Beauty and the beast: how a bat utilizes forests shaped by outbreaks of an insect pest

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Abstract

The consequences of different management strategies following natural disturbances are a matter of global concern. In former production forests around the Northern Hemisphere, the abandonment of intervention, such as removal of dead wood, after outbreaks of bark beetles has been increasingly promoted to regain more natural conditions. However, many focal species of conservation, such as the barbastelle bat *Barbastella barbastellus*, do not primarily depend on dead wood but might respond indirectly to disturbance-induced changes of forest structural attributes. We investigated the response of *B. barbastellus* foraging activity and roost selection by combining acoustic surveys, radio telemetry, and airborne light detection and ranging (LiDAR) to characterize *B. barbastellus* habitat use on different scales. *B. barbastellus* foraging activity increased with increasing canopy opening. Maternity colonies were recorded exclusively in trees killed by bark beetles. Bats preferred roost trees with a higher volume ($m^3 ha^{-1}$) of live trees in the surrounding, and trees with on average larger diameters than nearby control trees. Our results revealed that outbreaks of bark beetles result in forest structural attributes that are suitable habitat for *B. barbastellus*. Salvage logging, i.e., the removal of beetle-affected trees, generally deteriorates the positive effects of bark-beetle outbreaks on the foraging and roosting habitat of *B. barbastellus*. We recommend maintaining snags of large diameter if salvage logging is mandatory.

Introduction

A significant amount of terrestrial biodiversity is found in forests (Kumar Duraiappah, Naeem & Ash, 2005). Owing to their intensive economical use most Central European forests underwent a change in species composition and vegetation structure accompanied by dramatic species loss over the last centuries (Paillet *et al.*, 2010; Seibold *et al.*, 2015). In major parts of Europe, past forest management has transferred original forest stands into monotypic plantations of Norway spruce *Picea abies*, which has led to increased vulnerability to natural disturbances, such as windstorms and outbreaks of bark beetles (Coleoptera, Scolytinae) (Kulakowski *et al.*, 2016). Thus, natural disturbances are considered as a way to guide the restoration of commercial forests to more natural stages (Angelstam, 1998). Yet the standard management response to natural disturbances is salvage logging, i.e., the removal of affected trees (Lindenmayer, Burton & Franklin, 2012) due to concerns over forest safety, risk of wildfires,

spread of pests and productivity. However, salvage logging is accompanied by many negative effects on biodiversity, it negatively affected many species of conservation importance (Jonsson, Kruys & Ranius, 2005; Russo, Cistrone & Garonna, 2011; Thorn *et al.*, 2017) and the consideration of the positive effects of natural disturbances in forest management plans is still rare (see Schmiegelow *et al.*, 2006 for an example in burned forests). Nevertheless, a benign-neglect strategy has allowed natural disturbance dynamics to act without human interference in many protected areas in Central Europe (Kulakowski *et al.*, 2016).

During the last 50 years, the European spruce bark beetle *Ips typographus* affected an average of 2.9 million m^3 of forest per year in Central Europe (Schelhaas, Nabuurs & Schuck, 2003). Consequences of such outbreaks are a higher insolation in forest stands, an increase in the amount of spruce dead wood, especially standing dead trees, i.e., snags, and consequently a temporary increase in the cover of deciduous trees (Wermelinger, 2004). Besides economic

losses, outbreaks of *I. typographus* and the concomitant changes in stand structure also have multiple positive effects on biodiversity, such as an increase in species numbers in many taxonomic groups (Beudert *et al.*, 2015). Thus, *I. typographus,* the most severe pest insect in Europe (Wermelinger, 2004), has been promoted for increasing the conservation value of managed and protected forests (Müller *et al.*, 2008).

Monitoring programs after disturbances focus mainly on the number of species in and among taxonomic groups (Lehnert *et al.*, 2013; Beudert *et al.*, 2015). In contrast, changes in management plans (i.e., management actions following natural disturbances) often require evidence for an impairment of a single legally protected species owing to common management (Lindenmayer, Barton & Pierson, 2015) as outlined in the European Commission's Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (known as the Habitats Directive), which forms the foundation of European nature conservation policy. Yet, little is known about how the habitats of protected species are affected by outbreaks of *I. typographus*, particularly those species that do not primarily depend on dead wood.

The barbastelle bat *Barbastella barbastellus* is protected by Annexes II and IV of the European Habitats Directive. It has been recorded in Europe, North Africa and Asia. *B. barbastellus* is classified as near threatened in the IUCN redlist (www.iucnredlist.org) and as vulnerable or endangered in many countries of Central Europe (Hutson, Mickleburgh & Racey, 2001). *Barbastella barbastellus* hunts for moths along forest edges and along the canopy surface (Sierro & Arlettaz, 1997; Vaughan, 1997). It occurs in different forest types, especially in European beech *Fagus sylvatica* forests but also in pine and spruce forests, where it roosts mainly in tree cavities and behind loose bark (Steinhauser *et al.*, 2002; Russo *et al.*, 2004; Russo, Cistrone & Jones, 2005). Maternity colonies, whose protection is a priority aim of conservation legislation, are found in forests of low management intensity with a high amount of old and damaged trees (Russo *et al.*, 2010, 2015). These attributes are typically absent in commercially managed spruce-dominated forests, where salvage logging removes almost all damaged and injured trees (Lindenmayer *et al.*, 2012).

