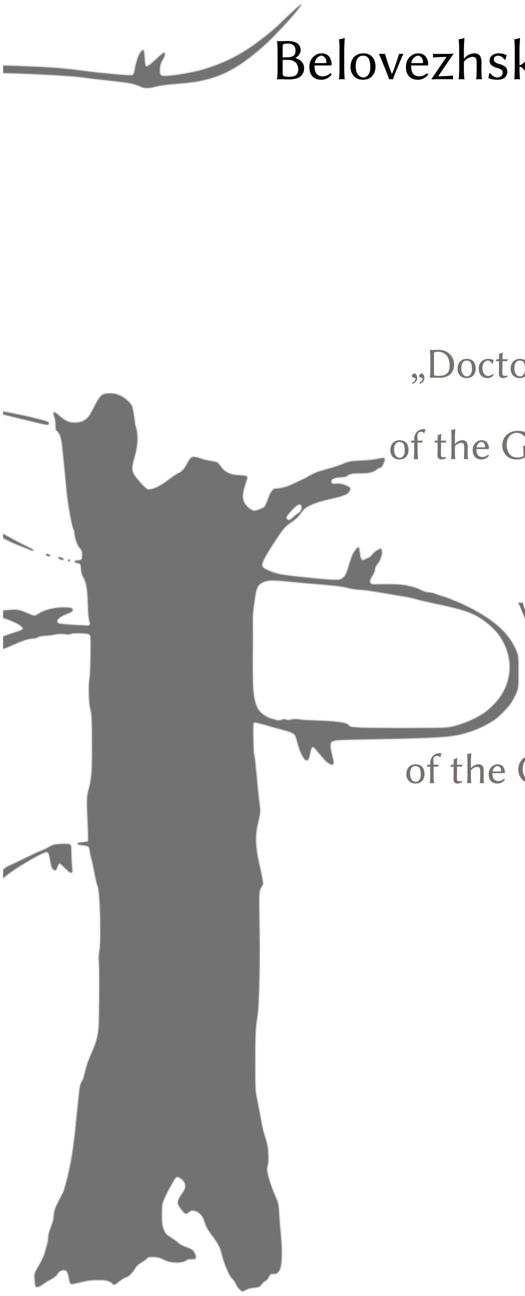
Bat activity and diversity in a temperate old-growth lowland forest –

Influence of horizontal and vertical structural heterogeneity on the bat assemblage of the Belovezhskaya Pushcha, Belarus



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SUMMARY

There are two different options to manage forests in the era of global climate warming, with partly opposing inferences. One is to reduce management or abandon it, as undisturbed forest ecosystems effectively store carbon and usually are relatively resilient against disturbance effects (Naeem 1998, Peterson et al. 1998, Bengtsson et al. 2000). Leaving forests untouched thus is an efficient climate change mitigation option. Another option is to reduce CO_2 emissions by the replacement of fossil fuels through timber-derived raw materials. Expanded use of forest products however entails a more intense forest management. These two opposing management perspectives need to be intertwined to define a compromise leading to truly climate-smart forestry (Verkerk et al. 2020). Most temperate bats rely on forested habitats for hunting or roosting. As three-dimensionally moving animals, they are especially sensitive to habitat alterations and are directly affected by forest management. Indeed, vegetation structure and species composition determine species-specific habitat use, arthropod prey occurrences and the availability of natural tree roosts. Forest bats are thus sensitive indicators of forest biodiversity.

The present thesis aimed at analysing horizontal and vertical activity patterns of temperate forest bats in a coherent temperate old-growth forest. The Belovezhskaya Pushcha (*BP*) lowland woodland complex can serve as a reference for the study of old-growth dynamics through the number of untouched forest patches present and its size stretching beyond the Polish-Belarusian border. Bat diversity in unmanaged stands was compared to managed stands in the Economic Activity Zone of the Belovezhskaya Pushcha National Park (*BPNP*). Moreover, species-specific preferences for natural tree roost attributes were extracted in a meta-analytical framework combining own data with datasets from literature.

We used automatically recording devices (*batcorder*) whose omnidirectional ultrasonic microphones are triggered by calls of echolocating or hunting bats. Bats were monitored simultaneously in natural canopy gaps and the adjacent forest interior within two forest communities in the Strictly Protected Zone of *BP*, namely Tilio-Carpinetum (broadleaved) and Querco-Pinetum (mixed-coniferous) stands. The impact of management was analysed by acoustically sampling managed Peucedano-Pinetum stands in the Economic Activity Zone of *BPNP*. A vertical *batcorder* setup in three forest heights analysed vertical stratification patterns of forest bats in canopy gaps and the adjacent forest interior.

Bat activity in canopy gaps was slightly higher for edge-space foraging bats compared to the forest interior, while bat richness was higher in gaps only in the species-poor mixed-coniferous stands. Vertical stratification was more pronounced in the forest interior than in canopy gaps, and vertical forest use clearly showed species-specific and seasonal differences. Bat diversity in *BPNP* was impacted by management with especially evenness being lower in homogenized human-altered managed coniferous forests. The activity levels of four strict forest species in the forest interior were negatively influenced by tree basal area (*B. barbastellus*, *P. pygmaeus*, *M. brandtii*) and positively influenced by the proportion of broadleaved trees (*P. pygmaeus*, *M. brandtii*, *M. nattereri*). *B. barbastellus* and *M. nattereri* were furthermore found to be tree roost specialists. While *B. barbastellus* favours loose bark of dead trees as day roosts, *M. nattereri* preferentially roosts in cavities or crevices in vital broadleaved trees.

Near-natural broadleaved forests are important habitats for temperate forest bat assemblages. The emulation of canopy gaps as a forest management strategy creates structurally heterogeneous forest stands that support a higher bat diversity through an increase in physical niches and foraging opportunities. Both the retention of snags and of large-sized vital trees offer essential roosting opportunities for forest bats and need to be integrated in close-to-nature forest management practices.

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CHAPTER 1

1 General Introduction

1.1 Old growth forests in Europe

The appearance of the European landscape has markedly been shaped by humans since the establishment of the first agricultural societies (Kaplan et al. 2009, Reick et al. 2010, Arneth et al. 2017). Forests have been heavily exploited for timber, game or as forest pastures. As a consequence, virgin or primeval (without or with very scarce human management impact) and old growth forests (possibly impacted by timber extraction in a more or less distant past) have become rare and constitute only 4% of the total European forest area (Forest Europe 2015). Remnants of primeval forests exist in the boreal and Eastern parts of Europe, but many of them are prone to fragmentation and further human exploitation (Korpel´ 1995, Wesolowski 2005, Potapov et al. 2017, Sabatini et al. 2018, 2021).

However, old growth forests provide habitat functions and resources not available in commercially used timber stands (e.g. Burrascano et al. (2008), Wirth et al. (2009), Petritan et al. (2013), Asbeck and Kozák (2021)). In the same line, these forests are known to provide essential ecosystem services such as freshwater storage and supply, carbon storage, or air purification, to mention only a few (Thompson et al. 2011, Strandberg and Kjellström 2018). Moreover, intact ecosystems are thought to be more resilient against disturbances, which is extremely important in a future climate marked by an increase in extreme weather events (Thompson et al. 2009, Gamfeldt et al. 2013).

Today´s impacts on forests differ from those since early human settlement. However, independent of the kind of impact, their importance increases since ecosystems are crossing tipping points beyond which deterioration cannot be reversed and beyond which degradation even accelerates (Reyer et al. 2015). Ironically, one way towards a reduction in the need for fossil fuel and non-renewable building materials is to increase the usage of timber-derived products (Food and Agriculture Organization of the United Nations (FAO) 2016). Therefore, a thoughtful or “climate-smart” forest management needs to be applied to keep these contradicting necessities in balance (Gutsch et al. 2018, Verkerk et al. 2020) Processes, dynamics and structures of old growth systems differ from managed systems in many ways. Mosaic structures with natural small-sized gaps occur where senescent trees die, and natural succession takes place in these newly created open habitats (Král et al. 2014, Feldmann et al. 2018). The three-dimensional forest structure in old-growth forests differs from managed forests through its multi-layered and multi-species structure (Franklin and Van Pelt 2004, Wirth et al. 2009b). Short rotation periods in managed forests impede trees from becoming mature. However, senescence in trees facilitates the development of tree-related microhabitats, which again creates habitats and resources for many species (Basile et al. 2020, Asbeck and Kozák 2021, Courbaud et al. 2021). The study of habitat use in old-growth forests is thus a prerequisite for the development of forest practices maximising biodiversity, ecosystem services and timber production.

1.2 Belovezhskaya Pushcha – a relic with a vivid history

Belovezhskaya Pushcha, or Białowieża forest (*BP*), is a forest complex of approximately 150,000 ha stretching beyond the Polish-Belarussian border. The climate is subcontinental with a mean annual air temperature of 7.3°C and an average annual precipitation of 625 mm (period 1985-2015, Boczoń et al. 2018). The forest complex belongs to the boreo-nemoral biogeographical region in the transition zone between temperate deciduous and boreal coniferous forests. The high predominance of syntaxa of the class Vaccinio-Piceetea and the high constancy of boreal species such as *Picea abies* (L.) H. Karst (Norway spruce) in broadleaved forest communities confirm the affiliation of this forest to the Eurasian taiga zone (Tsvirko and Grummo 2020).

This forested area is considered as one of the largest remaining and coherent old-growth forests in the Central European lowlands (Sabatini et al. 2018, Jaroszewicz et al. 2019). Although not untouched by humans, this woodland has experienced less disturbance than other European temperate woodlands and has never been cleared of forests since its establishment in the Atlantic period (5000-2500 AD, Mitchell and Cole (1998), Jaroszewicz (2004)). Forest composition has experienced direct or indirect human-induced changes since settlement in the forest surroundings took place in the 13th century. The forest complex, even though easily accessible and growing on fertile soils, experienced protection through its status as a hunting ground for ruling families and political rulers under differing political regimes since the 14th century (Wesolowski 2005, Bohn et al. 2017). During World War I and II, chaotic timber extraction took place in *BP* (Bohn et al. 2017). With the end of World War II and the beginning of the Soviet Regime, the forest was divided between Poland and the Belarussian Soviet Socialist Republic. On the Belarusian side, a nature reserve ("zapovednik") was established, and no systematic wide-scaled felling took place, but sanitary cuttings were partly carried out (Wesolowski 2005). Moreover, very high game stocking rates were temporarily exerting high pressure on the forest regeneration (Wesolowski 2005, Bohn et al. 2017). In the 1960s, further indirect human impacts took place in the straightening and deepening of water courses and draining of mires bordering the forest complex for hay production. It is only with the breakdown of the Soviet Union that the "Belovezhskaya Pushcha National Park" (*BPNP*) was founded in 1991 with an initial Core Zone of 5232 ha. Simultaneously, the central part of the *BPNP* was rewarded the title of a World Heritage Site. This area was extended and in 2014, a joint World Heritage Site over the Polish-Belarusian border was agreed upon.

On the Belarussian side, the Belovezhskaya Pushcha National Park (*BPNP*) covers a forested area of approximately 120,000 ha (~80% of its territory) and is divided into five Protection Categories (Nikiforov and Bambiza 2008, Bohn et al. 2017). It stretches over low undulating mounds of glacio-fluvial gravels, sands and clays at elevations of 134-202 m a.s.l. (Mitchell and Cole 1998, Nikiforov and Bambiza 2008, Jaroszewicz et al. 2019). Most forest communities belong to the Vaccinio-Piceetea class (64.4% of the *BPNP*´s area, Tsvirko and Grummo (2020)). Within this class, the Querco-Pinetum association on fresh sandy loam soils occupies 22.4% of *BPNP* (Tsvirko and Grummo 2020). The structurally complex tree layer is dominated by *Pinus sylvestris* L. (Scots Pine), *Quercus robur* L. (English oak) and *P. abies*. This association is marked by a well-developed combination of boreal and nemoral grass and shrub species and a dense moss cover (Tsvirko and Grummo 2020). A second widely distributed association within the Vaccinio-Piceetea are Peucedano-Pinetum stands. Most managed forests located in the Economic Activity Zone of the *BPNP* on fresh-sandy soils belong to this association. They are dominated by *P. sylvestris* in the tree layer, and the undergrowth is usually sparse with sometimes dense clumps of *P. abies* and *Q. robur*. The forest floor is continuously covered by mosses. Deciduous forests of the class Carpino-Fagetea represent nemoral broadleaved forests and constitute 12.2% of the *BPNP* (Tsvirko and Grummo 2020). These stands are mostly present in the central part of *BPNP* and are marked by a multi-species (5-7 species) and multi-layered tree structure (Tsvirko and Grummo 2020). *Q. robur* has a high constancy but makes up only a small percentage of the dense canopy. The most common tree species are *Carpinus betulus* L. (European hornbeam) and *Acer platanoides* L. (Norway maple) as shade and semi-shade tolerant species (Leuschner and Ellenberg 2017, Tsvirko and Grummo 2020).

The importance of the Belovezhskaya Pushcha for biodiversity lies in its size, coherence and its varying protection statuses which have saved forest patches from human exploitation. Several forest specialists have survived here in noticeable population sizes, like for example the White-backed Woodpecker *Dendrocopus leucotus* (Bechstein) or the European three-toed Woodpecker *Picoides tridactylus* (L.) among vertebrates (Wesolowski 1995, Jaroszewicz et al. 2019).

1.3 Ecology of Central European forest bats

With the beginning of the Holocene, the spreading of forests probably enabled the colonisation of Central and Northern Europe by many European bat species, while some species are assumed to have moved north with human infrastructure as substitute roosting opportunities (Dietz et al. 2009). This historical connection may explain the present importance of forested habitats for most European bat species (Meschede and Heller 2000, Dietz et al. 2009). Bats are affected by forest management on local and regional scales. On a local scale, they are affected by the vertical and horizontal forest structure and by the availability of roosting opportunities, by prey abundance and diversity, and by competition and predation, while landscape fragmentation and the connection between landscape elements and the diversity of adjacent landscape types act on a regional scale.

Forest bats use their habitat according to their ecomorphological adaptations including body size, wing size and form and echolocation call characteristics. Moreover, different foraging modes are utilised by insectivorous bats to catch prey. They range from feeding on arthropods from vegetation surfaces, the so-called gleaning, to trawling bats which catch arthropods from water surfaces and to aerial hawkers which catch airborne prey (Denzinger and Schnitzler 2013). Using these characteristics, bats can be classified into foraging guilds (Denzinger and Schnitzler (2013), Table 1.1). Safi and Kerth (2004) showed that a high habitat specialisation in temperate bats is related to a higher extinction risk. In the same line, Sagot and Chaverri (2015) showed that bat species specialised in one single dayroost type were exposed to higher extinction risks. These findings show that generally specialisation mechanisms in bats are correlated to extinction threat. Specialised forest bats like *Plecotus auritus* and *Myotis brandtii* are at high extinction risks due to their specialised hunting habitats but are quite generalist considering roosting preferences. *Nyctalus noctula* on the contrary hunts in uncluttered open habitats without a high habitat specialisation, but roost exclusively in woodpecker cavities in large deciduous trees. Thus, specialisations in habitat and roost choice have to be jointly considered to define a bat´s sensitivity to habitat transformation.

In Europe, 45 bat species are known to reproduce (BatLife Europe 2021). Of these, distribution ranges of 19 species spread over Central Europe and have been identified in Belarus (Shpak 2014). In *BP*, 17 bat species have been acoustically recorded, while 13 species have been shown to reproduce in this forest complex (Kurskov 1958, Rachwald et al. 2001, Ruprecht 2004, Demianchik and Demianchik 2006, Mazurska and Ruczynski 2008, Ruczynski and Bogdanowicz 2008, Demianchik 2013, Shpak 2014, Dombrovski et al. 2017, Dietz et al. 2018, Halat et al. 2021). *Myotis dasycneme*, *Vespertilio murin*us, *Eptesicus serotinus* and *Nyctalus lasiopterus* were not treated as forest bats in our study. Indeed, *V. murinus* and *E. serotinus* are strongly linked to human infrastructure for roosting and rely on open fields, vegetation structures in or around settlements or forest roads for hunting (Dietz et al. 2009, Halat et al. 2021, Rachwald et al. 2021). *M. dasycneme* hunts over water bodies and courses in *BP* by trawling insects from the water surface (Dombrovski et al. 2017). *N. lasiopterus* is hunting in the free air space, and both *M. dasycneme* and *N. lasiopterus* have only rarely been acoustically recorded in *BP* (Dombrovski et al. 2017). From the species considered as true forest species in *BP*, *M. alcathoe* has not yet been caught and a proof of its distribution range extending to this woodland yet has to be supplied. *M. mystacinus* has not been verified in *BP* since the separation from its sibling species *Myotis brandtii* in the 1970s (Dombrovski et al. 2017). Therefore, we restricted our study to the bat species listed in Table 1.1.

