ORIGINAL ARTICLE

Mono-specific forest plantations are valuable bat habitats: implications for wind energy development

Sascha Buchholz[1,2] · Volker Kelm[3] · Simon J. Ghanem[3]

Abstract

Near-natural or semi-natural forests such as relatively undisturbed and old deciduous or mixed woodland are considered worth protecting and ecologically valuable habitats for bat conservation. In contrast, mono-specific forest plantations are considered ecologically less valuable; thus, decision-makers recommend these plantations as suitable locations for wind power stations and therefore want to further expand wind turbines in these habitats. This is expected to have a strong negative impact on the landscape because forests would be cleared for wind turbine pads and access roads and wind turbines rise above the trees with adverse impacts for bats. Therefore, we argue that, in light of bat conservation, the suitability of forest plantations for wind energy development is not, per se, warranted and that implications of wind power stations, even in mono-specific forest plantations, should be assessed and evaluated. We conducted long-term bat activity monitoring and recorded bat echolocation calls above the canopies of different forest sites (coniferous monoculture plantations and semi-natural mixed deciduous forests) in Germany and compared different forest types in terms of species richness, total bat activity, activity of the three bat species groups and species composition. Generalised linear models revealed that forest type and the amount of forest biotopes did not enhance bat activity. Ordination showed that species composition was not affected by forest type, location and connectivity. Mono-specific forest plantations can harbour a diverse bat fauna with high species activity and are, therefore, valuable bat habitats just as near-natural or semi-natural woodlands are. Environmental impact assessment and mitigation measures are vital in all forest types before and after planning for wind energy turbines. In particular, future planning and approval processes must consider the importance of mono-specific forest plantations for bat species protection.

Keywords Chiroptera · Coniferous plantation · Environmental impact assessment · Renewable energy · Wind farm · Wind power · Woodland

Introduction

Woodlands are vital for many bat species by providing habitats, roosting sites and hunting grounds (e.g. Jantzen and Fenton 2013; Kalda et al. 2015; Charbonnier et al. 2016a). In general, the functional quality of woodlands is determined by a number of landscape and habitat parameters such as landscape connectivity and complexity (Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Fuentes-Montemayor et al. 2013). It has been widely shown that anthropogenic impacts negatively influence the distribution of forest bat species by affecting roosting and foraging habitats (fragmentation, Lesiński et al. 2007; habitat loss, Crampton and Barclay 1998; logging, Fukui et al. 2011). Furthermore, negative changes in bat density and diversity are often related to wind farms or wind turbines, respectively (Kunz et al. 2007a, 2007b; Horn et al. 2008; Cryan and Barclay 2009; Rydell et al. 2010), which is of particular importance because many bat species are endangered at global, national and regional levels (Mickleburgh et al. 2002; Jones et al. 2009).

In Germany, renewable energies are forecasted to rise to about 40–45% of the gross electricity consumption by 2025 to

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fulfil climate protection goals and up to 80% by 2050, with wind energy being the most important energy source (Informationsportal Erneuerbare Energien 2020). Aside from open landscapes, woodlands are considered potential locations for wind power stations. The German Federal Agency of Nature Conservation (BFN 2011) estimates that about 14% of existing German woodlands are suitable sites. In contrast to near-natural or semi-natural woodlands, mono-specific forest plantations are lower quality habitats for bats, and decision-makers are recommending them for wind power stations (e.g. MUGV Brandenburg 2011). Decision-makers argue that mono-specific forest plantations—characterised by one tree species (pine in NE-Germany) (Klimo et al. 2000)—are ecologically less valuable, as they emaciate the soil, are particularly sensitive to windfall and pests and are less diverse in plant and animal species (Klimo et al. 2000; MUGV Brandenburg 2011). Therefore, wind energy development in mono-specific forest plantations is seen as ecologically sound and, thus, has become the focus of attention of wind power operators (BFN 2011). The general consensus is therefore that the expansion of wind turbines in these plantations should be promoted although landscape changes are associated with this (for instance cleared forests for wind turbine pads and access roads as, wind turbines above the remaining forest patches).

In contrast, near-natural or semi-natural woodlands, such as deciduous and mixed deciduous forests, are considered worth protecting and ecologically valuable habitats, and several studies prove their importance for bat conservation (Kaňuch and Krištín 2005; Kaňuch and Celuch 2007; Zahn et al. 2008; Kalda et al. 2015). This is especially true in terms of wind energy development and its negative effects on bats and bat habitats. It is known that higher collision rates may occur due to higher bat activities above the canopy level (Grunwald and Schäfer 2007; Brinkmann et al. 2011; Zahn et al. 2014). Furthermore, indirect impacts, such as habitat loss, can be expected through logging, as many bat species strongly depend on tree holes as roosting sites (Meschede and Heller 2000; Dietz et al. 2009).