Foraging and roosting habitats of *B. barbastellus* can be influenced by outbreaks of *I. typographus* in multiple ways. For instance, the snags created can provide new roosts similar to those found beneath the bark of old European beeches (Russo *et al.*, 2004) and oaks *Quercus* sp. (Hillen, Kiefer & Veith, 2010). Furthermore, beetle-induced canopy opening might improve the hunting of prey by *B. barbastellus* in the increased open flight space, similar to that along forest edges (Müller *et al.*, 2012). On the other hand, the enhanced exposure might lead to a shortened foraging time, because of an increased risk of predation (Russo, Cistrone & Jones, 2007). Yet, it remains unclear to which extent *B. barbastellus* utilizes stands affected by outbreaks of *I. typographus* as roosting and foraging habitats, and this hampers evidence-based changes in common forest management.

By combining acoustic surveys and telemetry with high-resolution airborne light detection and ranging (LiDAR) data, we tested how forest stands affected by *I. typographus* are utilized by *B. barbastellus* as foraging and roosting habitats. We hypothesize that beetle-induced alteration of forest structural attributes (e.g., increasing canopy opening, increasing stand structural heterogeneity) lead to an increasing foraging activity of *B. barbastellus* (Müller *et al.*, 2012). Furthermore, we hypothesize that *B. barbastellus* select dead spruces killed by *I. typographus* as roosts (Russo *et al.*, 2015) in stands with high stand structural heterogeneity and a moderate canopy cover for a reduced exposure and risk of predation (Russo *et al.*, 2007).

Materials and methods

Study area

The study was conducted in the Bavarian Forest National Park, in southern Germany (48°54′N, 13°29′E), one of Europe's most heavily naturally disturbed areas (Thorn *et al.*, 2016). The national park consists of mixed mountain forests in areas below 1150 m a.s.l. composed of Norway spruce, European beech and silver fir *Abies alba* and high montane forests in areas above 1150 m a.s.l. naturally dominated by Norway spruce (Bässler, Müller & Dziock, 2010). Annual precipitation ranges between 1200 and 1800 mm, and mean annual temperature ranges between 3.8 and 5.8°C. Forest stands in the Bavarian Forest National Park have been affected by two severe outbreaks of *I. typographus* during the last 20 years (Müller *et al.*, 2008). Due to a benign-neglect strategy, these outbreaks led to increased structural heterogeneity and a mosaic of stands killed by *I. typographus* and vital stands nearby (Beudert *et al.*, 2015; Thorn *et al.*, 2016). Within this mosaic of killed and vital stands, we established 119 sampling points for acoustic surveys and seven locations for mist netting (Fig. 1). Due to the high severity of outbreaks of *I. typographus* in the study area the canopy cover around these sampling points ranged between 0 and 50% with a mean cover of $16 \pm 13\%$ (Fig. S2).