1.4 Research methods

Insectivorous bats use ultrasonic calls for orientation and/or for prey localisation. In most bats, these calls are emitted through the mouth, and echoes from clutter or prey allow them to exactly locate prey or obstacles. The emitted calls are species-specific with a habitat-dependent plasticity. For example, long and constant-frequent calls at low frequencies are typically emitted by open-space foragers. These large species possess narrow and long wings and prey on aerial insects in the free air space in fast flight. These same bats adapt their calls to more cluttered environments by integrating or augmenting the frequency-modulated part. Acoustic bat studies allow to collect large samples simultaneously at several plots and are a good choice when access to study plots is long or tedious. We chose an acoustic monitoring scheme to study bat activity and diversity in *BPNP*. We used automatic recording devices with

TABLE 1.1 Information on bat ecology of Central European forest bat species present in *BP*. Wing loading = body mass/wing surface area. FME= frequency of maximum energy, fm = frequency-modulated, qcf = quasi constant-frequent, cf = constant-frequent. *ESF* = edge-space forager, *NSF* = narrow-space forager, *OSF* = open-space forager. High wing loading mostly refers to large and fast-flying bats. In grey: species considered in the present thesis. Information from Dietz et al. (2009), Mueller et al. (2012), Denzinger and Schnitzler (2013).

Species	Summer roost	Prey	Hunting habitat	Foraging mode	Call type	Wing loading	Call length	FME	Guild
Barbastella barbastellus	Loose bark, crevices (on buildings behind panels)	Lepidoptera (Diptera, small Coleoptera...)	Forested areas, above or below canopy, along vegetation edges	Aerial hawking	fm	9.1	2.8	37	ESF
Eptesicus nilssonii	Behind wall panels, tree cavities	Small Diptera, Coleoptera, Lepidotpera	Boreal/montane forests, along vegetation edges, free air space	Aerial hawking	Fm/qcf	8.1	13	28.5	OSF
Myotis alcathoe	Crevices, loose bark	Diptera	Forests: Banks of streams, floodplain forests, crowns of deciduous trees	Aerial hawking	fm		4		NSF
Myotis brandtii	Tree hollows, crevices, loose bark, crevices on facades, in roof trusses	Lepidoptera, Arachnida, Diptera	Forests (especially moist forest types), (hedges)	Aerial hawking, gleaning	fm	7.1	4.5	46.5	ESF
Myotis daubentonii	Tree hollows, crevices in bridges or vaults	Chironomidea (Diptera, Aphidoidea, Ephemeropter, Neuroptera, Hymenoptera, Lepidoptera, Trichoptera)	Trawling above water (forests, orchards, parks along edges)	Trawling, aerial hawking	fm	7.0	5	43.5	ESF
Myotis mystacinus	Crevices in buidlings	Diptera, Lepidoptera, Hymenoptera, Neuroptera	Semi-open to open landscapes with hedgerows/groups of trees, human settlements and their surroundings	Aerial hawking (gleaning)	fm	7.1	4.5	46.5	ESF

Myotis nattereri	Tree hollows (buildings, rock crevices)	Arachnida, Opiliones, Diptera (Coleoptera, Lepidoptera)	Forests (parks, orchards, along water courses)	Gleaning (aerial hawking)	Fm	6.1	3.5	40	NSF
Nyctalus leisleri	Tree hollows	Lepidoptera, Diptera, Trichoptera	Forests, forest edges: above or under canopy, above water bodies, along forest roads	Aerial hawking	Cf (fm/qcf)	19.3	25	11.5	OSF
Nyctalus noctula	Woodpecker cavities (tree cavities	Diptera, Heteroptera, Trichoptera, Coleoptera, Lepidoptera	Water bodies/courses, forests	Aerial hawking	Cf/fm - cqf	16.1	22.5	16	OSF
Pipistrellus nathusii	Bark crevices, tree cavities	Diptera (Trichoptera, Aphidoidea, Neuroptera)	Near-natural forests, along linear vegetation/water structures	Aerial hawking	Fm/qcf	9.8	39	8.5	OSF
Pipistrellus pipistrellus	Crevices on buildings (loos bark)	Diptera	All habitats, forest preferred, hunting along edge structures	Aerial hawking	Fm/qcf	8.1	46	6	ESF
Pipistrellus pygmaeus	Buildings, tree hollows	Diptera, Hymenoptera, Neuroptera	Floodland forests, forests, along vegetation edges	Aerial hawking	Fm/qcf	8.1	54.5	6	ESF
Plecotus auritus	Cavities and vrevices on trees, buildings	Lepidoptera, Diptera, Coleoptera (Heteroptera, Orthoptera, Arachnida, Opiliones...)	Forests, forested areas around trees	Aerial hawking, gleaning	fm	7.1	30	3.5	NSF

omnidirectional ultrasonic microphones to record bat calls. These recorders are triggered by ultrasonic sounds with typical batcall characteristics. We opted for a whole-night monitoring design and used an activity index as a proxy for bat activity. We acoustically sampled bats while simultaneously collecting stand structural attributes on plot level. These structural variables were used to explain bat activity and bat species assemblages in managed and unmanaged stands of *BPNP*.

1.5 Research objectives

The overarching objectives of this thesis are to conclusively describe bat activity and diversity in a large and coherent unmanaged forest reserve. The focus lies on structural attributes of old-growth forests and on the role these attributes play for the insectivorous bat community present. On the horizontal scale, small-scale disturbances through single senescent trees dying off and opening the canopy by creating small canopy gaps were acoustically sampled (Chapter 2). I acoustically investigated the forest interior and naturally created adjacent forest gaps and collected data on gap size and vegetation structure. In Chapter 3, the focus is on the vertical height distribution of the bat species assemblage and its dynamics throughout the season. Therefore, I used a vertically hanging batcorder line to be able to record bat activity in the different forest strata. Chapter 4 finally describes bat diversity differences between managed and unmanaged forest stands of the Belovezhskaya Pushcha. I investigated bat activity in the forest interior of managed and unmanaged stands and associated forests structural variables to the activity differences observed. Moreover, the focus of this last chapter lies on the use of tree roosts by forest bat species. I applied a meta-analysis with own and literature data combined to investigate roosting niches in four dominant specialised forest species in *BP*.

In the frame of my study, I wanted to answer the following research questions:

- How do forest bats use different old growth stands in a large and coherent forest complex? (Chapter 2 and Chapter 3)
- What is the importance of small-scale canopy gaps for bats? (Chapter 2)
- How does bat activity differ depending on the bat species in different forest strata? (Chapter 3)
- Does vertical microhabitat use by insectivorous bats vary depending on the season? (Chapter 3)

- How does bat diversity differ between managed and unmanaged stands in *BPNP*? (Chapter 4)
- How do roosting preferences differ between different forest bat species? (Chapter 4)

In Chapter 5, the studies are synthesized to draw a comprehensive picture of bat activity and diversity in a large and coherent old growth forest complex. Further, this chapter addresses questions and issues that arose during my research and that should be in the focus of future research.

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CHAPTER 2

2 Shed light in the dark – how do natural canopy gaps influence temperate bat diversity and activity?

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2.1 Abstract

Globally, forests are under pressure to cope with an increasing human demand for forest products, while the need to protect forest biota increases. Old-growth forests are reference systems for the study of natural structures and processes in forest ecosystems. Results from such studies can be used to derive management practices that support and even foster biodiversity.

Most temperate bat species exhibit a high affinity towards forest habitats. We studied the foraging behaviour of temperate woodland bats in naturally created canopy gaps. The study took place in a large and coherent Central European lowland old-growth forest, the “Belovezhskaya Pushcha” in Belarus. We used passive acoustic recorders to assess the activity and diversity of bats in 12 natural canopy gaps and in adjacent forest interior control plots in two different forest habitats.

We found that the activity of open-space foragers and narrow-space foragers did not differ between forest gaps and the adjacent forest interior. The activity of edge-space foraging bats was higher in forest gaps. Bat diversity in mixed-coniferous forest stands was higher in canopy gaps. Gap size differently influenced bat guild activity. While the activity of open-space and narrow-space foragers did not vary with gap size, the activity of the edge-space foragers declined in broadleaved forests with increasing gap size. Bat diversity decreased with increasing gap size only in broadleaved forests.

Our results demonstrate the differential influence of small-scale disturbances in old-growth forests on temperate bat guilds. Furthermore, our study highlights the importance of native broadleaved forests for the temperate bat community.

Keywords: Temperate bats, old-growth forests, canopy gaps, near-natural forest management, Białowieża

2.2 Introduction

Contemporary forest management is confronted with the challenge to provide ecosystem services to society, while conserving and even fostering biodiversity (Bauhus et al. 2009, Kraus and Krumm 2013, Thom and Seidl 2016, FAO 2020). Diverse ecosystems provide resistance and resilience against disturbance impacts, and lead to a more stable provisioning of ecosystem services (Naeem 1998, Peterson et al. 1998, Bengtsson et al. 2000). In the face of climate change, these qualities of forest ecosystems become even more essential (Mueller et al. 2019). Consequently, an urgent question is how forests can be managed with minimal negative impacts on biodiversity, while maximizing timber yield.

Structurally heterogeneous forests with canopy gaps of different sizes and shapes are known to maintain biodiversity, as habitat diversity is higher (Gharehaghaji et al. 2012, Thom and Seidl 2016). In unmanaged forests, canopy openings originate from natural disturbances such as windthrows, wildfire or insect pests and from trees dying of old age (Firm et al. 2009, Muscolo et al. 2014, Thom and Seidl 2016). Old- growth forests with natural dynamics can thus serve as a reference system to assess the species assemblages, dynamics and structures in forest gaps and compare them to human-modified habitats (Schütz et al. 2016). The study of natural disturbance regimes in forests is one step towards an understanding of the consequences logging activities may entail (Bengtsson et al. 2000, Bauhus et al. 2009, Kraus and Krumm 2013). This knowledge can be implemented in a sustainable silvicultural practice emulating natural disturbances and supporting biodiversity conservation goals (Perera et al. 2004, Kern et al. 2017, Thom and Keeton 2020).

Most of the 45 European bat species are considered to require forest habitats to roost, forage or reproduce (Dietz et al. 2009, Russo et al. 2016). Depending on their echolocation call structure, wing morphology and body size, echolocating bats hunt preferentially in cluttered vegetation, along vegetation edges or in open areas (Aldridge and Rautenbach 1987, Denzinger et al. 2018). These ecomorphological adaptations can be described in the guild concept, grouping bat species that share similar adaptations and foraging strategies (Denzinger and Schnitzler 2013). As a highly mobile mammal group, the activity and occurrence of forest bats is directly (loss of tree roosts, loss or modification of hunting areas) and indirectly (decrease in prey availability, changes in microclimatic conditions) influenced by alterations of the forest structure as a result of forest management, such as the transition from a multi-layered canopy to a simpler, more homogeneous structure in even-aged production forests (e.g. Dodd et al. 2012, Jung et al. 2012, Burgar et al. 2015, Langridge et al. 2019). However, most studies on bats and forest gaps deal with harvest-created cut-blocks and do not account for differences between gaps of natural and man-made origin (Grindal and Brigham 1999, Patriquin and Barclay 2003, Schumann et al. 2003, Schliemann and Bockheim 2011). This does not reflect the situation of natural treefalls which create isolated open canopy islands in an otherwise closed forest matrix (Fukui et al. 2011, Tena et al. 2020). This difference between artificial and natural gaps can be important because skidder trails and roads are edge habitats used by bats in other ways than the closed forest vegetation (Menzel et al. 2002, Hein et al. 2009, Kalcounis-Rueppell et al. 2013, Rocha et al. 2017). Furthermore, the availability of standing and lying deadwood in natural gaps where stumps and snags are not removed induces a different arthropod community (Lachat et al. 2016, Seibold et al. 2016, Thorn et al. 2017, 2018). Arthropods developing or living in deadwood structures can be used as prey by some bat species, and lead to an increase in bat species diversity (Bouvet et al. 2016, Tillon et al. 2016). Moreover, old-growth forests host a different forest bat community compared to managed forest stands due to the presence of old-growth microhabitats such as cavities, cracks, and loose bark, offering more roosting opportunities (Vuidot et al. 2011, Regnery et al. 2013, Kortmann et al. 2018, Paillet et al. 2018).

To our knowledge, the study of Fukui et al. (2011) in Hokkaido, Japan, is the only one that analysed the influence of naturally created gaps in an old-growth forest on a temperate bat community. In Europe, undisturbed late-successional forests are highly fragmented and represent only 4% of the total forested area (Europe Forest 2015, Potapov et al. 2017). Therefore, the study of European forest bats in pristine habitats is possible in only a few forest complexes.

The goal of our study was to reveal the influence of single- or group-tree fallings in European old-growth forests on the activity and diversity of bats of the open-space forager (*OSF*), the edge-space forager (*ESF*) and the narrow-space forager (*NSF*) guilds. The findings of this study allow us to infer management tools appropriate to increase bat diversity in managed forests.

We chose the *Belovezhskaya Pushcha National Park* (*BPNP*) in Belarus as an old-growth reference forest (see 3.1). We hypothesized that

i) Bat guild activities differ between canopy gap and closed canopy plots
    a. *OSF*s are active mainly in canopy gaps due to their adaptation to open space
    b. *ESF*s are more active in canopy gaps compared to the closed canopy due to the presence of edge structures
    c. *NSF*s avoid canopy gaps and have higher activity levels under closed canopy

ii) Bat diversity in gaps is higher than under closed canopy

iii) Bat guild activity changes with gap size
    a. *OSF* activity increases with increasing gap size due to their adaptation to open space
    b. *ESF* activity reaches an asymptotic plateau with increasing gap size since the gap edge length increases asymptotically with gap area
    c. *NSF* activity decreases with increasing gap size due to their adaptation to cluttered vegetation

2.3 Methods

2.3.1 Site description

Our study took place in a woodland complex of approximately 150,000 ha stretching over the border of Belarus and Poland, the *Belovezhskaya Pushcha/Puszcza Białowieska* (*BP*). This forested area is one of the largest remaining and coherent old-growth forests in the Central European lowlands (Sabatini et al. 2018, Jaroszewicz et al. 2019).

The forest complex belongs to the boreo-nemoral biogeographical region in the transition zone between temperate deciduous forests and boreal coniferous forests. It is marked by a lack of beech (*Fagus sylvatica*) which dominates broadleaved forests in large parts of Central and Western Europe, and a high share of English oak (*Quercus robur*), European hornbeam (*Carpinus betulus*) and small-leaved lime (*Tilia cordata*). *Pinus sylvestris* is by far the prevailing tree species in about 60% of the forest stands on the Belarussian side of *BPNP*. *Quercus robur* is dominant in 3.5% of all forest habitats in *BPNP* – it is the most abundant broadleaved tree species besides *Alnus glutinosa* in the damp sites. *Picea abies*, at the southwestern border of its natural occurrence, is present in almost all stands with a low abundance (Falinski 1986, Nikiforov and Bambiza 2008).