To ensure environmentally sustainable energy production, the implications of wind power stations in mono-specific forest plantations versus near-natural or semi-natural woodlands should be assessed and evaluated. A number of studies highlighted the adverse effects of wind power stations for bats and bat habitats in woodlands (e.g. Brinkmann et al. 2011; Hötker et al. 2006; Aschoff et al. 2006, Kunz et al. 2007b), but most studies focused on near-natural or semi-natural woodlands while forest plantations have been nearly neglected in Europe (but see Kirkpatrick et al. 2017a). This is a drawback because the adverse effects of wind turbines may even be stronger through the attraction effects of wind turbines for bats (Cryan et al. 2014). We hypothesise that mono-specific forest plantations can be valuable bat habitats

and that stand type is not necessarily a predictor of bat activity as long as appropriate features such as tree holes, food availability and beneficial habitat structure or connectivity, respectively, are provided at the landscape and habitat level (Charbonnier et al. 2016b).

Methods

Field methods

We recorded bat echolocation calls with the batcorder system (Batcorder—ecoObs, Nuremberg, Germany) above the canopies of 24 different forest sites in Germany (Appendices Fig. 3 and Table 3). All sites were in proposed wind farms in a landscape dominated by different forest types. Bat activity can be highly variable with the daily variation of activity patterns being as high as the variation between different sites (Mathews et al. 2016, pers. observation). There are several guidelines recommending minimum buffer zones of 200 m to habitats of importance to bats (Rodrigues et al. 2015; Kelm et al. 2014). Consequently, we defined a 200-m radius for each location around the recording device to assess the environmental variables using QGIS 3.4 (Quantum GIS Development Team 2018 - © GeoBasis-DE/LGB, dl-de/by-2-0). In this radius, we calculated the amount of the forest biotopes (in percent) within each site and evaluated the available forest type and assigned it as a coniferous plantation (consisted of a single pine species (*Pinus sylvestris*)) or mixed deciduous forest (if at least 50% of the forest cover belonged to this category) (Table 1). All forest patches showed a similar age structure for around 50 years (± 20 years). To assess the connectivity, we measured all linear landscape elements, e.g. forest edges, hedges, roads or streams. We measured the distance (in m) from the recording device to the nearest forest edge that marked a change in habitat type (roads or streams were not considered) or water body. We defined water bodies as those with standing water and a minimum size of 8 × 8 m.

At each site, we recorded calls for 57–183 entire nights (sunset to sunrise) between April and November from 2011 to 2018. To ensure comparability, all surveys were conducted on mild nights (> 10 °C ambient temperature), without rain and low wind speeds (visual assessment with ≤ small branches moving, which according to the Beaufort scale is a maximum speed of 3.4–5.4 m/s). We detected the bat passes above the canopy with a batcorder fixed in a weatherproof box that was attached on a pole protruding the treetops about 1.5 m. The data transmission was facilitated via a GSM module, and the power supply was provided by a solar panel. All batcorders recorded the full frequency spectrum between 16 and 150 kHz in real time with a sampling rate of 500 kHz. We used a threshold of 27 dB and a pre-trigger of 400 ms for the recordings.

Table 1 Description of environmental variables

Variable name	Scale	Explanation
Amount of forest patches	Ratio	% in a 200-m radius around the study plot
Connectivity	Metric	Linear landscape elements in a 200-m radius, e.g. forest edges, hedges, streams, roads
Distance to the forest edge	Metric	Is the distance in metres from the study plot to the nearest forest edge
Distance to the next water body	Metric	Is the distance in metres from the study plot to the nearest water body (minimum pond size)
Forest type	Categorical	Coniferous plantation, mixed deciduous

We analysed the ultrasound recordings with the batIdent and bcAnalyze software (ecoObs, Nuremberg, Germany) to organise and identify species-specific echolocation calls. This software automatically measures the primary sound parameters of the recorded echolocation calls and calculates a probability value that a call is from a specific bat species. The software identifies bat echolocation calls from simultaneous recordings of up to three individuals per sequence (Runkel and Marckmann 2009). After the automatic analysis, we manually validated all echolocation calls for misidentifications and, when possible, identified additional calls following the criteria of species identification described in Hammer and Zahn (2009) and Skiba (2003). Where the recording quality allowed, we identified the following bats to species level: *Barbastella barbastellus*, *Eptesicus serotinus*, *Myotis daubentonii*, *Myotis myotis*, *Myotis nattereri*, *Nyctalus leisleri*, *Nyctalus noctula*, *Pipistrellus nathusii*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*. As some bat species are acoustically nearly indistinguishable, we combined the recordings of *Myotis brandtii* and *Myotis mystacinus* to the species group Mbra and the species *Plecotus auritus* and *Plecotus austriacus* to the species group Plecotus. Furthermore, we included all *Myotis*-like, *Nyctalus*-like, *Pipistrellus*-like and *Plecotus*-like calls in the categories *Myotis* sp., *Nyctaloid*, *Pipistrelloid* and *Plecotus* sp. For testing environmental effects on bat species composition and activity, we first classified all bat species following their collision risk at wind turbines as well as their foraging and echolocation behaviour to one of the three groups, *Nyctaloid* group (high collision risk—open space forager), *Pipistrelloid* group (medium collision risk—edge space forager) and *Myotis/Plecotus* group (low collision risk—narrow space forager). For detailed information about classifying bats in groups and guilds, see Denzinger and Schnitzler (2013). To describe bat activity, we counted the number of bat passes for each of the different species or groups. A 'bat pass' was defined as a sequence of at least two echolocation pulses of a passing bat (Thomas and West 1989). Therefore, we assume that the number of bat passes is highly correlated with bat activity. In addition to the already high reliability and precision of the batcorder system, we professionally calibrated all used microphones prior to their field use to warrant the same detectability under similar conditions. Consequently, all zero observations were regarded statistically as true absences of bats in a certain range.