Acoustic surveys

The foraging habitat on the 119 study plots (covering approximately 2000 ha in total) at 666 and 1332 m a.s.l. was surveyed with autonomous bat call recorders (batcorder 2.0; www.ecoobs.com) on 9–18 July 2015. Study plots were selected to cover the study area. We used 12 batcorders per night and distributed them across sites so that the entire study area was covered within each night. Hence, we sampled on 10 nights on 12 plots per night; on 9 July, one batcorder was non-functional, which resulted in a total of 119 different plots. The mean distance between two adjacent plots was 142 ± 126 m, the minimum distance was 10 m. We estimated the degree of correlation of all model residuals with geographic coordinates by means of spline correlograms to detect possible spatial autocorrelation (Bjørnstad & Falck,
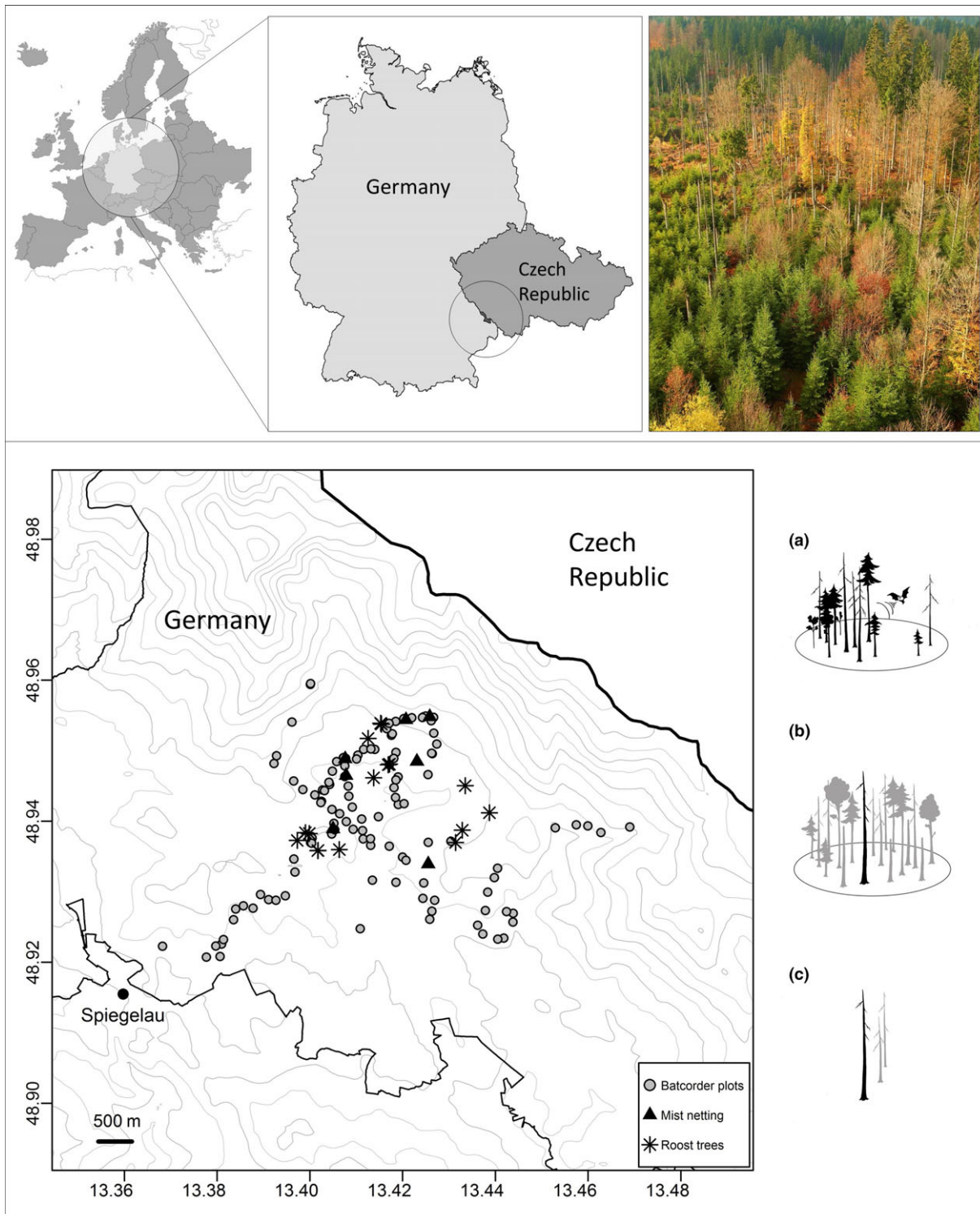
Figure 1 The Bavarian Forest National Park is located in Southwestern Germany at the border to the Czech Republic and was disturbed by several consecutive outbreaks of the European spruce bark beetle *Ips typographus* (picture in the right upper corner). The lower figure shows the location of 119 plots for acoustic surveys using batcorders, seven mist netting positions and 16 recorded roost trees within the national park to analyze (a) the influence on the foraging activity (i.e., number of echolocation calls) of the barbastelle bat *Barbastella barbastellus*, (b) the selection of roost surroundings, and (c) the selection of the roost tree itself. The roost trees contained maternity colonies of *B. barbastellus* in spruce stands killed by *I. typographus*. The interval between consecutive contour lines is 50 m. [Colour figure can be viewed at wileyonlinelibrary.com]

2001). We did not detect any spatial dependency in our model outputs (see Fig. S1 for details).

Bats were acoustically monitored 30 min before sunset until 30 min after sunrise. Surveys were conducted exclusively under good weather conditions on nights without rainfall and high wind speeds and with temperatures above 5°C. Recordings were accumulated at the plot level among sampling nights.

Batcorder recording settings were quality 20, threshold −36 bd; post-trigger 400 ms; critical call frequency 16 kHz. Species of recorded bats were identified using batIdent (ecoObs, Nürnberg Germany) whereas plotted recordings were additionally checked visually. Only recordings of *B. barbastellus* were used for further analyses.

Mist netting and radio telemetry

We captured bats with mist nets at forest glades and trails at seven different locations in the central part of the study area in July 2015 (Fig. 1). Nets were erected at dusk and controlled every 10 min. Captured bats were removed from the nets as quickly as possible. Lactating female *B. barbastellus* were tagged with a small 0.4 g radio transmitter from Biotrack Ltd., Wareham, UK (PIP AG 317) to locate the maternity colonies. Radio transmitters were fixed with a medical skin adhesive (Manfred Sauer GmbH) to the fur between the shoulder blades. The bats were held for 10 min until the adhesive dried and were then released. We followed tagged individuals until dawn to determine the approximate area of the chosen roost to facilitate the search the next day. Bats were radio-tracked using a portable 3-Element Yagi antenna (Biotrack Ltd.) and a THX-1000S radio receiver (Wildlife Materials, Inc., Murphysboro, IL, USA). Located maternity colony trees were marked and photographed. We measured diameter at breast height (DBH; cm) and tree height (m), visually estimated bark cover (%) and determined tree species and type (i.e., snag or vital tree) of every roost tree and of two control trees nearby from the ground, respectively. Control trees were the two next trees to the located roost with a DBH >7 cm. Individuals were tracked each day until the radio transmitter fell off to identify other roost trees if the tagged individual resettled in another tree. Every evening at dusk, we counted the number of bats flying out from maternity colonies. All steps during tagging and telemetry in this study were legally mandated with an animal welfare permit.

LiDAR parameters

We used LiDAR to acquire data on forest stands in the foraging environment. The study area was scanned with a Riegl LMS-Q680i sensor in July 2012 at a flight height of 650 m and an average point density of 30 points m^{-2} (Latifi *et al.*, 2016). Points were aggregated into 10 m × 10 m grids.