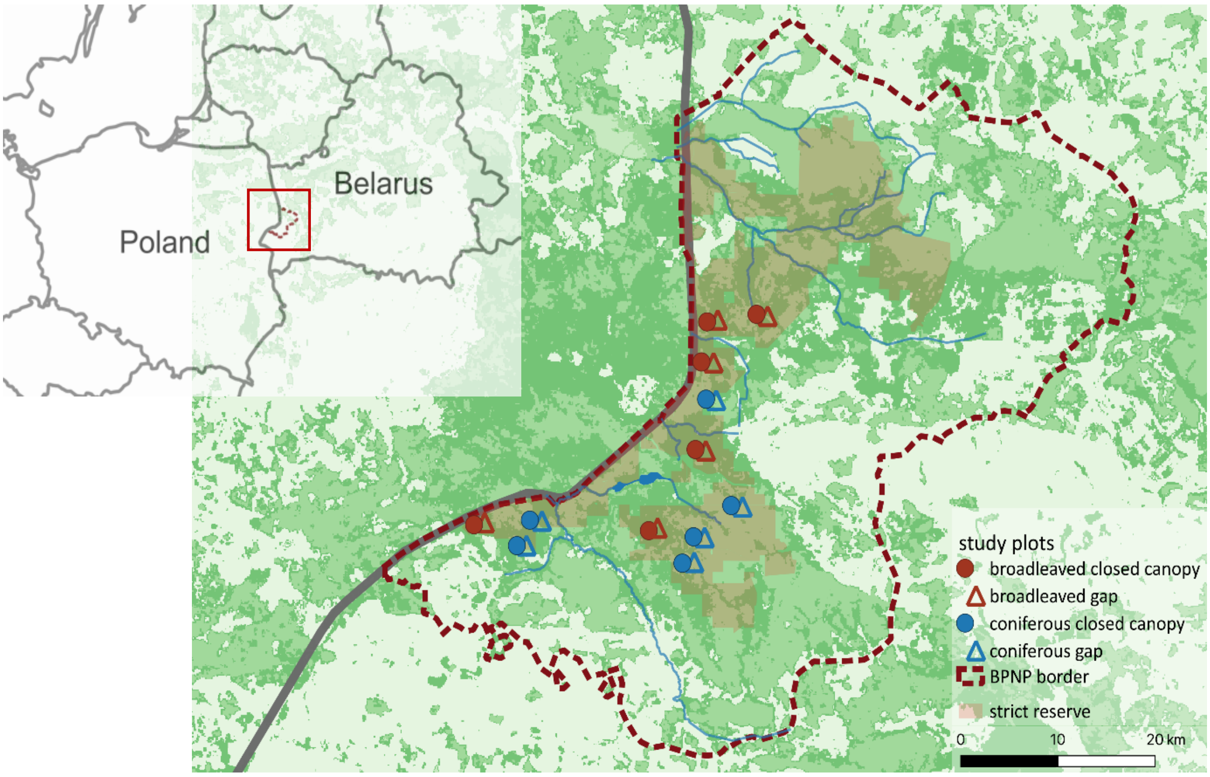

Figure 2.1 Location of the *BPNP*, and distribution of the sample plots within the strict reserve of *BPNP*. Grey line: country border. The 12 study plots with the corresponding gap and closed canopy subplots are shown for the two habitat types broadleaved and mixed-coniferous studied. The dashed red line shows the *BPNP* border, the shaded area corresponds to the strict reserve.

The dominating forest community on the Belarussian side is the mixed-coniferous Pino-Quercetum, a meso-oligotrophic plant community intermediate between the deciduous oak-hornbeam and the true coniferous forest stands. Mesotrophic habitats are occupied by the broadleaved forests of the Tilio-Carpinetum with *Quercus robur* and *Carpinus betulus* as the main tree species (Falinski 1986). Both forest types were chosen for comparison. The forest is situated at a mean altitude of 134–202 m.a.s.l. (Jaroszewicz et al. 2019). The climate is subcontinental with a mean annual air temperature of 7.3 °C and an average annual precipitation of 625 mm (period 1985–2015, Boczoń et al. 2018).

Our survey plots were located within the 57,000 ha of the strict reserve in the Belarussian National Park "*Belovezhskaya Pushcha*" and were not subject to any management practices (Buryi 2012). Six study plots were chosen in broadleaved forests (dominating tree species *Quercus robur*, except for one plot with dominating *Quercus petraea*) and six study plots in mixed-coniferous stands (dominating tree species *Pinus sylvestris*, Figure 2.1). All plots were located more than 2.7 km from each other. To minimize edge effects and the influence of anthropogenic infrastructure on bat activity, all study plots had a minimum distance of 1 km from the nearest settlement and 300 m from all forest paths. Since the presence of water is known to influence bat activity (Grindal 1998, Vindigni et al. 2009, Salvarina et al. 2018), all plots were located at least 1 km from water bodies or courses (except plot K6 at 500 m from a small watercourse).

Each plot included two subplots of differing canopy structures, namely one gap subplot and one subplot under closed canopy. These paired subplots were located between 70 and 330 m from each other (mean 145.5 +/- 47.7 m) and situated within a similar forest stand with respect to soil type, tree species composition and forest structure.

2.3.2 Bat sampling

Bats were monitored using a standardized acoustic stationary system (batcorder 3.0, EcoObs GmbH, Nuremberg, Germany) from June to September 2014. During each of six recording campaigns, one broadleaved plot (with one gap and one canopy subplot) and one mixed-coniferous plot (with one gap and one canopy subplot) were monitored simultaneously. Due to logistic challenges and technical issues, the survey campaigns differed in length. Each plot was surveyed during two campaigns between June and September, which resulted in a total of eight to 17 recording nights per subplot and a total of 300 recording nights (Table 2.1).

TABLE 2.1 Description of the acoustic survey campaigns. In each campaign, one broadleaved plot and one mixed-coniferous plot with two subplots each were simultaneously monitored. All plots were monitored repeatedly during 2 campaigns

Survey campaign	Time period	Recording nights
i	03.06.-10.06.	28
ii	11.06.-25.06.	58
iii	26.06-17.07.	69
iv	25.07.-06.08.	46
v	07.08.-20.08.	48
vi	21.08.-10.09.	51
Sum		300

Batcorders were mounted on a pole at a height of 2.0-2.5 m and ultrasonic microphones were oriented away from vegetation to record a maximum of bat passes. Ultrasonic microphones were slightly angled upwards (following Weller and Zabel (2002) and Britzke et al. (2013) for optimal bat detector positions). All batcorders were simultaneously purchased and calibrated by the manufacturer prior to the study. We used the recording mode "Auto-Timer" and the following recording settings: quality=20, threshold=-27dB, posttrigger = 400 ms, critical frequency = 16 kHz. Recordings automatically ran from half an hour after sunset until half an hour before sunrise.

In closed canopy subplots, batcorders were installed in the plot centre. In gaps, they were placed in vicinity of the assumed gap centre. Mean night-time temperature during all recording nights was above 8°C (weather station in Kamianiuki, 52.572938°N, 23.803277°E). Only two night-time precipitation events out of 18 were higher than 10 mm per night. Exploratory analyses did not show any influence of precipitation on bat activity, and all nights were included in the analyses.

2.3.3 Gap structural data

All treefall-gaps had been created by single or groups of fallen trees and varied in size and time of creation. All of them were isolated open patches in a closed forest matrix and were not connected to other open structures such as forest paths. Canopy openings *sensu* Runkle (1982) were measured taking bearings from the gap centre to the vertical ground projection of a tree crown beginning in eight directions. Vegetation density of all plants higher than 1.5 m was estimated as average percent coverage in four quadrants within 3 m around the gap centre.

2.3.4 Acoustic data analysis

Bat species were identified using their echolocation calls. All sequences were processed using the software batIdent (Runkel and Marckmann 2013), which automatically assigns species and probabilities to sequences. All sequences were manually verified using the software bcAnalyze2 (Runkel 2014), since combining automatic classification and manual post-validation is an effective method to identify bat echolocation calls (López-Baucells et al. 2019). Feeding buzzes and social calls were marked as such. The parameters used for manual verification can be found in Table A 2.1.

If possible, bat calls were assigned to a species, otherwise sonotypes were used (*Pipistrellus* sonotype for unidentified *P. Pipistrellus*, *P. pygmaeus* and *P. nathusii* calls, *Myotis* sonotype for unidentified *M. alcathoe*, *M. brandtii*, and *M. daubentonii* calls, nyctaloid sonotype for *E. nilssonii*, *E. serotinus*, *N. noctula*, *N. leisleri* and *V. murinus*). *Plecotus* spec. designates most likely *P. auritus* since *P. austriacus* has only episodically been recorded in *BP* (Sachanowicz et al. 2006). Most analyses were performed on guild level. Bat species were classified in the three guilds open-space foragers (*OSF*), edge-space foragers (*ESF*) and narrow-space foragers (*NSF*) following the classification of Mueller et al. (2012) (Table 2.2).

For species with distinct single calls such as *N. noctula*, the batcorder records each call in a single file if the posttrigger time of 400 ms is being exceeded. This may result in many recording sequences for one single bat pass. On the other hand, species hunting in front of the ultrasonic microphone produce many recordings. To even these effects out, bat activity can be expressed in activity indices instead of the number of bat passes per night (Miller 2001, Britzke et al. 2013). We used the number of 1-minute intervals per night as an activity index (see Mueller et al. (2012) for a similar methodology). The minute-count started with the first recording of this species. For one minute, no further calls of this species were counted. After the 1-minute period, the counting process for the respective species iterated. This way, the sequences recorded were transformed into minute-intervals. If more than one individual was clearly identifiable on one recording, it was counted as more than one minute-interval.

Forest type, canopy structure and mean night-time temperature were included as covariates into the models built to maximize a correct interpretation of the results. Each bat species

TABLE 2.2 Activity in total number of minute-intervals per night for the species and sonotypes identified from echolocation calls recorded.

Guild	Species	Closed canopy	Canopy gap	Sum	Proportion (%)
Edge-space foragers	Barbastella barbastellus	171	358	529	20.6
	Myotis brandtii	3	4	7	0.3
	Myotis daubentonii	2	0	2	0.1
	Myotis spp.	373	409	782	30.4
	Pipistrellus spec.	124	127	251	9.8
	Pipistrellus pipistrellus	19	29	48	1.9
	Pipistrellus pygmaeus	128	351	479	18.6
Narrow-space foragers	Myotis alcathoe	0	3	3	0.1
	Myotis nattereri	70	74	144	5.6
	Plecotus spec.	5	7	12	0.5
Open-space foragers	Eptesicus nilssonii	3	15	18	0.7
	Nyctalus leisleri	0	3	3	0.1
	Nyctalus noctula	6	18	24	0.9
	Nyctaloid	48	179	227	8.8
	Pipistrellus nathusii	21	16	37	1.4
	Vespertilio murinus	1	1	2	0.1
unidentified	Spec.	2	2	4	0.2
Sum		976	1596	2572	

Note: Activity is given separately for the canopy structures “canopy gap” and “closed canopy”. Proportion shows the proportional contribution in activity of the species or sonotype to the total activity recorded.

possesses a different echolocation call intensity. This again entails differing inter-species detection probabilities in the same habitat and under the same weather conditions (Britzke et al. 2013). Therefore, we compared bat guild and bat species activity patterns only within the same guild or species. Bat activity varies during the course of the night, between nights and throughout the season (Hayes 1997, Skalak et al. 2012, Vasko et al. 2020). We accounted for these patterns by temporal replicates and continuous monitoring throughout the night and season.

2.3.5 Statistical analyses

All statistical analyses were carried out using R version 4.0.0 (R Development Core Team 2019). Data were processed using the general guidelines in Zuur et al. (2010) and Zuur and Ieno (2016). Since both bat species and bat sonotypes were included in our analyses on bat diversity, the number of observed species/sonotypes per night and plot was denoted bat richness (confer Carr et al. (2020)).

Generalized linear mixed effects models were used to analyse

i) the effects of canopy structure (canopy gaps compared to closed canopy) on bat guild activity and bat richness

ii) the effects of gap size on bat guild activity and bat richness

using the package glmmTMB (Brooks et al. 2017) and following the guide of Benjamin M. Bolker et al. (2008).

We used plot as a random effect to account for the repeated night-time recordings on each plot, and for the potential similarity in species activity of the two adjacent subplots. The number of recording hours per night increased during the field season with increasing night length. Since these night-time recording hours strongly correlated with the survey campaign (i-vi, Table 2.1), we accounted for the increasing night length by integrating the survey campaign as a random factor into the model. The forest type was used as a predictor interacting with canopy structure and gap size respectively and mean night-time temperature was included as a control variable into the models. Regeneration density in gaps was positively correlated to gap size and excluded from models including gap size. The final model is presented using restricted maximum likelihood (REML).

The base equations for the models were

i) Bat activity/bat richness ~ canopy structure*forest type+ temperature + (1|plot) + (1|campaign)

ii) Bat activity/bat richness ~ gap size*forest type+ temperature + (1|plot) + (1|campaign)

For each response variable, we calculated a model set with and without the interaction term. Poisson, negative binomial and negative binomial zero-inflated distributions with a log-link were used for model calculation. Akaike´s Information Criterion (AIC) was used to choose the best fitting model from the set of models (Burnham and Anderson 2004). The model with the fewest parameters was selected when models were considered equivalent (ΔAIC<2). Model validation was done using the DHARMa package (Hartig 2020). Predictions used for plotting were calculated using the estimated marginal means from the emmip-function within the emmeans package (Lenth 2020).

2.4 Results

2.4.1 Bat richness and frequency of guilds

We collected 4165 recordings and identified 13 bat species and 3 sonotypes (*Myotis, nyctaloid, Pipistrellus*) assigned to the three bat guilds *ESF*, *OSF* and *NSF*. These sequences were transformed into 2572 minute- intervals. Seventy-seven percent of the total minute-intervals were attributed to *ESF*s with unspecified *Myotis* calls and calls from the Barbastelle bat *B. barbastellus* making up the biggest share (*Myotis* sonotype: 38%, *B. barbastellus*: 25%, *P. pygmaeus*: 23%), 18% were attributed to *OSF*s with unspecified *nyctaloid* calls as the main fraction and 5% to *NSF*s with the most common calls from the Natterer´s bat *Myotis nattereri* (Table 2.2). Four records could not be attributed to any species group. Since feeding buzzes (2.4%) and social calls (3.2%) only made up a very small part of the total recordings, we did not differentiate between different call types. During 103 of 300 recording nights, no bat calls were recorded.

2.4.2 Bat guild activity and bat richness in natural forest gaps

*OSF*s were recorded during only 24% of recording nights. The activity of *OSF* bats was higher in gaps than under closed canopy, but contrary to our hypotheses, this difference was not significant. *OSF*s did not show any forest type preference, but their activity was strongly and positively influenced by mean night-time temperature (Table 2.3 and Figure 2.2).

*ESF*s were recorded during 57% of all recording nights. In line with our hypotheses, bats adapted to edge habitats predominantly hunted in canopy gaps independent of the habitat type considered. They strongly and significantly preferred broadleaved over mixed-coniferous forests. Like *OSF*s, *ESF*s were more active with higher mean night-time temperatures (Table 2.3

TABLE 2.3 Effect of forest type, canopy structure and mean night-time temperature on bat guild activity, bat richness and the activity of the main *ESF* species.

		Intercept	habitat [coniferous]	canopy [gap]	temperature	habitat [coniferous] : canopy [gap]	ZI model
OSF activity	IRR (± SE)	0.00 (± 1.27)	0.57 (± 0.8)	3.55 (± 0.8)	1.45 (± 0.06)		0.38 (± 0.45)
	Stat.	-5.82	-0.67	1.52	6.57		-2.17
	p	<0.001	0.503	0.129	<0.001		0.030
ESF activity	IRR (± SE)	0.95 (± 0.8)	0.05 (± 0.4)	2.22 (± 0.4)	1.09 (± 0.03)		0.11 (± 0.34)
	Stat.	-0.06	-7.42	2.02	2.57		-6.51
	p	0.95	<0.001	0.044	0.010		<0.001
NSF activity	IRR (± SE)	0.27 (± 0.69)	0.12 (± 0.5)	1.27 (± 0.5)	1.05 (± 0.04)		
	Stat.	-1.89	-4.17	0.50	1.33		
	p	0.059	<0.001	0.617	0.185		
bat richness	IRR (± SE)	1.01 (± 0.45)	0.17 (± 0.27)	1.21 (± 0.21)	1.05 (± 0.02)	2.21 (± 0.35)	
	Stat.	0.02	-6.52	0.93	1.97	2.25	
	p	0.987	<0.001	0.350	0.049	0.025	
B. barbastellus activity	IRR (± SE)	0.06 (± 0.97)	0.10 (± 0.8)	2.63 (± 0.7)	1.16 (± 0.04)		0.11 (± 0.57)
	Stat.	-2.88	-3.12	1.30	3.54		-3.88
	p	0.004	0.002	0.192	<0.001		<0.001

Note: Results from generalized linear mixed models using negative binomial distributions for *OSF*, *ESF*, *NSF* and species activities with a zero-inflation part for *OSF*, *ESF* and the species activities and a Poisson distribution for bat richness. Model results are shown with restricted maximum likelihood. Effect of canopy gap tested against closed canopy, effect of mixed-coniferous habitat tested against broadleaved. Results are given on the response scale. N= 300 observations. random effects: 24 plots, 6 survey campaigns. IRR= Incidence Rate Ratios, SE=standard error. *OSF*: open-space foragers, *ESF*: edge-space foragers, *NSF*: narrow-space foragers, ZI=zero-inflated intercept.

and Figure 2.2). We analysed species-dependent activity differences between canopy gaps and closed canopy plots for the most commonly recorded species *B. barbastellus*, *Myotis* spec. and *P. pygmaeus* constituting the *ESF* guild. Barbastelle bats were more active in gaps compared to the forest interior, but this effect was not statistically significant (Table 2.3).