Data analysis

The data analysis was done using the free software package R-3.4.4 (R Core Team 2019). To test, if environmental variables (explanatory variables: amount of forest patches, connectivity, distance to forest edge, distance to next water body, forest type) had a significant effect (alpha = $P < 0.05$) on total bat activity, the species group activity and species numbers as response variables, we performed generalised linear models (GLM). Furthermore, we used the number of recording days as an offset variable to correct for different recording intensities. To avoid multicollinearity, we only included environmental parameters with correlations of $|r| < 0.7$. To compensate for the detected overdispersion, the standard errors were corrected using a quasi-Poisson GLM (Crawley 2007; Zuur et al. 2009). The most appropriate models were stepwise (backward) determined by analysis of deviance (Zuur et al. 2009). The residual deviance was used as a goodness-of-fit measure by calculating the pseudo-R^2 (Dobson 2002). Direct comparisons of categorical variable 'forest type' were conducted with post hoc Tukey's pairwise comparisons using R package LSMEANS.

In order to detect groupings of sample sites and the impact of environmental variables on species composition, bat frequencies were subjected to non-metric multidimensional scaling (NMDS) using VEGAN and MASS packages in R. For ordination, the frequencies of each species were square root transformed. NMDS is an iterative ordination method that places samples in a k-dimensional space using the ranked distances between them (McCune and Grace 2002). The ordination was based on the Bray-Curtis dissimilarity matrix. In search of a stable solution, a maximum of 100 random starts was used. We applied Kruskal's stress formula multiplied by 100, as given in McCune and Grace (2002). After two trials, two convergent solutions were found for a three-dimensional model. Afterwards, environmental data was fitted onto the ordination. The significance of the explanatory power of each variable was evaluated with a Monte-Carlo randomisation test (10,000 permutations) (Manly 1997) using R function 'envfit'.

Results

In all, we detected 10 bat species (Appendix Table 3). Most frequent were *Nyctalus noctula*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *Pipistrellus nathusii* that occurred at all study sites. Generalised linear models revealed that total bat activity (total bat passes) ($Chi^2 = 1.56$, $P = 0.20$, GLM) and number of bat species ($Chi^2 = 0.65$, $P = 0.42$, GLM) in coniferous plantations and mixed deciduous forests did not differ significantly (Fig. 1). Moreover, forest type did not significantly affect the activity level of the three species groups (Table 2), *Myotis*/*Plecotus* group ($Chi^2 = 0.48$, $P = 0.49$, GLM), *Nyctaloid* group ($Chi^2 = 0.83$, $P = 0.36$, GLM) and *Pipistrelloid* group ($Chi^2 = 2.82$, $P = 0.09$, GLM). Bat activity level in general ($Chi^2 = 3.87$, $P = 0.05$, GLM) and the activity level of the *Nyctaloid* ($Chi^2 = 3.72$, $P = 0.05$, GLM) and *Pipistrelloid* groups ($Chi^2 = 3.07$, $P = 0.08$, GLM) increased with closer distance to the next water body as a statistical trend. Also, as a statistical trend, the amount of forest patches negatively affected total bat activity ($Chi^2 = 3.40$, $P = 0.07$, GLM) and *Nyctaloid* group activity ($Chi^2 = 3.34$, $P = 0.07$, GLM) while *Myotis*/*Plecotus* species responded positively ($Chi^2 = 3.08$, $P = 0.08$, GLM). All other environmental variables had no impact on the activity levels of the groups or on the number of encountered species.

The NMDS based on the bat species activity level revealed no significant effects of the environmental variables (Fig. 2). None of the variables (connectivity, distance to forest edge, distance to next water body, forest or forest type) affected species groups (amount of forest patches: $F = 0.1$, $R^2 = 0.01$, $P = 0.96$; connectivity: $F = 0.4$, $R^2 = 0.02$, $P = 0.73$; distance to forest edge: $F = 0.4$, $R^2 = 0.02$, $P = 0.75$; distance to next water body: $F = 1.4$, $R^2 = 0.06$, $P = 0.25$; forest type: $F = 2.1$, $R^2 = 0.09$, $P = 0.10$; permutational multivariate analysis of variance with 9999 permutations).