We selected canopy opening (%), vertical forest heterogeneity (m) and broadleaved trees (%) to represent forest structures in the foraging habitat. To estimate the canopy

opening, we calculated the point ratio of returns higher than 2 m above ground to total returns (Latifi *et al.*, 2016). Vertical heterogeneity is the standard deviation of the mean height of the 10 m × 10 m grids in a 20-m radius. A high standard deviation indicates a high structural heterogeneity, i.e., a high number of trees with different heights in the 20-m radius, and a small standard deviation indicates that trees have the same height (Latifi *et al.*, 2016). To estimate the per cent of broadleaved trees, we used single-tree detection following Reitberger *et al.* (2007) to identify coniferous and deciduous trees >2 m in a 20-m radius. The per cent of broadleaved trees was calculated based on the sum of single-tree volume per 10 m × 10 m grid cell. In the roost surroundings (i.e., trees surrounding maternity colonies of *B. barbastellus*), we selected as predictors the volume of live trees (m^3 ha^{-1}), the per cent canopy opening and per cent broadleaved trees based on the results of single-tree detection in a 20-m radius. The volume of the detected trees was calculated using multiple linear regression and their height, crown size and tree species as predictors (Yao, Krzystek & Heurich, 2012). We then applied an active learning approach to distinguish live and dead trees based on the properties of the LiDAR point cloud and aerial images (Polewski *et al.*, 2016). Last, we randomly selected 10 000 trees throughout the study area to serve as pseudo-absence observations and to represent the heterogeneity of the study area as well as possible.

Statistical analyses

All statistical analyses where carried out in the free statistical software R 3.3.1. (www.r-project.org). First, we investigated the foraging activity (i.e., number of echolocation calls) dependent on forest structural attributes. We applied Poisson-linear mixed effects models (Bolker *et al.*, 2008), with the number of echolocation calls of *B. barbastellus* as response variable and canopy opening (%), vertical heterogeneity (m), and percentage of broadleaved trees (%) as predictors. We included the night as random effect to control for nights with higher or lower bat activity in general and an observation-specific random effect to control for Poisson over-dispersion (Elston *et al.*, 2001). This random effect enables the statistical handling of extreme outliers in Poisson-distributed data within our statistical model.

Second, we compared the surrounding (20-m radius) of selected roost trees (i.e., maternity colonies of *B. barbastellus*) with the surrounding of 10 000 randomly selected control trees (i.e., pseudo-absence) in the study area in a binomial linear model. We included volume of live trees (m^3 ha^{-1}), canopy opening (%) and broadleaved trees (%) as predictors in the model.

Third, the selected roost tree itself was compared to the next two trees >7 cm DBH to reveal tree parameters important for the establishment of maternity colonies of *B. barbastellus*. We applied binomial linear models with colony presence/absence as response variable and diameter at breast height (cm), tree height (m), and bark cover (%) as predictor variables.

Table 1 Results of generalized linear (mixed) models testing the influence of forest structural attributes on (a) foraging activity (i.e., number of echolocation calls); (b) selection of roost surroundings; and (c) selection of roost trees by the barbastelle bat *Barbastella barbastellus* in forest stands affected by outbreaks of the European spruce bark beetle *Ips typographus*. Boldface indicates significance

Response variable	Estimate	SE	z-value	P-value
(a) Foraging activity				
Intercept	$-9.76\ e^{-1}$	1.12	$-8.71\ e^{-1}$	0.384
Broadleaved trees (%)	$5.07\ e^{-1}$	$7.49\ e^{-1}$	$6.76\ e^{-1}$	0.449
Canopy opening (%)	**4.63**	**1.79**	**2.59**	**0.009**
Vertical heterogeneity (m)	$2.00\ e^{-1}$	$1.30\ e^{-1}$	1.54	0.125
(b) Roost surrounding				
Intercept	**−14.39**	**2.85**	**5.05**	**<0.001**
Broadleaved trees (%)	−2.76	1.61	−1.72	0.085
Canopy opening (%)	−2.29	3.40	$-6.74\ e^{-1}$	0.500
Volume of live trees (m³ ha⁻¹)	**1.72**	**$4.61\ e^{-1}$**	**3.72**	**<0.001**
(c) Roost tree				
Intercept	$-7.70\ e^{-1}$	1.13	$6.80\ e^{-1}$	0.496
Diameter (cm)	**$4.83\ e^{-2}$**	**$2.30\ e^{-2}$**	**2.10**	**0.036**
Height (m)	$-1.37\ e^{-2}$	$3.61\ e^{-2}$	$-3.80\ e^{-1}$	0.704
Bark cover (%)	$-5.18\ e^{-3}$	$1.26\ e^{-2}$	$-4.12\ e^{-1}$	0.680

Figure 2 (a) Volume of live trees (m³ ha⁻¹) in the surroundings of maternity colonies of the barbastelle bat *Barbastellus barbastellus*, i.e., 20-m radius around roosts located in spruces killed by European spruce bark beetles *Ips typographus*, compared to the volume of live trees in the surroundings of 10 000 randomly selected trees. (b) Diameter at breast height (DBH; cm) of 16 trees housing maternity colonies of *B. barbastellus* compared to DBH of 32 nearby control trees.

Results

The acoustic surveys yielded 1859 recordings of *B. barbastellus*. Testing these recordings against LiDAR parameters [canopy opening (%), vertical heterogeneity (m), and broadleaved trees (%)] revealed that the number of recorded *B. barbastellus* calls increased with increasing canopy opening in a 20-m radius around the batcorder (Table 1).