*NSF*s were recorded during 26% of all recording nights. Contrary to our hypotheses, the activity patterns of *NSF*s did not reveal a preference towards closed canopy plots. *NSF*s clearly avoided coniferous forests and predominantly hunted in broadleaved habitats. *NSF*s did not show any temperature-sensitivity (Table 2.3 and Figure 2.2).

Bat richness was higher in canopy gaps compared to closed canopy plots only in coniferous forest plots. Contrary to our hypotheses, bat richness in broadleaved stands did not differ between the forest interior and canopy gaps (Figure 2.2, see contrasts Table A 2.2). Bat richness was generally higher in broadleaved stands compared to mixed-coniferous plots. High night-time temperatures had a slight positive influence on bat richness (Figure 2.2, Table 2.3).

		Intercept	habitat [coniferous]	canopy [gap]	temperature	habitat [coniferous] : canopy [gap]	ZI model
P. pygmaeus activity	IRR (± SE)	0.32 (± 1.22)	0.03 (± 0.8)	1.74 (± 0.7)	1.03 (± 0.05)		0.23 (± 0.41)
	Stat.	-0.95	-4.36	0.75	0.57		-3.52
	p	0.343	<0.001	0.456	0.571		<0.001
Myotis spec. activity	IRR (± SE)	0.87 (± 1.02)	0.05 (± 0.5)	1.57 (± 0.5)	1.04 (± 0.05)		0.07 (± 0.57)
	Stat.	-0.14	-6.16	0.93	0.88		-4.60
	p	0.889	<0.001	0.354	0.379		<0.001

Note: Results from generalized linear mixed models using negative binomial distributions for *OSF*, *ESF*, *NSF* and species activities with a zero-inflation part for *OSF*, *ESF* and the species activities and a Poisson distribution for bat richness. Model results are shown with restricted maximum likelihood. Effect of canopy gap tested against closed canopy, effect of mixed-coniferous habitat tested against broadleaved. Results are given on the response scale. N= 300 observations. random effects: 24 plots, 6 survey campaigns. IRR= Incidence Rate Ratios, SE=standard error. *OSF*: open-space foragers, *ESF*: edge-space foragers, *NSF*: narrow-space foragers, ZI=zero-inflated .

2.4.3 Influence of gap size on bat guild activity and bat richness

Gap sizes ranged from 56 to 265 m^2. Median gap size in broadleaved plots was 87 m^2, whereas median gap size in mixed-coniferous plots was 134 m^2.

Gap size did not significantly influence the activity of *OSF*s. The activity of *ESF*s was negatively influenced by gap size only in broadleaved forest stands (Table 2.4 and Figure 2.3, see contrasts in Table A 2.3). The most commonly recorded species within the *ESF* guild were differently influenced by gap size. The activity of *B. barbastellus* and *Myotis spec.* decreased with increasing gap size (only significant for *Myotis spec.* in broadleaved forests), whereas *P. pygmaeus* tended to have higher activity levels in larger gaps (results not statistically significant). *NSF*s were not significantly influenced by gap size in their activity (Table 2.4, Figure 2.3).

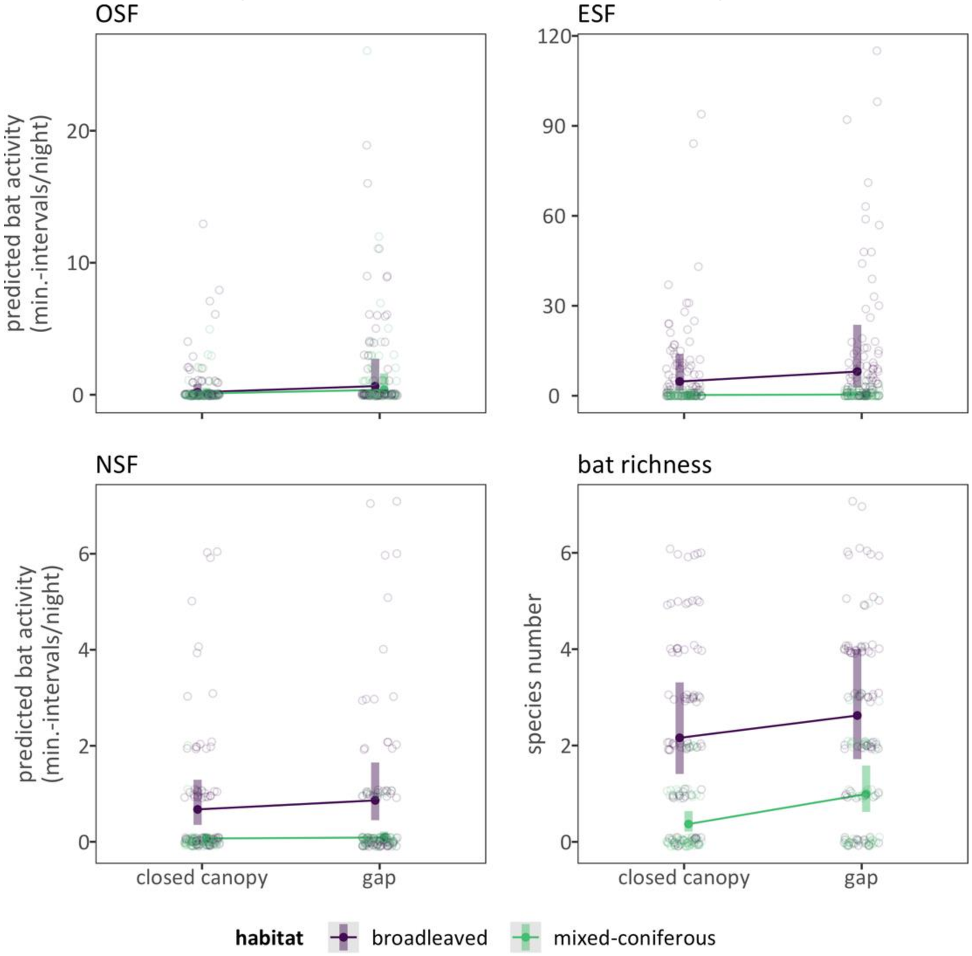

Figure 2.2 Predicted bat activity/bat richness in canopy gaps and under closed canopy in minute-intervals per night for both habitats broadleaved and mixed-coniferous. Confidence intervals from negative binomial (*OSF*, *ESF* and *NSF* activity) and Poisson (bat richness) generalized linear mixed models at population-level. The zero-inflation part is not considered for the prediction calculation. Note the differences in axis scales among guilds. *OSF*: open-space foragers, *ESF*: edge-space foragers, *NSF*: narrow-space foragers.

Bat richness in canopy gaps was differently influenced by gap size depending on the habitat type. In broadleaved plots, bat richness decreased with increasing gap size, whereas in mixed-coniferous habitats, bat richness showed a slight increase with increasing gap area (Figure 2.3, Table 2.4, contrasts in Table A 2.4). This pattern was caused by a decrease in the number of species or species groups belonging to the *ESF*s, which induces the exact same pattern as considering the whole bat richness (Table 2.4, contrasts in Table A 2.5).

2.5 Discussion

Acoustic sampling methods possess pitfalls that have to be addressed (Gannon et al. 2003, Britzke et al. 2013). Bats are assumed to have an acoustic detection probability below one, and actual occurrences are thus generally underestimated (Gorresen et al. 2008). Detection probabilities vary with changing vegetation clutter and weather conditions and between species (Yates and Muzika 2006, Gorresen et al. 2008, Britzke et al. 2013, Bender et al. 2015).

We tried to compensate for detection differences due to habitat heterogeneity by sampling the same habitat type at multiple plots. Bat detection probability between canopy gaps and closed canopy plots may differ due to varying degrees of openness. However, batcorders under closed canopy were placed with distance from vegetation clutter to minimize attenuation effects on bat calls. In the studies of Yates and Muzika (2006) and Bender et al. (2015), vegetation density influenced bat occupancy more than detection probability of bats, and Obrist et al. (2011) only found minimal attenuation effects of foliage on bat calls. Therefore, we are confident that the trends we identified between canopy gaps and closed canopy plots are not substantially influenced by differences in detection probability.

Our data include a high number of nights where no bat calls were recorded (34%). We estimate that this high proportion is due to our study design. We wanted to quantify the importance of inner gaps and gap edge structures compared to the forest interior, and we therefore intentionally did not sample at heavily frequented foraging areas such as water bodies and courses, or linear forest edges used as commuting structures. Moreover, the number of bat passes recorded has to be set in relation to the size of the forest complex studied. We recorded bat passes of the same magnitude than other bat studies using ultrasonic recording techniques in temperate or boreal old-growth forest stands (Grindal 1998, Humes et al. 1999, Kennedy et al. 2014).

Seasonal or within-night temporal activity adaptions are important behavioural responses to resource allocation, to predation risk, to differing abiotic conditions or as a competition

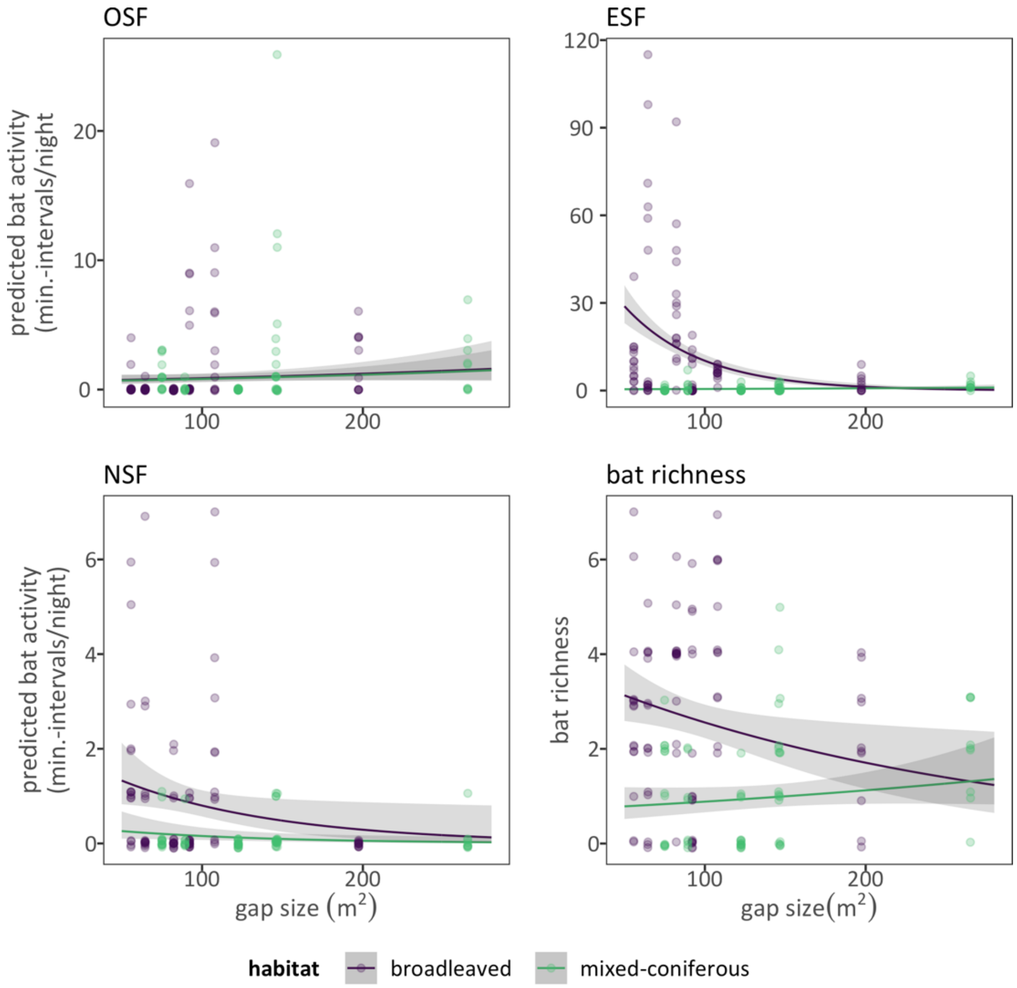

Figure 2.3 Predicted bat activity/bat richness with increasing gap size for the two habitat types broadleaved and mixed-coniferous. Confidence intervals from negative binomial (*OSF*, *ESF* and *NSF* activity) and Poisson (bat richness) generalized linear mixed models at population-level. The zero-inflation part is not considered for the predictions. Note the differences in axis scales among guilds. *OSF*: open-space foragers, *ESF*: edge-space foragers, *NSF*: narrow-space foragers.

avoidance strategy (Hayes 1997, Ciechanowski et al. 2007, 2009, Mueller et al. 2013, Roeleke et al. 2018, Rocha et al. 2020, Vasko et al. 2020). We did not consider time activity shifts in our study but focused on spatial activity and diversity differences. We think that differences in prey abundance both during one night and during the season along with temperature differences between canopy gaps and closed canopy plots are the major drivers of temporal activity shifts in our study. However, since we considered small gap openings, these differences are expected to occur on a rather small scale.

TABLE 2.4 Effect of habitat, gap size and mean night-time temperature on bat guild activity, bat richness, *ESF* richness and the activity of the most recorded species in the *ESF* guild.

		Intercept	gap area	hab[con]	temp	gap area: hab[con]	ZI-Model
OSF activity	IRR (±SE)	0.00 (±0.00)	1.01 (±0.01)	0.56 (±0.81)	1.40 (±0.14)		
	Stat.	-3.27	0.99	-0.40	3.41		
	p	0.001	0.324	0.688	0.001		
ESF activity	IRR (±SE)	5.81 (±0.83)	0.98 (±0.00)	0.00 (±0.80)	1.18 (±0.04)	1.03 (±0.01)	0.07 (±0.60)
	Stat.	2.12	-5.45	-7.26	3.69	4.83	-4.51
	p	0.034	<0.001	<0.001	<0.001	<0.001	<0.001
NSF activity	IRR (±SE)	1.92 (±1.25)	0.99 (±0.01)	0.30 (±0.79)	0.98 (±0.07)		
	Stat.	0.52	-1.14	-1.53	-0.35		
	p	0.603	0.254	0.126	0.726		
bat richness	IRR (±SE)	0.77 (±0.57)	1.00 (±0.00)	0.17 (±0.49)	1.11 (±0.03)	1.01 (±0.00)	
	Stat.	-0.45	-1.52	-3.6	3.15	1.82	
	p	0.651	0.128	<0.001	0.002	0.069	
ESF richness	IRR (±SE)	1.57 (±0.64)	0.99 (±0.00)	0.04 (±0.63)	1.07 (±0.04)	1.02 (±0.00)	
	Stat.	0.70	-2.63	-5.13	1.71	3.29	
	p	0.484	0.008	<0.001	0.088	0.001	
B. barbastellus	IRR (±SE)	0.33 (±1.50)	0.99 (±0.01)	0.21 (±1.00)	1.18 (±0.06)		
	Stat.	-0.74	-1.31	-1.55	2.68		
	p	0.456	0.191	0.121	0.007		
P. pygmaeus	IRR (±SE)	0.34 (±2.14)	1.01 (±0.01)	0.02 (±1.67)	1.00 (±0.08)		
	Stat.	-0.50	0.48	-2.28	-0.03		
	p	0.616	0.634	0.023	0.973		
Myotis spp.	IRR (±SE)	2.91 (±1.43)	0.98 (±0.01)	0.00 (±1.63)	1.1 (±0.070)	1.02 (±0.01)	
	Stat.	0.75	-1.77	-3.34	1.30	1.87	
	p	0.455	0.077	0.001	0.194	0.062	

Note: Results from generalized linear mixed models using negative binomial distributions for *OSF*, *ESF*, *NSF* and species activities, with a zero-inflation part for *OSF* and *ESF* activity, and a Poisson distribution for bat richness and *ESF* richness. Model results are shown with restricted maximum likelihood. Effect of mixed-coniferous habitat tested against broadleaved. Results are given on the response scale. N= 148 observations. Random effects: 12 plots, 6 survey campaigns. IRR=Incidence Rate Ratios, SE= standard error. *OSF*: open-space foragers, *ESF*: edge-space foragers, *NSF*: narrow-space foragers. ZI = zero-inflated intercept, hab = habitat, con = mixed-coniferous, temp = temperature. Significant effects in bold

2.5.1 *OSF* activity in canopy gaps

OSF bats in our study were equally active in canopy gaps and under closed canopy independent of the forest type and independent of the gap size considered.