## Discussion

Impact of forest type

It is well known that near-natural or semi-natural woodlands, such as deciduous and mixed deciduous forests, are ecologically valuable bat habitats; thus, they are considered worth protecting (e.g. Jantzen and Fenton 2013; Kalda et al. 2015; Charbonnier et al. 2016a, 2016b). However, we found no significant differences in bat densities in mixed deciduous forest and mono-specific forest plantations. Given that none of the bat groups responded to forest type, we encourage a change of thinking regarding the ecological value of mono-specific forest plantations for bats. Even if forest plantations

are ecologically critical, they still provide a habitat with equally high bat activity as near-natural or semi-natural woodlands (Pereira et al. 2016; da Silva et al. 2019). Moderate silvicultural methods can also promote bat diversity (Kirkpatrick et al. 2017a), such as harvesting, which creates a patch mosaic with different tree densities (Perry et al. 2007; Blakey et al. 2016; Kirkpatrick et al. 2017b).

Kalda et al. (2015) found only a minor impact of forest type on bat diversity. They concluded that natural and anthropogenic woodlands could be seen as a single land-cover type regardless of the dominating tree species. In addition, Glendell and Vaughan (2002) found forest plantations to be suitable habitats for bats, as they showed that bats similarly forage in semi-natural and plantation woodlands. Bats depend on a variety of landscape and habitat properties, for example forest edge structures for commuting and foraging (Hein et al. 2009; Kelm et al. 2014; Morris et al. 2010; Jantzen and Fenton 2013), open patches (Loeb and O'Keefe 2006; Perry et al. 2007; Kirkpatrick et al. 2017b), diverse surrounding landscape compositions (Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Heim et al. 2018), water bodies (Morris et al. 2009; Heim et al. 2018) and roosting sites (Kühnert et al. 2016; Coronado et al. 2017; Dietz et al. 2018). However, all these features potentially exist in all diverse, near-natural and mono-specific forest plantations (Cruz et al. 2016; Kirkpatrick et al. 2017a). According to Ruczyński et al. (2010) and Toth et al. (2015), woodland bats may change their roost site preferences and could, thus, occupy habitats previously considered less suitable. Runkel (2009) observed that bats generally use a wide range of forest habitats, but only a few specialists succeed in niche partitioning in forests with a low spacing between trees. Our results show that many open and edge space species, such as *Pipistrellus pipistrellus*, *Pipistrellus nathusii*, *Eptesicus serotinus* and *Nyctalus noctula*, also had high activity in coniferous forestry zones which adds to findings of Kirkpatrick et al. (2017b) for Sitka spruce (*Picea sitchensis*) plantations. All these species are negatively affected by wind energy development (Brinkmann et al. 2011) and at risk from wind turbines (Müller et al. 2013).

Differences in species composition naturally occur across different regions; however, other drivers—such as landscape composition, habitat structure and stand origin—are comparable (Kalda et al. 2015). In our study, species composition was not influenced by forest type, even though *Pipistrellus* species usually show a preference for open patches in forests, such as thinnings and windbreaks (Kirkpatrick et al. 2017b), which are habitat conditions that rather occur in mixed deciduous forests. However, *Pipistrellus pipistrellus* is a generalist species that can reach high densities in manifold landscapes (Davidson-Watts et al. 2006). Moreover, *Myotis daubentonii* can use open space landscapes (Kalda et al. 2015) but strongly depends on ponds and lakes as primary foraging habitats