Within the same time period, we caught 25 individuals of *B. barbastellus* (12 males and 13 females) and tagged six lactating females to locate maternity colonies using radio telemetry. These females used one to five different roost trees during the survey; we located 16 roost trees between the 9 and 18 July in total in an area of approximately 600 ha (Fig. 1). The distance between different roost trees of one tagged individual ranged from a few meters to 1 km. Statistical analyses of LiDAR parameters [volume of live trees (m³ ha⁻¹), canopy opening (%) and broadleaved trees (%)] revealed that the surroundings of roost trees had a significant higher volume of live trees than the surrounding of control trees (Fig. 2a and Table 1).

We counted 1–21 adult individuals of *B. barbastellus* leaving a single roost tree at dusk. Juveniles were not yet able to fly at the time. All maternity colonies of *B. barbastellus* were located beneath loose bark of spruces killed by *I. typographus* (Fig. 3). The 16 trees that carried maternity colonies had significantly larger diameters than 32 nearby control trees (Fig. 2b and Table 1). The median DBH
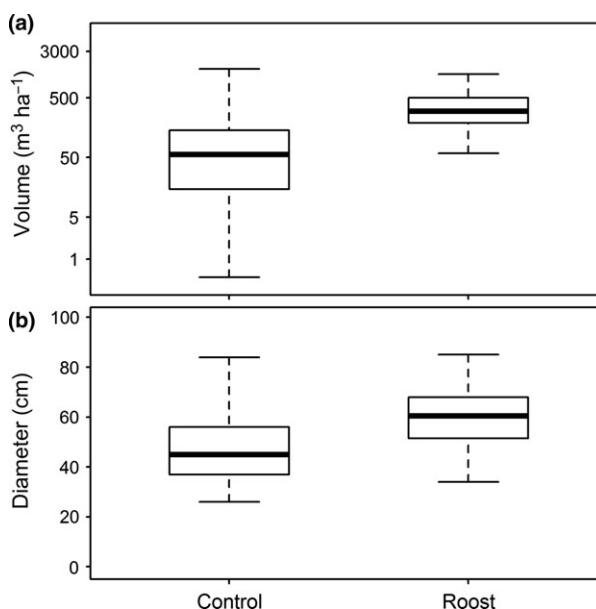
of the roost trees was 60.5 cm, whereas the median DBH of control trees was 45 cm (Fig. 2b).

Discussion

Our results demonstrated that forest stands shaped by outbreaks of *I. typographus* are utilized by *B. barbastellus* in various ways. Bat foraging habitats were improved by the beetle-induced increase in canopy opening. Roost surroundings were characterized by a larger volume of live trees compared to surroundings of randomly selected trees, which indicated that the bats use trees in semi-open stands as roosts. Maternity colonies were found in beetle-killed spruces larger than the nearby control trees; the colonies were located beneath loose bark.

Our results reveal the potential of *I. typographus* to create and improve habitats for a species listed in the Annexes II and IV of the Habitat Directive. However, the effects of severe pest infestations are not always favorable for species of conservation concern. For example, populations of the Mt. Graham red squirrel *Tamiasciurus hudsonicus grahamensis* in Arizona, USA, seriously declined after a sequence of different insect outbreaks and the subsequent dieback of spruces and firs (Koprowski, Alanen & Lynch, 2005). The response of a certain species depends on the affiliation to a structural component that gets influenced by natural disturbances and post-disturbance management strategies. For example, bark insectivorous birds profit from bark beetle outbreaks and the

Figure 3 Position of maternity colonies of the barbastelle bat *Barbastellus barbastellus* located beneath loose bark (arrows) of Norway spruces *Picea abies* killed by European spruce bark beetles *Ips typographus* in the Bavarian Forest National Park, Central Europe. [Colour figure can be viewed at wileyonlinelibrary.com]

concomitant dieback of infested trees because of the increasing food availability (Drever, Goheen & Martin, 2009). On the other hand, farmland birds in Mediterranean pine forests profit from the habitat opening caused by post-fire salvage logging (Rost *et al.*, 2012). In the case of *B. barbastellus* not the food availability but the fissures between bark and trunk that create roosting possibilities are favorable. Nevertheless, forest stands affected by outbreaks of *I. typographus* are not only utilized by *B. barbastellus*, but likewise host the rare fungus *Antrodiella citronella* (Bässler & Müller, 2010) and support populations of endangered saproxylic beetle species (Müller *et al.*, 2010).

Importance of canopy opening in foraging habitats

Our study revealed an increasing foraging activity with increasing canopy opening. This finding is in line with the study of Jung *et al.* (2012), who recorded foraging individuals of *B. barbastellus* in open forests with a low amount of understory, and with the studies of Runkel (2008) and Hillen *et al.* (2011), who recorded *B. barbastellus* individuals on linear structures, such as forest glades, forest trails and edges.

Canopy opening generally leads to increasing growth of herbaceous plants, which may serve as a food source for many species of nocturnal moths, which in turn are the main prey of *B. barbastellus* (Vaughan, 1997). However, the abundance of nocturnal moths is remarkably higher in single- and multi-layered spruce–beech stands than in logged and unlogged stands killed by bark beetles (Thorn *et al.*, 2015). Thus, increasing foraging activity appears to be the result of increased prey accessibility rather than increased prey amount.