*OSF*s are adapted to track ephemeral and unpredictable congregations of flying insects and to fly over large distances to reach attractive hunting grounds (Shiel et al. 1999, Waters et al. 1999, Safi et al. 2007, Mueller et al. 2012, Charbonnier et al. 2014). Many studies revealed higher activity levels or more occurrences of *OSF* species in gaps compared to the forest interior (Crome and Richards 1988, Menzel et al. 2002, Patriquin and Barclay 2003, Owen et al. 2004, Froidevaux et al. 2014). We recorded a generally low level of *OSF* activity, even in forest gaps. We attribute this to the fact that the vast plains surrounding *BPNP* were more attractive foraging areas than the small canopy gaps we studied. *OSF* calls recorded under closed canopy stem from bats foraging above the forest canopy whose high-intensity calls penetrate through the forest canopy. The open space above a forest potentially represents an important foraging habitat for *OSF*s, as shown by Kalcounis et al. (1999) and Mueller et al. (2013). Gaps can thus be interpreted as an extension of the outer canopy surface.

*OSF*s in our study were recorded equally often in broadleaved and mixed-coniferous habitats. We assume that the ephemeral and unpredictable insect abundances in open spaces are less dependent on the type of vegetation beneath or surrounding them compared to abundances of foliage-dwelling arthropods. Similar to our findings, Patriquin and Barclay (2003) did not detect any presence and activity differences between different forest types for the *OSF* *Lasionycteris noctivagans* in boreal mixed-wood forests in Alberta, Canada.

In accordance with our findings, we support the hypothesis from Fukui et al. (2011) who showed that *OSF* bats did not respond to gap size but were active in the open space above the canopy, independent of the forest canopy structure below. However, the small bandwidth of the gap sizes we considered restricts the interpretation of our results. Other studies in artificially created canopy openings found opposite trends (e. g. Menzel et al. (2002), Ford et al. (2005)).

2.5.2 *ESF* activity in canopy gaps

*ESF*s preferred hunting in forest gaps and their activity decreased in larger gaps. We recorded higher *ESF* activity levels in broadleaved forests compared to mixed-coniferous stands.

*ESF*s are mid-sized bats specialized to hunt aerial arthropods along structural vegetation edges with their high prey availability (Deans et al. 2005, Mueller et al. 2018). We assume that the large amount of unspecified *Myotis*-calls predominantly belonged to *M. brandtii*, whose presence was verified via mist-netting (Dietz et al. 2018).

Supporting our findings, Kusch et al. (2004) and Mueller et al. (2013) found a preference of *Myotis* and *Pipistrellus* bats for open canopy areas or inner forest edges. Other studies found contrasting activity patterns for different species grouped together in our *ESF* guild (Renner et al. 2018, Carr et al. 2020, Tena et al. 2020). We believe that the generally strong affinity for broadleaved forests in this guild is linked to a more abundant and species-rich arthropod community, especially when considering phytophagous arthropods, compared to coniferous forests (Brandle and Brandl 2001, Gossner 2008, Leidinger et al. 2019).

A reduced prey availability in large gaps compared to smaller gaps might be a reason for the decline in *ESF* activity with increasing gap size, but this suggestion has to be supported by further research. Considering artificially created gaps, Menzel et al. (2002) found lower activity levels of the *ESF Lasiurus borealis* in large gaps compared to small gaps, whereas Ford et al. (2005) did not detect an influence of minimum gap width on the detection probability of this species. In natural gaps, Fukui et al. (2011) found a preference for medium-sized gaps in *ESF* bats.

2.5.3 *NSF* activity in canopy gaps

NSF bats in our study had similar activity levels in canopy gaps and under closed canopy. With increasing gap size, *NSF* activity levels decreased, likely because the forested vegetation character of the gaps diminished and became less attractive for these bats.

M. nattereri was the species most commonly recorded within the *NSF* guild. We cannot infer from our results on *Plecotus auritus* since we recorded too few call sequences from this species. Natterer´s bats feed mainly on dipteran insects and on spiders and are specialized on prey perception close to or within the vegetation by aerial hawking and gleaning (Siemers and Schnitzler 2000, Swift and Racey 2002, Siemers and Swift 2006). Patriquin and Barclay (2003) found the gleaning bat *Myotis septentrionalis* to forage preferably in intact forest patches in Alberta, Canada. In the study of Ford et al. (2005), the detection probability of *NSF*s was higher with increasing canopy cover. Similarly to our results however, Tena et al. (2020) did not identify a gap effect for the gleaning bat *Plecotus* spec. We assume that the clearings in our study offered enough regeneration vegetation, and consequently valuable prey for Natterer´s bats to use these gaps for gleaning.

The strong preference of *M. nattereri* for broadleaved forests we observed supports results from previous studies on species from this guild (Entwistle et al. 1996, Smith and Racey 2008, Murphy et al. 2012). Indeed, many studies suggest a higher arthropod diversity in crowns of broadleaved trees, especially of oak trees (Floren et al. 2008, Mupepele et al. 2014, Leidinger et al. 2019; but see Korenko et al. (2011) for contradictory findings in canopy spiders). Similarly, Smith and Racey (2008) found that *M. nattereri* avoided coniferous stands because they are too dense. Consistent with our hypotheses and in accordance with findings from Fukui et al. (2011) for a *NSF* species, gap size negatively influenced the foraging activity of *M. nattereri.*

2.5.4 Bat richness in canopy gaps

Natural gaps promoted bat diversity in mixed-coniferous stands, even though bat richness in these forests in our study was generally very low. These stands possess a relatively dense canopy layer, and canopy openings offered foraging areas for bat species otherwise largely precluded from these forests. Tena et al. (2020) also found a higher bat richness in gaps compared to control points in pine woods of the Guadarrama Mountains in Central Spain, since they were used by edge-foragers and forest-dwelling species alike.

In broadleaved forests with a higher general bat diversity, bat richness did not differ between gaps and the forest interior and decreased in larger gaps. Broadleaved forests offered adequate hunting grounds for more species even in the forest interior and provided at least occasional foraging habitats for all species detected. These results support findings from Celuch and Kropil (2008) from the Carpathian Mountains and from Renner et al. (2018) and Carr et al. (2020) who identified structurally heterogeneous forests and forests more than 30 years after management abandonment to be the most species rich.

Gap size had a differential influence in broadleaved and mixed-coniferous stands on bat richness. The larger the canopy gaps in coniferous stands, the higher the forest heterogeneity which likely drives the increase in bat richness for this otherwise species-poor forest stands. Considering broadleaved forests, the decreasing richness within the *ESF* guild is the most influencing factor for the lower bat richness with increasing gap size. This is due to the fact that the *ESF* guild in our study was the most species-rich guild with several species with comparable occurrences.

2.5.5 Conclusions and implications for forest management

We showed that small-scale disturbances in old-growth forests are valuable habitat components for forest bats. In mixed-coniferous stands, they led to an increase in bat richness, and in all forest habitats considered, they were more actively used than the forest interior especially by *ESF* species. An emulation of natural disturbances typical for the forest habitat considered, i.e. the selective logging of trees as implemented in the plenter or group plenter systems, has the potential to promote bat species diversity, with no negative impacts on *NSF*s and *OSF*s. These forest management practices should be regarded as a part of the integrative instruments recommended by Kraus and Krumm (2013).

Especially for *OSF* species, the area above the forest canopy remains understudied. We need more information on differences between the forest interior, the space above the canopy and gaps of different sizes in arthropod density and diversity and their use by *OSF* bats, to elucidate the mechanisms behind the patterns observed in our study.

We want to highlight the general importance of forest bats as potential surrogate species for forest conservation measures: different bat species rely on differing tree species and tree microhabitats for roosting, such as woodpecker holes, stem crevices or loose bark. Bats could be grouped according to general roost-site characteristics into roosting- guilds as has been done by Drake et al. (2020) for North American forest bat species. Combined conservation actions considering both roosting and hunting preferences of forest bat guilds should therefore benefit a variety of other organisms and biodiversity aspects (Regnery et al. 2013, Paillet et al. 2018, Basile et al. 2020). Quantitative research in this field would be an important step towards the development of concrete conservation tools for forest managers.

Our results highlight the important role of broadleaved forests for bat species diversity and activity. Natural forests built of native broadleaved tree species that are allowed to follow the natural regeneration cycle are of outstanding importance for conserving the biota of the temperate forest biome in Europe and elsewhere (Selva et al. 2020).

2.6 CRediT authorship contribution statement

Maude Erasmy: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Christoph Leuschner:** Writing - review & editing. **Niko Balkenhol:** Writing - review & editing. **Markus Dietz:** Conceptualization, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

2.7 Declaration of Competing Interest

The authors declare that there is no conflict of interest.

2.8 Acknowledgements

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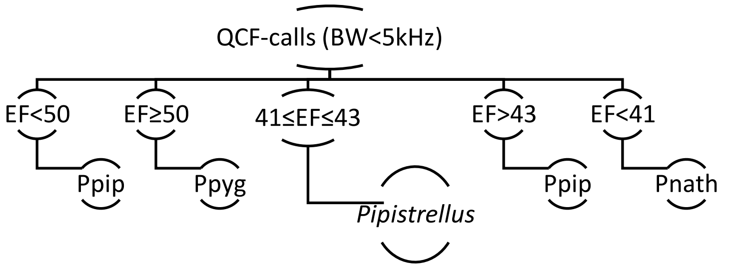
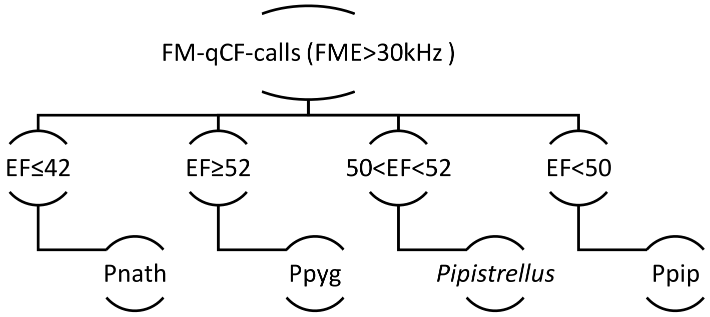
2.10 Appendix

Table A 2.1 Rules used for species identification. EF: end frequency, SF: start frequency, BW: bandwidth, qCF: quasi-constantfrequent, FM: frequency-modulated, FME: frequency of maximum energy. All call properties are given in kHz-units. Pnath: *Pipistrellus nathusii*, Ppip: *P. pipistrellus*, Ppyg: *P. pygmaeus*, Malc: *Myotis alcathoe*, Mbart: *M. brandtii*, Mdaub: *M. daubentonii*, Mdas: *M. dasycn*eme, Mnat: *M. nattereri*, Nycleis: *Nyctalus leisleri*, Nycnoc: *N. noctula*, Enil: *Eptesicus nilssonii*, Eser: *E. serotinus*, Vmur: *Vespertilio murinus*.

<table>
<tr><td colspan="2">*Pipistrellus* sonotype</td></tr>
<tr><td>Automatic identification:</td><td>Manual identification:</td></tr>
<tr><td>All sequences ≥ 90% probability and >5 calls/sequence accepted</td><td>If < 5 automatically recognized calls: minimum 2 extra calls verified manually (of lower quality)</td></tr>
<tr><td></td><td>If <90% probability:

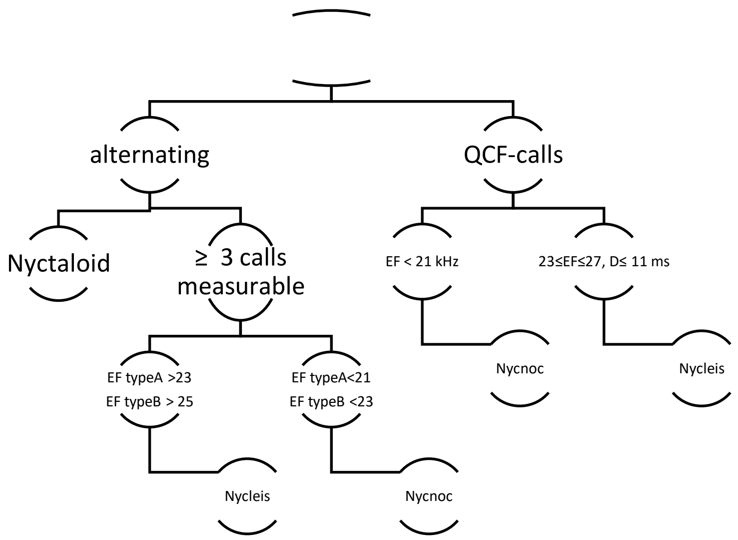




</td></tr>
<tr><td colspan="2">*Myotis* sonotype</td></tr>
<tr><td>Automatic identification:</td><td>Manual identification:</td></tr>
<tr><td>Mbart and Mdaub >80%: accepted</td><td>Mnat: SF>120, EF around 20 → BW>100 when good calls, high FME (>50 kHz), convex shape: all identified (and checked) calls accepted as species evidence</td></tr>
<tr><td>Mdas changed into Myotis spec. or Enil (see details for this species)</td><td>Malc: identified manually with expert opinions</td></tr>
<tr><td><5 calls recognized: changed into Myotis spec. (except Mnat: identification possible even if no calls automatically identified)</td><td></td></tr>
<tr><td>Mbart, Mdaub: <80%: changed into Myotis spec.</td><td></td></tr>
</table>

Nyctaloid sonotype

Automatic identification:	Manual identification:
<5 calls: changed into Nyctaloid Vmur: >80% accepted Enil: >80% accepted Nyctief → Nyctaloid Nycmi → Nyctaloid	



Plecotus auritus

Automatic identification

All sequences accepted

Barbastella barbastellus

Automatic identification:	Manual identification:
Often not recognized, since e.g. calls too low	Alternating calls, easily recognizable, first call loud, 2.5 ms long, SF 36 kHz, EF 28 kHz; second call qCF/FM pulse, SF 44 kHZ, EF 29 kHz, 4.5 ms long

TABLE A 2.2 Contrasts from a Poisson generalized linear mixed model for bat richness in different forest types under different canopy structures on the response scale. Plot and period included as random effects.

forest type	contrast	ratio	SE	df	t-ratio	p-value
broadleaved	closed canopy / gap	0.823	0.171	298	-0.935	0.351
coniferous	closed canopy / gap	0.372	0.107	298	-3.450	<0.001

TABLE A 2.3 Estimates for the slope of gap size from a generalized linear mixed negative-binomial zero-inflated model at an average mean night-time temperature for *ESF* activity. Contrast from the same model for *ESF* activity.

forest type	gap size trend	SE	df	lower cl	upper cl
deciduous	-0.025	0.005	144	-0.034	0.016
coniferous	0.005	0.004	144	-0.002	0.013

contrast	estimate	SE	df	t-ratio	p-value
deciduous-coniferous	-0.030	0.006	144	-4.832	<0.001

TABLE A 2.4 Estimates for the slope of gap size from a generalized linear mixed Poisson model at an average mean night-time temperature for bat richness. Contrast from the same model for bat richness.

forest type	gap size trend	SE	df	lower cl	upper cl
deciduous	-0.004	0.003	146	-0.011	0.001
coniferous	0.003	0.002	146	-0.002	0.007

contrast	estimate	SE	df	t-ratio	p-value
deciduous-coniferous	-0.007	0.004	146	-1.821	0.071

TABLE A 2.5 Estimates for the slope of gap size from a generalized linear mixed Poisson model averaged over mean night-time temperature for *ESF* richness. Contrast from the same model for *ESF* richness.

forest type	gap size trend	SE	df	lower cl	upper cl
deciduous	-0.009	0.003	146	-0.015	-0.002
coniferous	0.006	0.003	146	0.000	0.012

contrast	estimate	SE	df	t-ratio	p-value
deciduous-coniferous	-0.015	0.005	146	-3.287	0.001

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Chapter 3

3 Three-dimensional stratification pattern in an old-growth lowland forest: how does height in canopy and season influence temperate bat activity?

