high diversity of beetles found on old (>150 years) solitary trees in sparsely wooded meadows (cf. Ranius 2002), despite a low local DWV.

Forest history and conservation

The high diversity of the fauna preferring sun-exposed oak wood located in low forest strata suggests that this resource had to be rather common in the past. This is consistent with the claims that European lowland woods would be rather sparse in a natural state (Rackham 1998; Vera 2000; Peterken 2001), with sunshine reaching lower parts of tree trunks and fallen logs. This is further supported by the preference of some beetles, considered to be relics of primeval woodlands, for large-diameter trees (Ranius and Nilsson 1997; Buse et al. 2007), because such trees only rarely grow within close-canopy stands. It also corresponds with sunshine preferences of specialised woodland species in such groups as butterflies (Warren 1991; Benes et al. 2006), epigeic invertebrates (Grgic and Kos 2005; Spitzer et al. 2008) or herbs (Peterken and Francis 1999; Strandberg et al. 2005). Further, it explains a high diversity of specialised “edge species” in European biota (e.g., Magura 2002).

Until recently, the professed goal of woodland reserves in Central Europe has been a non-intervention strategy, allowing for the operating of natural ecosystem dynamics (Christensen et al. 2005; Vrska et al. 2006). Given the preferences of a high number of specialised woodland species from multiple groups, it is increasingly clear that such strategy is inappropriate, or even contradictory to sustaining native biodiversity. Whatever factors maintained the open woodland structure in a “pristine” state, they likely operated on scales much larger than remnant areas of present lowland woods (cf. Kirby 2004; Johnson and Miyanishi 2007). The space limitation differentiates

European lowland from mountain woods. While enough space for disturbance dynamics is still available in mountains (e.g., Jonasova et al. 2005), the open canopy structure of lowland woods has been preserved for centuries by once-common management practices, such as woodland pasture or coppicing, operating in a patchy, mosaic-like manner. It seems plausible that these practices “packed” entire disturbance dynamics into relatively small forest remnants, thus preserving the biodiversity of original woodlands.

It follows that besides retention of dead wood, small-scale canopy-opening practices, such as coppicing, should be reinstated in reserves still harbouring sensitive oak-feeding saproxylic fauna. Restoring such practices has been advocated to benefit, e.g., butterflies (Warren 1991; Freese et al. 2006) or birds (Fuller and Henderson 1992) and our results suggest that they should benefit saproxylic beetles as well. A failure to re-establish such practices will lead to gradual impoverishment of saproxylic fauna, even if dead wood supply is increased.

For commercial forests, the policy of enhancing dead wood supply will yield the best results if dead wood is retained at sun-exposed situations, such as along roads and tracks, or within mantles separating forests and non-forest lands. With increasing demand for fuel-wood, even return to coppicing may become profitable, especially in less productive locations (Utinek 2004).

We do not imply that no species benefit from ongoing woodland closure—on the contrary, preference for shaded dead wood is expectable among insects attacking wood in an advanced state of decay (Jonsell et al. 1998) and among those depending on wood of shade-tolerant tree species (Jonsson et al. 2005). Requirements of such species should be accommodated in reserves, e.g., by exempting parts of reserves from restoring open canopy conditions. Still, many of the species preferring close-canopy conditions seem to be rather common at present, probably benefiting from canopy closure in reserves and from prevailing high-forest management elsewhere. An example represented in this study, the widely polyphagous *Leiopus nebulosus* (cf. Sláma 1998), was abundant in both shaded and sun-exposed baits. A recent study of effects of canopy closure on epigeic invertebrates demonstrated that species with narrow distribution preferred open stands, whereas close stands were preferred by widespread generalists (Spitzer et al. 2008). As open woodlands contain a mosaic of sunny and shady places, shady conditions are always present there. The argument that opening-up woodlands may harm the biodiversity of shade-preferring species is hence unjustified. The current threat to the biodiversity of European lowland woods is the absence of the sun in the closed forest, not the absence of shade in the open forests.

Conclusions

The finding that oak-associated xylophagous beetles preferentially breed in sun-exposed wood located in woodland understorey supports the claims that European oak-dominated woodlands had to be rather sparse in their natural state. It is thus crucial to restore the open woodlands by coppicing, coppicing with standards or forest pasture whenever it is feasible. In commercial forests, the positive effect of dead wood left for the benefit of biodiversity will be substantially enhanced if substantial amount of the dead wood was sun-exposed, rather than located in shady understorey.

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