The accessibility of prey is crucial for aerial hunting species that use echolocation. In contrast to predators that use their olfactory senses to detect their prey, physical barriers are a serious constraint during hunting for bats that use echolocation, such as the greater mouse-eared bat *Myotis myotis*, which is not able to reach crickets on the ground surface when ground vegetation is to dense (Rainho, Augusto & Palmeirim, 2010). *Barbastella barbastellus* is smaller than *M. myotis*. Thus, acoustical clutter, which prevents sufficient prey detection by echolocation, might play a more important role for *B. barbastellus*. Similarly, the silver-haired bat *Lasionycteris noctivagans*, which is about the same size as *B. barbastellus,* prefers open forest patches over thinned or intact patches because of acoustical clutter in dense vegetation (Patriquin & Barclay, 2003). Such acoustical clutter produced by the surroundings interferes with the target echo and hence complicates the processing of relevant information (Schnitzler & Kalko, 2001). Some species cope with this problem with special adaptions of their echolocation system (Schnitzler & Kalko, 2001) and wing morphology (Dietz, Dietz & Siemers, 2006). The northern long-eared bat *Myotis septentrionalis*, for example, can forage in dense vegetation because of its lower wing loading (Norberg & Rayner, 1987) and shows no vegetation avoidance behavior (Patriquin & Barclay, 2003). Species that lack such morphological adaptions are not able to hunt in dense vegetation (Müller *et al.*, 2012) and thus might benefit from canopy opening.

The effect of prey abundance, on the other hand, should be negligible for *B. barbastellus*. During observations of the response of different forest bat species in south-western France on the abundance of moths, *B. barbastellus* did not

increase activity when moth densities increased (Charbonnier *et al.*, 2014). Müller *et al.* (2012) also concluded that foragers that hunt along vegetation like *B. barbastellus* should not be influenced by the amount of prey.

In the analysis of acoustic survey data, the possibility of a sampling effect should be taken into account. The range of the batcorder is presumably lower in denser vegetation and might therefore detect fewer sonic signals, as has been discussed in earlier studies (Law, Anderson & Chidel, 1999; Patriquin *et al.*, 2003). However, *B. barbastellus* calls at a relatively high frequency of about 40 kHz (Denzinger, Schaub & Schnitzler, 2001). Patriquin *et al.* (2003) showed that higher frequencies of 40 kHz are equally detectable in different types of forest stands. A previous study in the Bavarian Forest National Park showed that *B. barbastellus* hunts mainly below the tree tops in this study area. Furthermore, also individuals flying above the canopy should have been detected since the canopy cover around our batcorder plots was relatively low (16 ± 13%; see Fig. S2). A sampling effect should therefore be negligible.

Importance of the volume of live trees in roost surroundings

Our study revealed a preference of *B. barbastellus* for roosts in trees with a high volume of live trees in the surroundings. One reason for this preference for semi-open stands could be that open habitats have a negative effect on the emergence time at dusk, which leads to a reduced foraging period. Russo *et al.* (2007) compared the time of evening bat emergence in open areas and dense forests while considering light levels and demonstrated that bats roosting in dense vegetation emerged earlier than those roosting in open habitats. Russo *et al.* (2007) concluded that the vegetation allocates cover and therefore better protection against predators, which allows the bats to start foraging earlier in the evening for crepuscular insects. This factor might be especially crucial for females with offspring.

Importance of a large diameter for roost trees

In our study, individuals of *B. barbastellus* roosted beneath loose bark of dead trees, as did bats in beech forests in Italy (Russo *et al.*, 2004). Maternity colonies of *B. barbastellus* were found in trees with a DBH larger than those of nearby control trees. This preference might be explained by the increasing amount of bark with increasing tree diameter and hence and increasing amount of flaking bark, i.e., the chances of find a suitable bark cavity are higher in trees with a larger DBH.

Not only old beeches (Russo *et al.*, 2004), oaks (Hillen *et al.*, 2010) and pines (Steinhauser *et al.*, 2002) but also Norway spruce trees killed by *I. typographus* are suitable roosts for *B. barbastellus*. Thus, the tree species itself might be of subordinate importance for the roost selection of *B. barbastellus* as long as small cavities are present. Indeed, Kühnert *et al.* (2016) found *B. barbastellus* in Switzerland

exclusively behind window shutters and Ancillotto *et al.* (2014) recorded maternity colonies in rock crevices in Abruzzo, where *B. barbastellus* is thought to compensate the general absence of trees with the availability of a high amount of prey.

Conclusions

Our results highlight the capacity of forests affected by *I. typographus* as suitable habitats for *B. barbastellus*. This underlines the potential of commercially managed spruce forests for the conservation of species, particularly since major parts of European forests have been transformed to spruce monocultures (Brus *et al.*, 2011). Outbreaks of *I. typographus* in these managed forests can be utilized as restorative tool for forest management to improve habitat quality by an increase in structural diversity. In this case, it improved foraging as well as roosting habitats for *B. barbastellus* [e.g. Jonášová & Prach (2004) and Angelstam (1998)]. However, a mosaic of stands with different tree densities can only be obtained by avoiding all salvage logging operations. Small, scattered groups of trees infested by *I. typographus* are commonly overlooked in commercially managed spruce forests, which results in dry snags with a low pest hazard (Wermelinger, 2004). Such snags could be retained to provide suitable roosts for *B. barbastellus*, without increasing the risk of pest outbreaks, particularly since the economic value of such snags is about 20–30% lower than logged healthy spruce wood. On the other hand, if salvage logging is required, we recommend that snags of large diameter be maintained.