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3.1 Abstract

The study of animal–habitat interactions is of primary importance for the formulation of conservation recommendations. Flying, gliding, and climbing animals have the ability to exploit their habitat in a three-dimensional way, and the vertical canopy structure in forests plays an essential role for habitat suitability. Forest bats as flying mammals may seasonally shift their microhabitat use due to differing energy demands or changing prey availability, but the patterns are not well understood. We investigated three-dimensional and seasonal habitat use by insectivorous bats in a temperate lowland old-growth forest, the Belovezhskaya Pushcha in Belarus. We acoustically sampled broadleaved and mixed coniferous plots in the forest interior and in gaps in three heights during two reproductive periods (pregnancy/lactation vs. postlactation). In canopy gaps, vertical stratification in bat activity was less pronounced than in the forest interior. Vertical activity patterns differed among species. The upper canopy levels were important foraging habitats for the open-space forager guild and for some edge-space foragers like the Barbastelle bat *Barbastella barbastellus* and the soprano pipistrelle *Pipistrellus pygmaeus*. *Myotis* species had highest activity levels near the ground in forest gaps. Moreover, we found species-dependent seasonal microhabitat shifts. Generally, all species and species groups considered except *Myotis* species showed higher activity levels during postlactation. *Myotis* species tended toward higher activity in the forest interior during postlactation. P. *pygmaeus* switched from high activity levels in the upper canopy during pregnancy and lactation to high activity levels near the ground during postlactation. We conclude that a full comprehension of forest bat habitat use is only possible when height in canopy and seasonal patterns are considered.

Keywords: Bialowieza forest, gaps, insectivorous bats, seasonality, three-dimensional habitat use

3.2 Introduction

Forests are three-dimensionally structured ecosystems, where plant species and resources are heterogeneously distributed in time and space (Muscolo et al. 2014, Perry et al. 2018). Knowledge about how this three-dimensional heterogeneity impacts the spatio-temporal behaviour of forest animals is essential for the formulation of conservation measures (e.g. Charbonnier et al. (2014), Alder et al. (2020), Ruczynski and Barton (2020)). The forest canopy as the upper layer of vegetation formed by tree crowns is a particularly important habitat and resource element used by vertebrate and nonvertebrate forest animals (Lowman et al. 2013, Nakamura et al. 2017).

A few decades ago, forest research was restricted to ground-based methods due to technical limitations and inferences on species interactions and population dynamics within the canopy were mainly deduced from ground observations (Lowman et al. 2013, Nakamura et al. 2017). The development of new technologies such as canopy access facilities (e.g., cranes) and remote sensing systems (e.g., drones) led to an increasing accessibility of forest canopies (Basset et al. 2003, Unterseher et al. 2007, Jung et al. 2012, Lowman et al. 2012, 2013, Froidevaux et al. 2016, Nakamura et al. 2017, Ozanne et al. 2021). Vertebrates using the forest canopy for moving, feeding, or resting actively choose their microhabitats by vertically switching between forest layers. This has been shown for birds (Pearson 1971, Shaw et al. 2002, Walther 2002, Jayson and Mathew 2003, Acharya and Vijayan 2017, Rajaonarivelo et al. 2020), gliding squirrels (Krishna et al. 2016), or monkeys (Enstam and Isbell 2004, Li 2007, Pinheiro et al. 2013) in different climatic regions. Bats as three-dimensionally moving organisms can exploit the forest canopy, the free space above the canopy and the interstrata free space. Studies on the role of tree crowns for bats originated in the tropics, where a number of studies revealed vertical stratification of various diversity metrics caused by species-inherent ecomorphological constraints and specializations in foraging behaviour (Bernard 2001, Kalko and Handley 2001, Henry et al. 2004, Ramos Pereira et al. 2010, Rex et al. 2011, Carvalho et al. 2012, Tiago Marques et al. 2016, Duya et al. 2017, Gregorin et al. 2017, Fraixedas Nunez et al. 2019, Silva et al. 2020). Such height stratification patterns were also found for arthropods across climatic regions (Stork and Grimbacher 2006, Oguri et al. 2014, Basset et al. 2015, Ashton et al. 2016). In temperate regions worldwide, studies focusing on the three-dimensional space use in forest bats have not yet revealed consistent height patterns (United States: Hayes and Gruver (2000), Menzel et al. (2005), Kennedy et al. (2014), Australia: Adams et al. (2009), New Zealand: Scrimgeour et al. (2013)). In Europe, Froidevaux et al. (2014) did not detect any layer preferences (ground vs. canopy) within guilds. Plank et al. (2012) found species-dependent activity differences between strata and according to Collins and Jones (2009) and Mueller et al. (2013), species or species group activities and species assemblages differed between canopy layers.

In the forest interior, forest bat activity is more strongly confined to certain heights than at forest edges such as forest tracks or water bodies (Adams et al. 2009, Tiago Marques et al. 2016). In the absence of vegetation clutter, the flight heights used by bats are not determined by physical constraints but are rather depending on species-dependent prey preferences. Indeed, bats' choice of adequate foraging habitats results from an interaction of prey species and their abundances (Andreas et al. 2012b, Ferreira et al. 2017, Salvarina et al. 2018), current energy requirements (Russ et al. 2003, Lucan and Radil 2010, Ruczynski et al. 2017), and local competitive interactions (Andreas et al. 2012a, Roeleke et al. 2018, Vasko et al. 2020). Differing seasonal habitat requirements can thus be reflected in seasonal height use shifts, as Plank et al. (2012) and Staton and Poulton (2012) showed for temperate bats. Seasonal shifts in bat activity have been shown furthermore to occur between habitats (Russ et al. 2003, Lucan and Radil 2010, Kelm et al. 2014, Heim et al. 2016, Ferreira et al. 2017, Roeleke et al. 2018, Vasko et al. 2020).

We acoustically sampled the vertical height use of a temperate forest bat assemblage in a European lowland old-growth forest. We compared the activity of guilds, the activity of dominant species, and species community composition in two forest habitats for the ground, mid, and high canopy layer in the forest interior and in canopy gaps for the two time periods pregnancy/parturition and lactation/postlactation. This way, we were able to assess seasonal preferences in three dimensions both locally (vertically in the forest interior and adjacent gaps) and at a broader spatial scale (broadleaved vs. mixed coniferous forests).

Specifically, we hypothesized that

i) stratification of bat activity is more accentuated in the forest interior than in forest gaps

ii) forest layers are differently used by guilds and species depending on their ecomorphology and prey preferences

iii) forest layers are differently used by guilds and species depending on the reproductive season.

3.3 Material and Methods

3.3.1 Study area

The study was conducted in the "Belovezhskaya Pushcha" National Park (*BPNP*) in Western Belarus. The National Park is largely dominated by temperate and hemiboreal woodlands (approximately 80% of the total 153,000 ha, Nikiforov and Bambiza (2008)) at elevations of 134–202 m a.s.l. and is part of the Belovezhskaya Pushcha/ Puszcza Białowieska (*BP*) forest complex which extends beyond the Polish–Belarusian border (Jaroszewicz et al. 2019). The climate is subcontinental, with a mean annual air temperature of 7.3°C and an average annual precipitation of 625 mm (period 1985–2015, Boczoń et al. (2018)). Mixed coniferous forests are the prevailing vegetation, reflecting the transitional character of *BP* between nemoral broadleaved and boreal coniferous forests (Nikiforov and Bambiza 2008). *Pinus sylvestris* L. (Scots pine) is the dominating tree species in more than half of the forest stands on the Belarusian side of *BP* (Falinski 1986, Nikiforov and Bambiza 2008). Besides *Alnus glutinosa* L. (common alder) in swamp forests, English oak (*Quercus robur* L.), European hornbeam (*Carpinus betulus* L.), and small-leaved lime (*Tilia cordata* Mill.) form broadleaved mixed forests on sites not influenced by groundwater. In almost all forest stands in *BP*, *Picea abies* (L.) H. Karst. (Norway spruce) is present as an admixture (Falinski 1986).

Our study plots were located within the "strict reserve" of the National Park, where management activities are prohibited on an area of 57,000 ha. To guarantee independent sampling of bats as flying mammals, all plots were located more than 7 km from each other. All plots were at least 1 km away from the nearest settlement to avoid anthropogenic influences and at least 300 m from external forest borders to minimize edge effects. Furthermore, plots were located more than 1 km distant to water bodies or courses to reduce the influence of water on bat activity (Grindal 1998, Fukui et al. 2006, Vindigni et al. 2009, Salvarina et al. 2018).

Our study design covered two different habitat types for comparison. Four plots were located in mixed Pino-Quercetum stands (mixed coniferous forest), which represent the dominating forest community on the Belarusian side of *BP* (Falinski 1986). These forest stands are dominated by *P. sylvestris* with varying admixtures of *P. abies* in the upper canopy and *P. abies* and *Q. robur* in the second tree layer. The understory was dominated by young *Picea* trees which create rather dense inner stands with respect to available flight space. Four plots were located in broadleaved Tilio-Carpinetum stands, a mesotrophic forest community with frequently *Q. robur* and more rarely *Tilia cordata* or *Acer platanoides* dominating the uppermost canopy layer, and a rather dense subcanopy created mainly by *C. betulus* and *P. abies*. The forest interior was less dense compared to mixed coniferous stands due to lower stem densities. Each plot consisted of two subplots, with an average distance of 154 ± 85 m from each other. One subplot was located in the forest interior, and the other in an adjacent forest gap. All gap plots had been created by fallen trees and were located within the forest matrix, without connections to other open structures.

3.3.2 Bat sampling

We used acoustic recording techniques to estimate bat activity. Devices automatically recording ultrasound were deployed at the plots (batcorder 3.0, EcoObs GmbH Nuremberg). We used the recording mode “Auto-Timer” and the following recording settings: quality = 20, threshold = −27 dB, post-trigger = 400 ms, critical frequency = 16 kHz. Recordings automatically ran from sunset until 1 h after sunrise. Following recommendations from Weller and Zabel (2002) and Britzke et al. (2013), omnidirectional ultrasonic microphones were slightly inclined upward and the space surrounding them was void of vegetation clutter to minimize detection probability bias.

In each subplot, batcorders were installed at three heights to collect a three-dimensional acoustic image of bat activity along a vertical gradient in the plot centre. In the forest interior, batcorders were placed at the plot centre (see 3.3.4 Stand structural data). In gaps, batcorders were placed in the subjective gap centre. A rope-and- pulley system was used to suspend the batcorders. With a slingshot, we shot an auxiliary rope into a suitable branch fork. By means of this auxiliary rope, we pulled up the final string to which batcorders were attached at three heights. If no adequate tree was present in the gap centre, we shot auxiliary ropes in two suitable trees on each side of the gap. This way, a rope was stretching from one side of the gap to the other side at canopy height. In the gap centre, batcorders were attached to this rope using a vertically hanging line. We anchored the line in this central position with side ropes and tent pegs.

We investigated bat activity in three heights within each subplot. Ground sampling (low stratum, space dominated by tree stems, and understory vegetation) was established at an average height of 3 m (SD = 0.7 m, min = 1.6 m, max = 4.2 m). Midcanopy sampling (mid stratum, space of subcanopy trees) was conducted at 11 m (SD = 1.2 m, min = 9 m, max = 12.8 m) and high-canopy (high stratum, space between subcanopy and canopy trees) sampling at 19 m (SD = 3.7 m, min = 13.1 m, max = 26.6 m). We tried to evenly spread the three batcorders over the height spectrum. However, we were not able to position the highest batcorder at the crown-top level of the tallest trees (Figure 3.1 and Figure A 3.1).

The batcorder array was set up simultaneously in a gap subplot and the neighbouring forest interior subplot. For technical reasons, the number of recording nights per batcorder differed between 3 and 12 nights (mean 8 recording nights, SD = 2.5). Sampling took place on 72 nights between 31 May and 4 September 2015. To catch seasonal effects on bat activity, we considered two time periods with similar sampling effort for each habitat and canopy structure (period I: 192 samples, period II: 196 samples; Table 3.1). However, while period I included samples from four plots (accordingly eight subplots) per habitat, in period II only 3 plots (corresponding to six subplots) per habitat were sampled (Table 3.1). Due to technical problems, the highest batcorder in subplot E2 in broadleaved gaps was not working in period I; however, all synchronously recorded sequences in the other heights were included in the analyses, since the models used allow for differing sample sizes. Period I until July 3rd included gestation, parturition, and lactation of the offspring, while period II encompassed weaning of the young and the beginning of their independent flights (Table A 3.1). Temperature was measured internally in each batcorder and stored every 15 min (Figure A 3.2). On ten nights, precipitation events of low impact took place (0.3–5.5 mm per night, measured between 18:00 and 6:00). All precipitation nights were included in the analyses, since exploratory analyses did not show any influence of these rare and low-intensity events on bat activity. Every height stratum in each habitat and canopy structure type was sampled between 29 and 37 nights during our field campaign.

3.3.3 Acoustic data analysis

We collected acoustic bat calls and used these recordings to identify bat species. The software batIdent (EcoOb GmbH) identifies species and assigns identification probabilities. López-Baucells et al. (2019) found that a combination of automatic and manual methods is effective in identifying bat calls. Hence, we used a combination of automatic bat call identification and manual postvalidation of these assignments using the software bcAnalyze2 (EcoOb GmbH). Parameters and literature used for manual species identification are given in Erasmy et al.

(2021). Bat calls not identified to species were combined into sonotypes. Recently, 16 bat species have been described for the Belarusian side of *BP* (Dietz et al. 2018). We used the *Pipistrellus* sonotype for calls from unidentified *P. Pipistrellus* and *P. pygmaeus*, *Myotis* sonotype for unidentified calls from *M. alcathoe*, *M. brandtii*, and *M. daubentonii*, and *nyctaloid* sonotype for unidentified calls from *E. nilssonii*, *E. serotinus*, *N. noctula*, *N. leisleri*, and *V. murinus*. A few calls were attributed to *Plecotus* spec. These calls most probably refer to *Plecotus auritus* since *P. austriacus* has only rarely been recorded in *BP* (Sachanowicz et al. 2006). We performed a first set of statistical analyses on bat guild level and used the guild attribution of bat species following Mueller et al. (2012) and Erasmy et al. (2021). Edge-space foragers (*ESF*) included *B. barbastellus*, *P. pipistrellus*, *P. pygmaeus*, *M. brandtii*, *M. daubentonii*, *M. alcathoe* and not further specified *Myotis* spec., narrow-space foragers (*NSF*) comprised *Plecotus auritus* and *M. nattereri*, and open-space foragers (*OSF*) *P. nathusii*, *N. leisleri*, *N. noctula*, *E. nilssonii*, *E. serotinus*, *V. murinus*, and all not further specified *nyctaloid* calls.

When analysing bat recordings, we cannot distinguish between one individual recorded several times and several individuals recorded once. For this reason, Hayes (1997) and Kalcounis et al. (1999) proposed the use of an activity index instead of the number of recorded sequences as a method to take account of this issue. We used the number of 1-minute intervals with bat calls per night as an activity index (see Mueller et al. (2012) for a similar methodology and Erasmy et al. (2021) for a detailed description of this index). This index evens out the effects of very high activity levels produced by species hunting in front of the microphone or by species with intercall intervals exceeding the post-trigger time (e.g. *N. noctula*).

Individual bat species differ in echolocation call intensities. This induces varying interspecies detection probabilities in the same habitat and under identical weather conditions (Britzke et al. 2013). We therefore refrained from comparing activity patterns between guilds or species. Detection probabilities within species vary with vegetation clutter and weather conditions (Yates and Muzika 2006, Gorresen et al. 2008, Britzke et al. 2013, Bender et al. 2015). All batcorders in the forest interior were surrounded by vegetation-free space to create similar recording situations and to minimize attenuation effects on bat calls through leaves and branches. We sampled the same habitat type at multiple plots with differing vegetation structures surrounding our batcorders. Since we were interested in habitat effects on bat activity, we are confident that these differing forest structural patterns from within the same habitat are suited to account for detection probability differences due to vegetation clutter.

Our batcorder array sampling synchronously at three heights possessed a pitfall: Since every microphone was recording on a single device, high-intensity bat calls were likely to reach the neighbouring batcorder microphone and thus trigger the same activity recording in adjacent batcorders. We therefore manually checked all recordings, identified calls with the same timestamp from the same species/sonotype at neighbouring batcorders, and assigned them to the batcorder with the strongest signal (Tiago Marques et al. 2016).