Fig. 1 Bat activity and number of bat species (mean and standard error of the mean) in coniferous plantations and mixed deciduous forest did not differ significantly between both forest types (bat activity: $Chi^2 = 1.56$, $P = 0.20$, GLM; number of bat species: $Chi^2 = 0.65$, $P = 0.42$, see Table 2). For bat activity, additional post hoc Tukey's pairwise comparisons of categorical variable 'forest type' have been conducted:
$z.ratio = 1.23$, $P = 0.22$
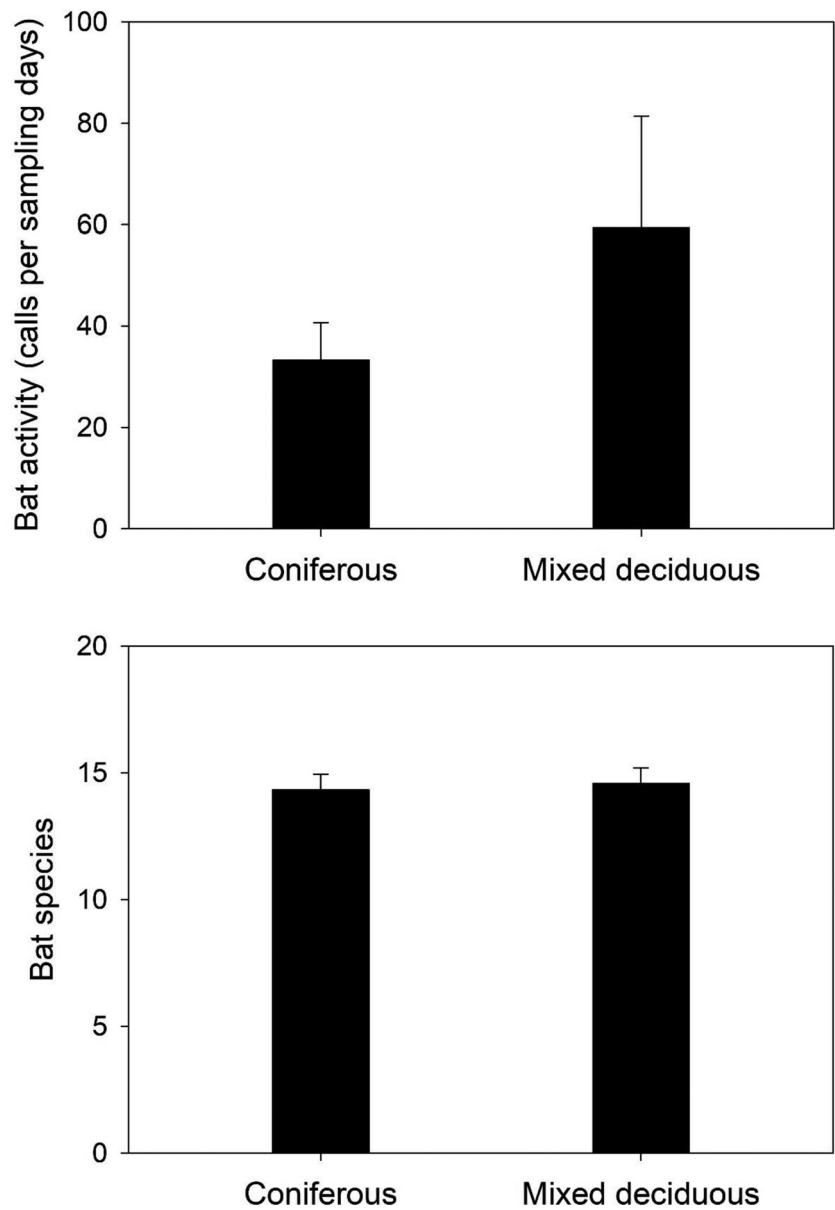
(Glendell and Vaughan 2002; Dietz et al. 2009). In general, *Myotis* species are known to select habitat structure over forest type. Thus, bats of the *Myotis* genus are able to negotiate cluttered woodland interiors (Glendell and Vaughan 2002).

Table 2 Regression results (quasi-Poisson GLM). Positive effects on dependent variables are expressed as ↑ (for increasing) and negative ones are expressed as ↓ (for decreasing)

Response	Amount of forest patches	Connectivity	Distance to the forest edge	Distance to the next water body	Forest type
Total bat passes all groups	$Chi^2 = 3.40$, $P = 0.07$ (↓)	$Chi^2 = 0.40$, $P = 0.53$	$Chi^2 = 1.33$, $P = 0.25$	$Chi^2 = 3.87$, $P = 0.05$ (↓)	$Chi^2 = 1.56$, $P = 0.21$
Species number	$Chi^2 = 1.53$, $P = 0.22$	$Chi^2 = 0.26$, $P = 0.61$	$Chi^2 = 2.24$, $P = 0.26$	$Chi^2 = 1.26$, $P = 0.26$	$Chi^2 = 0.65$, $P = 0.42$
Myotis/Plecotus group	$Chi^2 = 3.08$, $P = 0.08$ (↑)	$Chi^2 = 0.20$, $P = 0.65$	$Chi^2 = 1.92$, $P = 0.17$	$Chi^2 = 1.32$, $P = 0.25$	$Chi^2 = 0.48$, $P = 0.49$
Nyctaloid group	$Chi^2 = 3.34$, $P = 0.07$ (↓)	$Chi^2 = 0.36$, $P = 0.54$	$Chi^2 = 1.29$, $P = 0.26$	$Chi^2 = 3.72$, $P = 0.05$ (↓)	$Chi^2 = 0.83$, $P = 0.36$
Pipistrelloid group	$Chi^2 = 2.62$, $P = 0.11$	$Chi^2 = 0.32$, $P = 0.57$	$Chi^2 = 1.05$, $P = 0.31$	$Chi^2 = 3.07$, $P = 0.08$ (↓)	$Chi^2 = 2.82$, $P = 0.09$

Impact of spatial variables

There were no significant effects of forest type, but we found that distance to the next water body had a positive impact on the activity level of the *Nyctaloid* group, as well as on the overall bat activity. Water bodies play an important role as a bat habitat, as they are visited for drinking, offer an abundance of prey (Fukui et al. 2006) and are landmarks for bat orientation and navigation (Serra-Cobo et al. 2000).