Acknowledgments

References

Ancillotto, L., Cistrone, L., Mosconi, F., Jones, G., Boitani, L. & Russo, D. (2014). The importance of non-forest landscapes for the conservation of forest bats: lessons from barbastelles (*Barbastella barbastellus*). *Biodivers. Conserv.* **24**, 171–185.

Angelstam, P.K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* **9**, 593–602.

Bässler, C. & Müller, J. (2010). Importance of natural disturbance for recovery of the rare polypore *Antrodiella*

citrinella Niemelä & Ryvarden. *Fungal Biol.* **114**, 129–133.

Bässler, C., Müller, J. & Dziock, F. (2010). Detection of climate-sensitive zones and identification of climate change indicators: a case study from the Bavarian Forest National Park. *Folia Geobot.* **45**, 163–182.

Beudert, B., Bässler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N. & Müller, J. (2015). Bark beetles increase biodiversity while maintaining drinking water quality. *Conserv. Lett.* **8**, 272–281.

Bjørnstad, O.N. & Falck, W. (2001). Nonparametric spatial covariance functions: estimation and testing. *Environ. Ecol. Stat.* **8**, 53–70.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135.

Brus, D.J., Hengeveld, G.M., Walvoort, D.J.J., Goedhart, P.W., Heidema, A.H., Nabuurs, G.J. & Gunia, K. (2011). Statistical mapping of tree species over Europe. *Eur. J. Forest Res.* **131**, 145–157.

Charbonnier, Y., Barbaro, L., Theillout, A. & Jactel, H. (2014). Numerical and functional responses of forest bats to a major insect pest in pine plantations. *PLoS ONE* **9**, 1–8.

Denzinger, S.A., Schaub, B.A. & Schnitzler, H. (2001). Echolocation by the barbastelle bat, *Barbastella barbastellus*. *J. Comp. Physiol. A.* **187**, 521–528.

Dietz, C., Dietz, I. & Siemers, B.M. (2006). Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). *J. Mammal.* **87**, 1241–1251.

Drever, M.C., Goheen, J.R. & Martin, K. (2009). Species – energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology* **90**, 1095–1105.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001). Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology* **122**, 563–569.

Hillen, J., Kiefer, A. & Veith, M. (2010). Interannual fidelity to roosting habitat and flight paths by female western barbastelle bats. *Acta Chiropt.* **12**, 187–195.

Hillen, J., Kaster, T., Pahle, J., Kiefer, A., Elle, O., Griebeler, E.M. & Veith, M. (2011). Sex-specific habitat selection in an edge habitat specialist, the western barbastelle bat. *Ann. Zool. Fenn.* **48**, 180–190.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001). *Global status survey and conservation action plan: microchiropteran bats*. Gland: IUCN.

Jonášová, M. & Prach, K. (2004). Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. *Ecol. Eng.* **23**, 15–27.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood - Lessons for dead wood management. *Silva Fenn.* **39**, 289–309.

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J. & Kalko, E.K.V. (2012). Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *J. Appl. Ecol.* **49**, 523–531.

Koprowski, J.L., Alanen, M.I. & Lynch, A.M. (2005). Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Cons.* **126**, 491–498.

Kühnert, E., Schönbächler, C., Arlettaz, R. & Christe, P. (2016). Roost selection and switching in two forest-dwelling bats: implications for forest management. *Eur. J. Wildl. Res.* 6–9.

Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T. & Bebi, P. (2016). A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems.
For. Ecol. Manage. 2–7.

Kumar Duraiappah, A., Naeem, S. and Ash, N., WRI & (UNEP-WCMC), M.E.A.B. (2005) *Ecosystems and human well-being: biodiversity synthesis*. Washington (DC): World Resources Institute.

Latifi, H., Heurich, M., Hartig, F., Müller, J., Krzystek, P., Jehl, H. & Dech, S. (2016). Estimating over- and understorey canopy density of temperate mixed stands by airborne LiDAR data. *Forestry* **89**, 69–81.

Law, B.S., Anderson, J. & Chidel, M. (1999). Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. *Biol. Cons.* **88**, 333–345.

Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J. & Müller, J. (2013). Conservation value of forests attacked by bark beetles: highest number of indicator species is found in early successional stages. *J. Nat. Conserv.* **21**, 97–104.

Lindenmayer, D.B., Burton, P.J. & Franklin, J.F. (2012). *Salvage logging and its ecological consequences*, 1st edn. Washington: Island Press.

Lindenmayer, D., Barton, P. & Pierson, J. (2015). *Indicators and surrogates of biodiversity and environmental change*. Clayton South: CSIRO Publishing.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T. & Duelli, P. (2008). The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodivers. Conserv.* **17**, 2979–3001.

Müller, J., Noss, R.F., Bussler, H. & Brandl, R. (2010). Learning from a "benign neglect strategy" in a national park: response of saproxylic beetles to dead wood accumulation. *Biol. Cons.* **143**, 2559–2569.

Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H. & Brandl, R. (2012). Aggregative response in bats: prey abundance versus habitat. *Oecologia* **169**, 673–684.

Norberg, U.M. & Rayner, J. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations,

flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. B. Biol. Sci.* **316**, 335–427.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Outila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* **24**, 101–112.