3.3.4 Stand structural data

In gaps, we estimated gap area following Runkle (1982) by determining the edge of crowns in eight directions from the gap centre. Gap sizes ranged from 56 to 265 m$_2$, with an average gap size in broadleaved plots of 78 ± 23 m^2 and an average gap size of 156 ± 77 m^2 in mixed coniferous (Figure 3.2).

Plots in the forest interior were established on an area of 1000 m^2 (17.8 m radius around the batcorder as the plot centre). We measured the height of 12–18 trees per plot and used the nonlinear regression equation reported by Petterson (1955) to predict the height of all trees not measured. These height measures were used for depicting the plot height profiles of trees within the plot (forest interior subplots) or surrounding the gap (forest gap subplots) for the two habitat types considered (Figure 3.1).

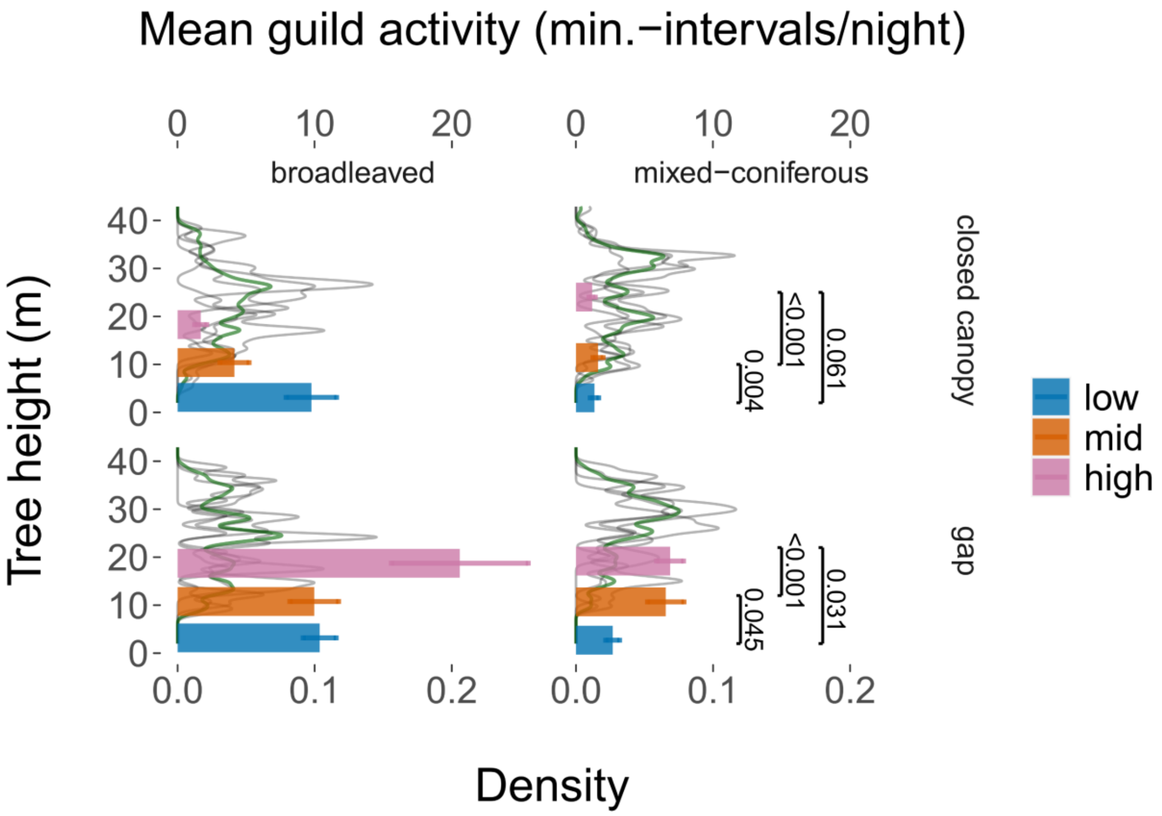

FIGURE 3.1 Density function of tree height profiles in individual subplots (light grey, n=4) and averaged over all plots (thick green line). Bars show the mean night-time activity (+/- standard error) in minute-intervals/night for total bat guild plotted at the mean batcorder heights. Significant p-values of post-hoc Tukey-tests adjusted for multiple comparisons for the three height levels for both habitats combined from the Generalized linear mixed model fitting total bat activity. Blue: high, rose: mid, orange: low batcorder stratum.

3.3.5 Statistical analyses

All statistical analyses were performed within the R 4.0.3 software environment (R Development Core Team 2019). To test for the influence of structural and seasonal effects on bat activity, separate models were fitted for total bat activity, for the activity of each bat guild (*OSF*, *ESF*, and *NSF*) and of each of the dominant species within each guild with the 1-min activity index as a response variable. To disentangle species-dependent activity differences within the *ESF* guild, the activities of the main *ESF* species (Barbastelle bat, soprano pipistrelle, and *Myotis* spec.) were separately fitted. *Myotis brandtii* (7% of *ESF* activity) and not further identified *Myotis* spec. (20% of *ESF* activity) were first analysed in separate analyses. The patterns identified were qualitatively identical, and their activity data were jointly analysed as *Myotis* spec. to increase sample size. We fitted linear mixed models using the package glmmTMB (Brooks et al. 2017) and validated model assumptions with the DHARMa package (Hartig 2020). We accounted for seasonal variations in bat activity by monitoring throughout the summer and by integrating Julian date as a random factor (n = 72, total bat activity model) or two recording periods corresponding to pregnancy/lactation and postlactation period as fixed effect into our models (all other models; Hayes (1997), Skalak et al. (2012), Vasko et al. (2020)). Subplot (n = 16) was added as a random factor to account for subplot-dependent variation not captured by the predictors used. A set of candidate models including all two-way interactions between height, canopy openness (gap vs. forest interior), season (pregnancy/lactation vs. postlactation), and forest habitat (broadleaved vs. mixed coniferous) were fitted for each guild/species with assumed negative-binomial distributions. Mean nighttime temperature was added as a simple predictor, since several studies identified temperature as an important predictor both for bat and insect activity (e.g. Dajoz (2000), Mueller et al. (2012), Wolbert et al. (2014), Froidevaux et al. (2021)). Post hoc testing for effects with more than two levels was done using Tukey's honestly significant difference test with a correction factor for multiple comparisons using the pairs function within the emmeans package (Lenth 2020). The best fitting and most

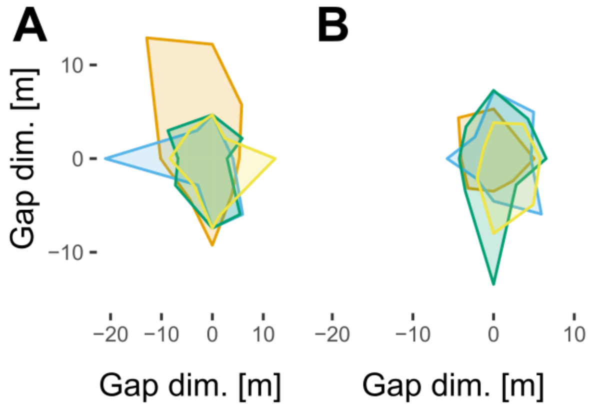

Figure 3.2 A) and B) Projected gap areas of the coniferous (n=4) and broadleaved (n=4) forest sites in a projected coordinate system with 0 as the plot-centre where the batcorder was placed and gap dimensions showing the extent of each gap site in differently coloured shades.

parsimonious model from this candidate set was identified using Akaike's information criterion adapted for small sample sizes (AICc) and chosen within AICc values below 2 (Burnham and Anderson 2004, Brewer et al. 2016). All candidate models including their differences in AICc values are shown in Table A 3.2. Moreover, we calculated marginal R^2-values for the best fitting model using the Nakagawa equation (Table A 3.2; Nakagawa and Schielzeth (2013), Lüdecke et al. (2021)). The best model is presented using restricted maximum likelihood (REML). Predictions used for plotting were calculated using the emmeans package (Lenth 2020).

We applied nonmetric multidimensional scaling based on the Bray−Curtis similarity metric on species activity data to describe species assemblages (function metaMDS from the R package 'vegan', Oksanen et al. (2020)). This function was applied to the activity data of all species/species groups present with more than 20 min-intervals in the field campaign. *V. murinus*, *Plecotus* spec., *M. alcathoe*, *M. dasycneme*, and *E. serotinus* were excluded from this multivariate analysis due to their rare observation.

3.4 Results

3.4.1 General patterns of bat activity

During 72 measuring nights, we recorded a total of 4316 bat call sequences (transformed into 2507 min-intervals per night). During 90 of the 388 batcorder sessions, no bat calls were recorded. The recordings were assigned to the three guilds *OSF*, *ESF*, and *NSF*, with 72% of the total activity belonging to *ESF* species, 24% to *OSF* and 4% to *NSF* species. 64.5% of the activity data could be assigned to one of the 13 species identified, and the remaining sequences were

TABLE 3.1 Fitted effects for total bat activity from a generalized linear mixed model with negative-binomial distribution assumed (n=388).

Predictors	IRR ± SE	Stat.	p
habitat [mixed coniferous]	0.35 ± 0.15	-2.42	**0.015**
structure [gap]	2.09 ± 0.93	1.66	0.098
height [mid]	0.55 ± 0.10	-3.25	**0.001**
height [high]	0.34 ± 0.07	-5.39	**<0.001**
mean night-time temperature	1.11 ± 0.03	4.29	**<0.001**
structure [gap] * height [mid]	2.18 ± 0.53	3.22	**0.001**
structure [gap] * height [high]	5.40 ± 1.39	6.52	**<0.001**

Note: Random effects: subplot=16 levels, date=72 levels. IRR=incidence rate ratio, SE=standard error. Habitat fitted against broadleaved, canopy structure "gap" against the forest interior, and heights against the ground layer.

attributed to species groups or sonotypes (see 3.3.3 Acoustic data analysis). 73% of the total activity observed in the study was recorded in broadleaved forests and 27% in mixed coniferous forests. About a quarter of total activity (27%) was observed in the forest interior and 73% in gaps. Bat total activity was evenly distributed over all three heights (high: 37%, mid: 29%, ground: 33%; Table A 3.3 summarizes the raw data).

Total bat activity revealed opposing height patterns between forest gaps and the forest interior. In gaps, the highest activity was recorded in the upper canopy, and activity levels were lower with decreasing heights (Table 3.1). In the forest interior, however, the highest activity levels were recorded at the ground, with lower activity levels higher in the canopy (Table 3.1; Figure 3.1).

None of the species identified was recorded exclusively in either habitat, canopy structure, or height. However, differences in the proportional activity spent in each microhabitat became evident on species level (Figure 3.3). N. *noctula* was detected proportionally more often in gaps (81% of the total *N. noctula* activity) and in the upper canopy (81%) in mixed coniferous habitats (74%; Figure 3.3). *P. nathusii* bats spent almost their total activity in gaps (88%) and in the upper

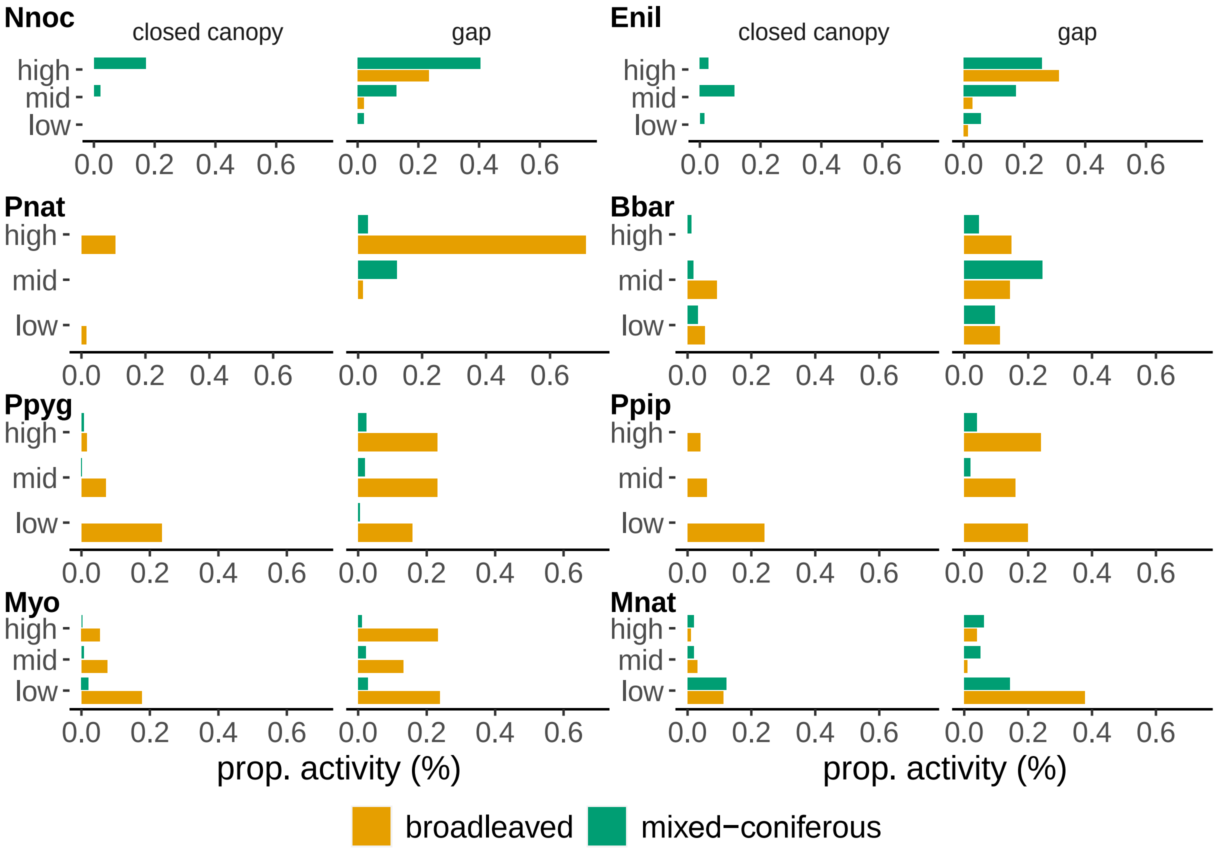

Figure 3.3 Proportional species activity spent in the habitat structures considered relative to the total activity of this species in minute-intervals/night for dominant species. Nnoc = *Nyctalus noctula*, Enil = *Eptesicus nilssonii*, Pnat = *Pipistrellus nathusii*, Bbar = *Barbastella barbastellus*, Ppyg = *Pipistrellus pygmaeus*, Ppip= *P. pipistrellus*, Myo = *Myotis* spec. (all *Myotis* spec. except *M. natteri*), Mnat = *M. natteri.*

canopy (85%) in broadleaved forests (85%; Figure 3). *B. barbastellus* was equally active in broadleaved and mixed coniferous habitats but spent more time in gaps (79% of activity) with half of its activity at the midcanopy layer (50%; Figure 3.3). *P. pygmaeus* bats generally spent most of their activity in gaps (67%) distributed equally over all three heights (Figure 3.3). In the forest interior, they were most active at the ground (71% activity spent; Figure 3.3). 94% of their total activity was spent in broadleaved forests. *P. pipistrellus* showed a proportional time activity pattern similar to *P. pygmaeus* (Figure 3.3). *Myotis* spec. spent most of their activity in broadleaved forests (91%) and were detected slightly more often in forest gaps (67%) and at the ground (46%; Figure 3.3). M. *nattereri* foraged in both habitat types, especially at the ground level (76%) and in forest gaps (68%; Figure 3.3).

3.4.2 Guild-dependent activity stratification

Calls belonging to *OSF*s were recorded in 36% of sample nights. The best model fitting *OSF* activity revealed a differing height activity pattern between canopy gaps and the forest interior (Table 3.2): In gaps, *OSF*s were significantly more active in the upper canopy stratum, whereas their predicted activity levels for midcanopy heights and the ground were negligible (Figure 3.4). In the forest interior, however, both mid-and high-canopy heights revealed significantly higher *OSF* activity levels compared to the ground batcorder (Figure 3.4). *OSF*s were equally active in broadleaved and mixed coniferous forests, and temperature was significantly and positively influencing *OSF* activity levels (Table 3.2). Most calls from the *OSF* guild were unidentified *nyctaloid* calls (60% of all *OSF* calls). *E. nilssonii* and *P. nathusii* accounted for 12% and 11%, respectively, of *OSF* calls. Species models for this guild were not fitted due to a low number of observations for single species.