Habitat connectivity is a very important driver for bat diversity and density, while fragmentation and isolation, in contrast, negatively affect bats (Gorresen and Willig 2004; Yates and Muzika 2006; Lesiński et al. 2007) especially in the presence of wind turbines (Roscioni et al. 2014). The amount of forest area did not affect our three functional bat groups. However, generally, the amount of forest enhances bat activity, which corroborates the great importance of woodlands (e.g. Jantzen and Fenton 2013; Kalda et al. 2015; Neece et al. 2018). In contrast, higher stocking levels and lesser
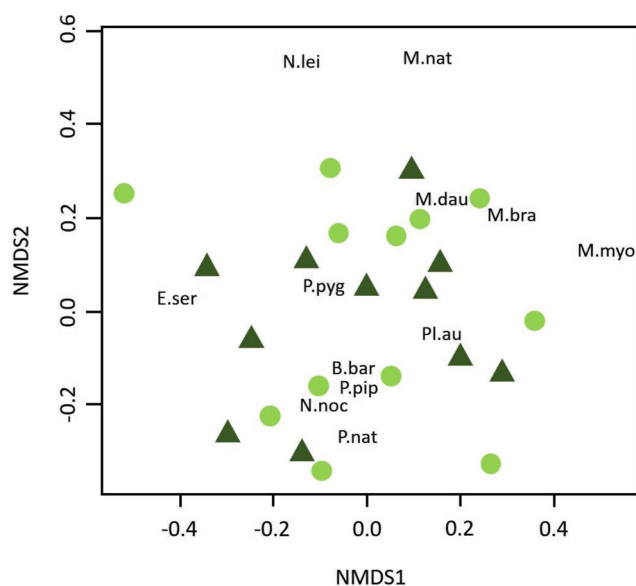

Fig. 2 Ordination plot (NMDS, 2 dimensions, stress = 0.18) based on bat species activity (number of bat passes). Forest types are displayed as triangles (= coniferous plantations) and circles (= mixed deciduous forests). Environmental variable did not affect species distribution (amount of forest patches: $F = 0.1$, $R^2 = 0.01$, $P = 0.96$; connectivity: $F = 0.4$, $R^2 = 0.02$, $P = 0.73$; distance to forest edge: $F = 0.4$, $R^2 = 0.02$, $P = 0.75$; distance to next water body: $F = 1.4$, $R^2 = 0.06$, $P = 0.25$; forest type: $F = 2.1$, $R^2 = 0.09$, $P = 0.10$; Permutational multivariate analysis of variance with 9999 permutations). Species abbreviations: B.bar = *Barbastella barbastellus*, E.ser = *Eptesicus serotinus*, M.bra = *Myotis brandtii/mystacinus*, M.dau = *Myotis daubentonii*, M.myo = *Myotis myotis*, M.nat = *Myotis nattereri*, N.lei = *Nyctalus leisleri*, N.noc = *Nyctalus noctula*, P.nat = *Pipistrellus nathusii*, P.pip = *Pipistrellus pipistrellus*, P.pyg = *Pipistrellus pygmaeus*, Pl.au = *Plecotus auritus/austriacus*

distances between tree trunks can decrease the activity of certain species (Runkel 2009). This is especially true for *Pipistrellus* species and barbastelle bats (*Barbastella barbastellus*) that are active in semi-open airspace and are dependent on thinnings (Kaňuch and Krištín 2005; Dietz et al. 2009).

Impact of wind development in plantations

Harvesting operations in forests do not differ crucially from interventions in monoculture plantations. They are usually excluded from any BACI (before-after-control-impact design, Smith 2002) examination (Mortimer 2006) and nevertheless lead to fragmentation, depreciation or loss of habitats (Farneda et al. 2015). The impact of wind turbine construction in forests is no exception at first, as habitat alteration through linear clearings for the installation and maintenance may result in habitat alteration or roost loss as well (Meschede and Heller 2000). Still, the extent of interference in plantations varies greatly depending on the tree species planted. While the loss of roosting opportunities due to felling in *Picea sitchensis* plantations is limited (Kirkpatrick et al. 2017a), several bat species are affected by possible roost loss in *Pinus nigra* and *Pinus sylvestris* plantations (Mortimer 2006, pers. observation). The main difference between the impact of harvesting and wind turbine construction is the possible attraction effects for bats at wind turbines (Cryan et al. 2014). Habitat alteration, attracting lights or accumulated insect prey at wind turbines, may also foster an increased bat activity in forest plantations due to increased foraging opportunities especially for *Nyctalus* or *Pipistrellus* species (Ober et al. 2020; Kirkpatrick et al. 2017a). Installed wind turbines could act as an ecological trap in the newly emerged foraging areas (Tscharntke et al. 2012). Yet, a comparative study with a broad dataset of 193 nacelle height monitoring surveys showed that the overall activity at nacelle height is not necessarily higher at wind turbines in forest habitats compared to open habitats (Reers et al. 2017). Our results show a high bat activity over the canopy of monocultural plantations. Moreover, Reers et al. (2017) argue that bat activity also needs to be measured at the lowest rotor outreach. Thus, longer-term monitoring of possible impact zones should be considered for wind turbines with larger rotor diameter. Currently, the evaluation of negative effects of wind energy development in forests is limited because bat fatality searches are incredibly difficult; the heterogeneous environment of forest grounds hinders finding possible carcasses or carcasses may get caught in the surrounding trees (an umbrella effect). Snapshot acoustic monitoring or the limits of carcass searches may underestimate the collision risk for bats in forested areas.