Patriquin, K.J. & Barclay, R.M.R. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *J. Appl. Ecol.* **40**, 646–657.

Patriquin, K.J., Hogberg, L.K., Chruszcz, B.J. & Barclay, R.M.R. (2003). The influence of habitat structure on the ability to detect ultrasound using bat detectors. *Wildl. Soc. Bull.* **31**, 475–481.

Polewski, P., Yao, W., Heurich, M., Krzystek, P. & Stilla, U. (2016). Combining active and semisupervised learning of remote sensing data within a renyi entropy regularization framework. *IEEE J. Select. Topics Appl. Earth Obs. Remote Sens.* **9**, 2910–2922.

Rainho, A., Augusto, A.M. & Palmeirim, J.M. (2010). Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. *J. Appl. Ecol.* **47**, 850–858.

Reitberger, J., Heurich, M., Krzystek, P. & Stilla, U. (2007). Single tree detection in forest areas with high-density LiDAR data. *Int. Arch. Photogram. Remote Sensing Spatial Inf. Sci.* **36**, 139–144.

Rost, J., Clavero, M., Brotons, L. & Pons, P. (2012). The effect of postfire salvage logging on bird communities in Mediterranean pine forests: the benefits for declining species. *J. Appl. Ecol.* **49**, 644–651.

Runkel, V. (2008). *Mikrohabitatnutzung syntoper Waldfledermäuse. Ein Vergleich der genutzten Strukturen in anthropogen geformten Waldbiotopen Mitteleuropas*. PhD Thesis, Naturwissenschaftliche Fakultät Friedrich-Alexander-Universität, Erlangen-Nürnberg.

Russo, D., Cistrone, L., Jones, G. & Mazzoleni, S. (2004). Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biol. Cons.* **117**, 73–81.

Russo, D., Cistrone, L. & Jones, G. (2005). Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats *Barbastella barbastellus*. *Ecography* **28**, 769–776.

Russo, D., Cistrone, L. & Jones, G. (2007). Emergence time in forest bats: the influence of canopy closure. *Acta Oecol.* **31**, 119–126.

Russo, D., Cistrone, L., Garonna, A.P. & Jones, G. (2010). Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats. *Biodivers. Conserv.* **19**, 2501–2515.

Russo, D., Cistrone, L. & Garonna, A.P. (2011). Habitat selection by the highly endangered long-horned beetle

Rosalia alpina in Southern Europe: a multiple spatial scale assessment. *J. Insect Conserv.* **15**, 685–693.

Russo, D., Febbraro, M.Di, Cistrone, L., Jones, G., Smeraldo, S., Garonna, A.P. & Bosso, L. (2015). Protecting one, protecting both? Scale-dependent ecological differences in two species using dead trees, the rosalia longicorn beetle and the barbastelle bat. *J. Zool.* **297**, 165–175.

Schelhaas, M.J., Nabuurs, G.J. & Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. *Glob. Change Biol.* **9**, 1620–1633.

Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A. & Koivula, M. (2006). Reconciling salvage logging of boreal forests with a natural-disturbance management model. *Conserv. Biol.* **20**, 971–983.

Schnitzler, H.-U. & Kalko, E.K.V. (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* **29**, 382–390.

Sierro, A. & Arlettaz, R. (1997). Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecol.* **18**, 91–106.

Steinhauser, D., Burger, F., Hoffmeister, U., Matez, G., Teige, T., Steinhauser, P. & Wolz, I. (2002). Untersuchungen zur Ökologie der Mopsfledermaus, *Barbastella barbastellus* (Schreber, 1774), und der Bechsteinfledermaus, *Myotis bechsteinii* (Kuhl, 1817), im Süden des Landes Brandenburg. *Schriftenr. Landschaftspflege. Naturschutz* **71**, 81–98.

Thorn, S., Hacker, H.H., Seibold, S., Jehl, H., Bässler, C. & Müller, J. (2015). Guild-specific responses of forest Lepidoptera highlight conservation-oriented forest management - Implications from conifer-dominated forests. *For. Ecol. Manage.* **337**, 41–47.

Thorn, S., Bässler, C., Svoboda, M. & Müller, J. (2016). Effects of natural disturbances and salvage logging on biodiversity - Lessons from the Bohemian Forest. *For. Ecol. Manage.* **388**, 113–119.

Thorn, S., Bässler, C., Burton, P.J., Cahall, R.E., Campbell, J.L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hutto, R.L., Lee, E.-J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.-B., Zmihorski, M. & Müller, J. (2017). Impacts of salvage logging on biodiversity- a meta-analysis. *J. Appl. Ecol.* https://doi.org/10.1111/1365-2664.12945

Vaughan, N. (1997). The diets of British bats (Chiroptera). *Mammal Rev.* **27**, 77–94.

Wermelinger, B. (2004). Ecology and management of the spruce bark beetle *Ips typographus* - A review of recent research. *For. Ecol. Manage.* **202**, 67–82.

Yao, W., Krzystek, P. & Heurich, M. (2012). Tree species classification and estimation of stem volume and DBH based

on single tree extraction by exploiting airborne full-waveform LiDAR data. *Remote Sens. Environ.* **123**, 368–380.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Spline correlograms of model residuals of (a) foraging habitat, (b) roost surrounding and (c) roost trees to test for spatial dependence.

Figure S2. Canopy cover in the 20-m surroundings of all batcorder plots with a mean cover of $16 \pm 13\%$.