Conclusions

Mono-specific forest plantations can be considered just as valuable bat habitats as near-natural or semi-natural woodlands. This is especially true when water bodies are existent in the immediate vicinity because these habitats have an overall positive effect on bat activity. While many studies use acoustic snapshots to compare bat activity or even conduct risk assessment during planning processes, our study strongly demonstrates the importance of long-term monitoring above the canopy to evaluate bat activity. All forest types potentially harbour a diverse bat fauna with high species activity. Therefore, wind turbine development in mono-specific forest plantations is far from ecologically sound. Our results suggest that environmental impact assessments and mitigation measures are vital in all forest types before and after planning for wind energy turbines. In this context, it is mandatory to include the entire bat fauna by also focussing on species hunting above the canopy level, because migration behaviour and species composition may differ among different forest strata. We are aware that industrial wind energy production is needed to meet the growing demand for energy but, if bat activity is high, we need to include mitigation measures for all habitat types to assure sustainable development.

Appendix 1

Fig. 3 Location of the study region in Germany (**a**) and location of study plots (dots = coniferous plantations and triangles = deciduous mixed forests) (**b**). Inlet **c** shows an example of a study site together with the landscape configuration. The coordinates can be taken from Appendix Table 3
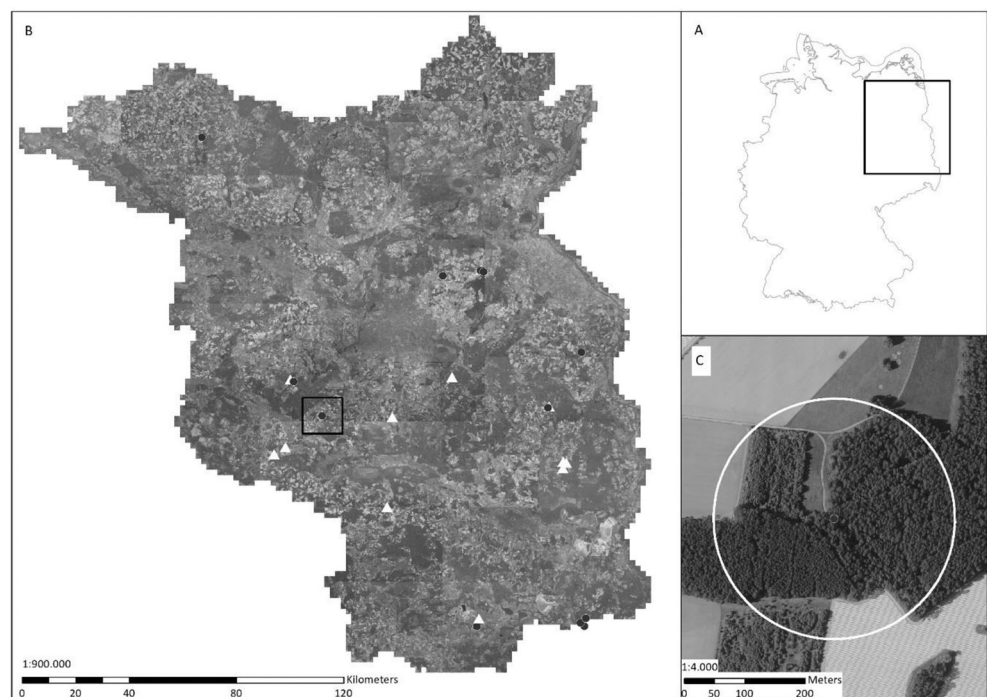
Appendix 2

Table 3 Raw data

Species

Site	Coordinates N	E	Forest type	Distance	Connect	Forest	Dist. water	Sample days	Total calls	Species richness	Bbar	Eser	Mdau	Mmyo	Mnat
S1	52.209301	12.994693	Deciduous mixed	20	526	78.8	2288.48	120	7552	7	2	63	1	0	0
S2	53.131853	12.281886	Deciduous mixed	9	371	67.6	1785.97	132	5377	9	2	164	0	5	44
S3	52.327387	12.816236	Coniferous	67	1300	85.2	1892.01	118	3414	9	0	12	5	2	1
S4	52.321702	12.833637	Deciduous mixed	438	892	100	2306.7	106	29,832	7	77	922	0	0	2
S5	52.437083	14.407141	Deciduous mixed	20	1126	12.3	557.95	94	3859	6	8	4	0	0	0
S6	52.711300	13.851796	Coniferous	905	0	100	1968.43	133	2775	7	8	0	7	0	0
S7	52.709137	13.847546	Deciduous mixed	183	402	95.7	1354.22	149	3046	10	23	16	14	2	2
S8	52.705288	13.864434	Deciduous mixed	69	132	89.8	759.3	149	4587	10	20	70	13	5	1
S9	52.069321	14.313989	Coniferous	66	1502	62.5	1449.37	171	2594	8	2	3	3	2	0
S10	52.064800	14.331467	Coniferous	325	1725	100	1726.15	92	1085	5	0	7	0	0	0
S11	52.073611	12.738917	Coniferous	235	846	100	1896.64	175	6461	8	7	41	1	0	3
S12	51.907136	13.360436	Coniferous	655	1753	99	370.63	168	2026	10	1	2	3	2	3
S13	51.512111	13.857972	Deciduous mixed	45	771	80.2	2483.12	57	899	5	0	6	0	1	0
S14	51.537869	13.868861	Coniferous	35	2443	93.6	510.9	63	3513	7	2	0	3	0	2
S15	52.09886	12.800883	Coniferous	6	0	62.1	1984.15	121	3513	9	4	40	2	0	2
S16	52.254468	14.233894	Coniferous	164	491	97.5	2022.65	136	4565	9	7	13	3	0	1
S17	52.250753	14.227750	Deciduous mixed	193	556	100	2890.41	140	6013	7	2	19	2	0	0
S18	52.210028	13.377722	Coniferous	30	990	36.8	1131	183	19,198	9	1	542	1	0	2
S19	52.689167	13.640000	Deciduous mixed	3	402	36.3	1797.74	145	18,243	8	7	3	0	2	0
S20	52.046885	14.312772	Coniferous	318	2008	99.2	336.9	164	5078	8	2	10	0	3	1
S21	52.348281	13.700361	Coniferous	290	2644	90.5	1642.63	134	2520	6	0	16	1	0	0
S22	51.516972	14.436722	Deciduous mixed	62	1043	66.9	1258.4	88	829	7	1	2	0	1	0
S23	51.528111	14.414944	Deciduous mixed	140	682	96	1098.81	147	2671	10	2	5	8	6	5
S24	51.543556	14.443361	Deciduous mixed	508	1184	93.1	525.35	153	3523	10	12	69	5	1	1

Species   Species groups

Site	Nlei	Nnoc	Pnat	Ppip	Ppyg	Mbra	Myotis sp.	Nyctaloid	Pipistrelloid	Plecotus sp.
S1	0	4309	269	2034	31	0	3	667	0	9
S2	11	1266	220	1004	13	9	57	1809	0	11
S3	1	1683	224	875	209	9	31	239	0	7
S4	11	2660	171	4404	4876	3	38	16,253	95	20
S5	0	2007	494	867	6	1	3	314	17	4
S6	7	1424	110	756	29	1	35	256	24	1

Functional group

Site	Group total	Nyctaloid group	Pipistrelloid group	Myotis group	Myotis/Plecotus group
S1	7541	5197	2334	10	19
S2	5364	3961	1237	166	177
S3	3407	2023	1308	76	83
S4	29,812	20,210	9546	56	76
S5	3778	2387	1384	7	11
S6	3017	1832	1114	71	72

Table 3 (continued)

S7	6	1306	114	986	14	4	24	365	0	6	2766	1785	919	62	68
S8	9	1667	263	1510	37	4	41	732	0	8	4559	2634	1810	115	123
S9	0	1592	241	116	284	0	30	188	0	14	2578	1882	641	55	69
S10	0	746	128	24	21	0	5	117	9	2	1083	895	182	6	8
S11	1	3589	354	398	6	1	4	1410	1	5	6447	5677	759	11	16
S12	1	1376	133	66	5	5	17	295	3	11	2014	1763	207	44	55
S13	0	157	91	595	0	0	8	16	0	5	974	522	332	120	125
S14	0	1259	311	1609	6	5	70	142	8	8	3503	1452	1934	117	125
S15	10	1722	98	506	12	1	12	809	0	16	3493	2852	616	25	41
S16	3	3248	193	398	181	4	27	326	39	11	4547	3687	811	49	60
S17		4005	227	672	450	2	28	348	114	9	6002	4474	1463	65	74
S18	5	6372	775	1981	24	2	18	8073	494	12	19,185	15,879	3274	32	44
S19	6	8350	1068	6401	50	1	20	2020	38	8	18,228	10,630	7557	41	49
S20		2898	282	213	512	4	159	613	0	27	5049	3773	1007	269	296
S21	0	1982	167	26	2	0	4	251	0	0	2520	2317	195	8	8
S22	0	415	78	46	4	6	29	159	0	7	821	636	128	57	64
S23	2	1343	138	101	9	6	52	413	362	17	2650	1941	610	99	116
S24	1	1127	186	167	1	5	26	1478	5	62	3447	3030	359	58	120

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