*ESF*s were active during 68% of all sample nights. The most parsimonious model showed a significantly differing height pattern between gaps and the forest interior (Table 3.2): In gaps, *ESF*s were equally active over the three heights considered (Table 3.2). In the forest interior, however, *ESF*s were most active at the ground (estimated marginal mean (EMM) activity from the model: 1.8 min-intervals/ night; Figure 3.4). Generally, broadleaved forests were significantly preferred by *ESF* bats (Table 3.2). Activity within this guild significantly increased with higher mean nighttime temperatures (Table 3.2). Height use in Barbastelle bats (23% of *ESF* activity) differed depending on the canopy structure. Barbastelle bats' activity in canopy gaps was highest at mid heights (Figure 3.4). In the forest interior, Barbastelle bats were significantly more active at the ground and at mid heights compared to the highest layer. Barbastelle bats did not prefer any of the two habitat types, broadleaved or mixed coniferous (Table 3.2). In both habitat types, they were significantly more often recorded in gaps (Table 3.2). Temperature was

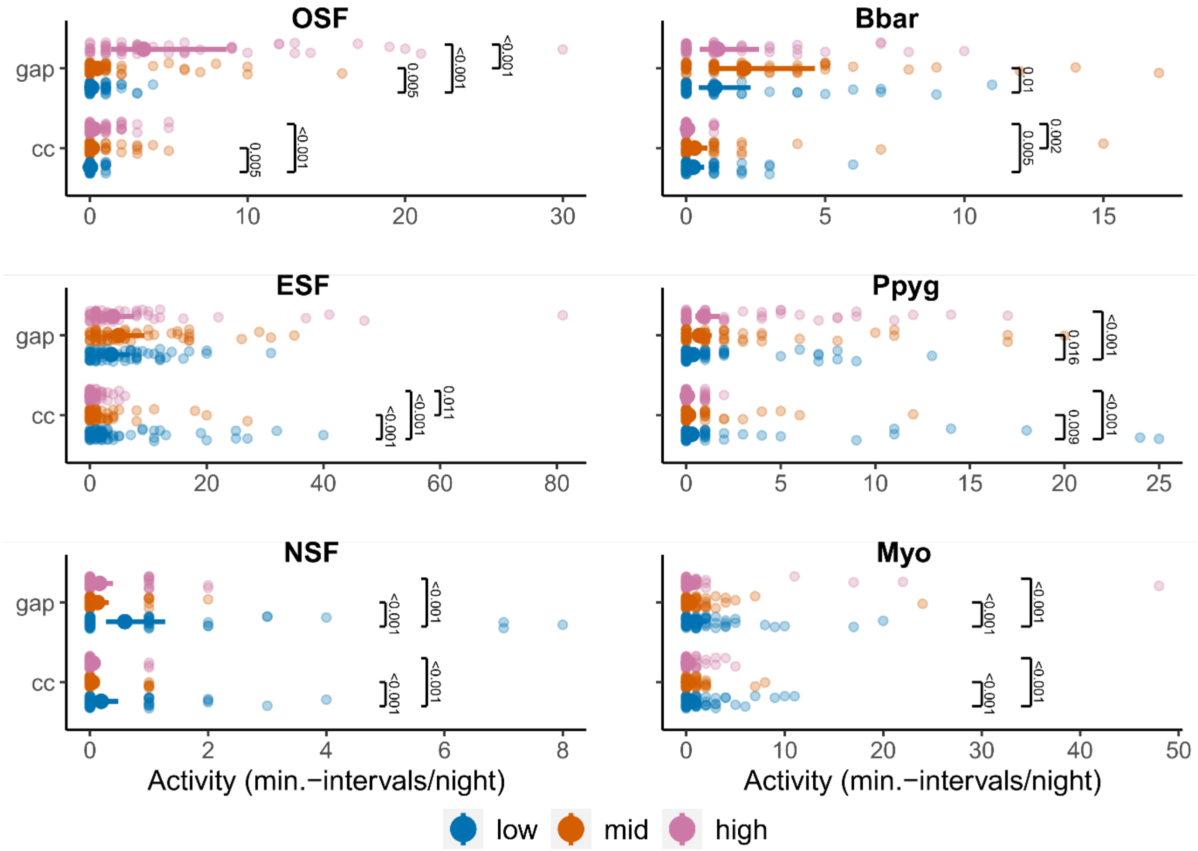

FIGURE 3.4 Estimated marginal means from the GLMMs for bat guild and species activity with 95% confidence levels as errorbars. Raw activity data are plotted as transparent points in the background. For *OSF*s, the highest datapoint (69 minute-intervals/night) was excluded from the plot for a better visualisation. Significances of contrasts were corrected using Tukey´s post-hoc test for multiple comparisons. *OSF*: open-space foragers, *NSF*: narrow-space forager, *ESF*: edge-space forager, Myo: *Myotis* spec. (*Myotis brandtii* and undefined *Myotis* spec. combined), Bbar: *B. barbastellus*, Ppyg: P. *pygmaeus*. Coloured bars indicate the three batcorder heights low (blue), mid (orange) and high (rose).

not influencing Barbastelle activity (Table 3.2). Soprano pipistrelles made up 33% of the *ESF* activity. They showed an overall activity pattern similar to the one described for the *ESF* guild as a whole. The best fitting model showed a differing height activity pattern between gaps and the forest interior (Table 3.2). Soprano pipistrelles used the whole vertical canopy spectrum in canopy gaps, with significant higher activity levels in the highest layer (Figure 3.4). In the forest interior, however, their activity was restricted to the ground, with significant lower activity levels recorded both for the mid and high heights (Figure 3.4). Soprano pipistrelles preferred hunting in broadleaved forests; their activity levels in mixed coniferous forests were negligible (EMMs 0.056 ± 0.02 min-intervals/ night; Table 3.2; Figure 3.4). Mean nighttime temperatures had a positive influence on soprano pipistrelles' activity levels (Table 3.2). *Myotis* species showed equal activity levels in canopy gaps and in the forest interior and they significantly preferred hunting in broadleaved forests (Table 3.2). Considering height segregation, *Myotis* species were most active at the ground (Figure 3.4). *Myotis* activity was increasing with increasing nighttime temperature (Table 3.2).

TABLE 3.2 Fitted effects of forest structure parameters on the activity of bat guilds and dominant species/species groups.

		height [mid]	height [high]	structure [gap]	habitat [C]	period [II]	temp	height [mid] * period [II]	height [high] * period [II]	height [mid] * structure [gap]	height [high] * structure [gap]	structure [gap] * period [II]	structure [gap] * height [mid]	structure [gap] * height [high]
OSF	*IRR ± SE*	7.47 ± 6.34	29.31 ± 23.62	2.76 ± 2.45	3.28 ± 2.32	4.9 ± 3.89	1.13 ± 0.03	0.55 ± 0.45	0.09 ± 0.07	0.73 ± 0.38	3.42 ± 1.76	2.38 ± 0.91		
	Stat.	2.37	4.19	1.14	1.68	2	4.17	-0.73	-3.18	-0.6	2.38	2.27		
	p	**0.018**	**<0.001**	0.254	0.094	**0.045**	**<0.001**	0.464	**0.001**	0.549	**0.017**	**0.023**		
ESF	*IRR ± SE*	0.44 ± 0.12	0.32 ± 0.09	2.02 ± 0.95	0.2 ± 0.09	1.52 ± 0.31	1.06 ± 0.02	1 ± 0.27	0.43 ± 0.12	3.07 ± 0.85	5.21 ± 1.59			
	Stat.	-3.04	-3.96	1.5	-3.53	2.05	2.54	0.01	-2.99	4.07	5.39			
	p	**0.002**	**<0.001**	0.135	**<0.001**	**0.041**	**0.011**	0.992	**0.003**	**<0.001**	**<0.001**			
NSF	*IRR ± SE*	0.22 ± 0.07	0.28 ± 0.09	6.75 ± 4.59	0.66 ± 0.37	3.23 ± 1.67	1.03 ± 0.05					0.21 ± 0.13		
	Stat.	-4.5	-4.09	2.81	-0.73	2.27	0.61					-2.61		
	p	**<0.001**	**<0.001**	**0.005**	0.466	**0.023**	0.541					**0.009**		
Bbar	*IRR ± SE*	1.17 ± 0.4	0.18 ± 0.1	3.99 ± 2.49	0.85 ± 0.49	1.6 ± 0.35	1.01 ± 0.03						1.72 ± 0.71	6.05 ± 3.69
	Stat.	0.47	-3.14	2.23	-0.28	2.15	0.29						1.31	2.95
	p	0.636	**0.002**	**0.026**	0.783	**0.031**	0.772						0.19	**0.003**

Note: All generalized linear mixed models were fitted assuming negative-binomial distributions. Random effects: subplot=16 levels, 388 observations. Significant effects are shown in bold. IRR=incidence rate ratio, SE=standard error. Habitat mixed coniferous (C) compared against broadleaved, heights (mid, high) compared against ground, structure (canopy gaps against the forest interior), sampling period I against period II. Temp = mean night-time temperature.

Ppyg	*IRR ± SE*	0.64 0. ±	0.45 ±	1.17 ±	0.05 ± 0.02	5.99 ± 1.82	1.11 ±	0.43 ±	0.19 ± 0.08	4.68 ± 1.69	13.34 ±	
		0.26	0.21	0.59			0.03	0.17			5.73	
	Stat.	-1.08	-1.74	0.32	-6.37	5.9	3.45	-2.12	-4.05	4.28	6.03	
	p	0.279	0.081	0.746	**<0.001**	<0.001	0.001	0.034	**<0.001**	**<0.001**	**<0.001**	
Myotis	*IRR ± SE*	0.51 ±	0.67 ±	2.76 ±	0.11 ± 0.06	1.14 ± 0.42	1.11 ±	0.74 ±	0.33 ± 0.14			0.41 ±
		0.15	0.2	1.57			0.04	0.31				0.16
	Stat.	-2.23	-1.37	1.79	-4.08	0.37	2.63	-0.72	-2.57			-2.27
	p	**0.026**	0.172	0.074	**<0.001**	0.713	**0.009**	0.473	**0.01**			**0.023**

Note: All generalized linear mixed models were fitted assuming negative-binomial distributions. Random effects: subplot=16 levels, 388 observations. Significant effects are shown in bold. IRR=incidence rate ratio, SE=standard error. Habitat mixed coniferous (C) compared against broadleaved, heights (mid, high) compared against ground, structure (canopy gaps against the forest interior), sampling period I against period II. Temp = mean night-time temperature.

NSF bats were recorded in 18% of recording nights. They were significantly more active at the ground compared to mid-and high-canopy layers and did not show any preference for a certain forest type (Figure 3.4). *NSF* activity levels in canopy gaps were higher than in the forest interior and were not influenced by mean nighttime temperatures (Table 3.2). *NSF*s were dominated by *Myotis nattereri*, with 89% of all *NSF* call sequences from this species.

A clear pattern evident from the nonmetric multidimensional scaling was the species segregation between broadleaved and mixed coniferous plots, which mainly spread along the first NMDS axis explaining the greatest variance (Figure 3.5A; stress values of 0.14 with k = 3 dimensions and a maximum of 5 00 permutations starting from the previous best solution). The resulting linear fit (R^2) was 0.883. Nyctaloids were associated mainly with mixed coniferous plots, while *Myotis* and *Pipistrellus* species were more closely linked to broadleaved plots. The NMDS plot did not show a segregation between canopy structures (Figure 3.5B). Canopy height was depicted as a gradient in Figure 3.5C using a contour plot with isolines representing identical height levels. A clear transition from *N. noctula* and *E. nilssonii* over the *nyctaloid*s (active at the highest canopy) to *M. brandtii* and *Myotis* spec. (most active at the ground) became apparent. Barbastelle bats, Pipistrelle bats, and Natterer's bats were occupying intermediate height positions in ordination space (Figure 3.5C).

3.4.3 Seasonal activity pattern

OSF species showed higher activity levels in the second period considered except for the highest canopy layer. Here, activity levels did not differ between periods (canopy gaps) or were higher in period I (forest interior; Figure 3.6). The *ESF* guild showed a tendency toward higher activity levels in period II with a significant increase only in the ground layer (Figure 3.6). For *ESF* species, we considered the dominating species separately. Barbastelle bats showed a tendency toward a higher activity in period II with no differences between height layers or canopy structures (Figure 3.6). Soprano pipistrelles showed activity increases in the second period for mid-and low-canopy layers (Figure 3.6). *Myotis* species were the only group to show significantly higher activity levels in the first period considered, for all height levels in canopy gaps and for the highest canopy layer in the forest interior (Figure 3.6). *NSF* species revealed seasonal activity shifts depending on the canopy structure. Activity was significantly higher in period II in the forest interior but did not show seasonal variations in canopy gaps (Figure 3.6).

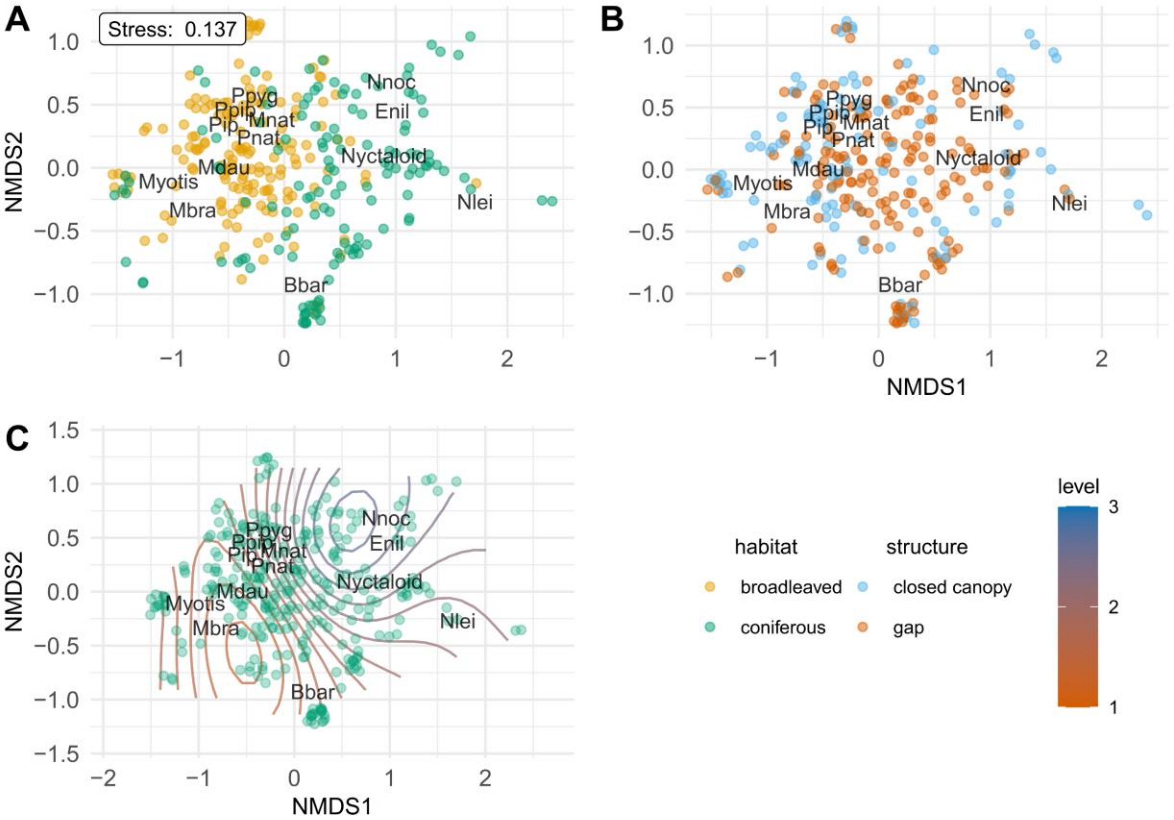

FIGURE 3.5 NMDS plots showing 2 of 3 dimensions for A) habitat, B) canopy structure and C) height levels depicted as isolines (levels1-3). Bbar = *Barbastella barbastellus*, Enil = *Eptesicus nilssonii*, Mbra = *Myotis brandtii*, Mdau = *M. daubentonii*, Mnat = *M. nattereri*, Pip = *Pipistrellus* spec., Ppip = *P. pipistrellus*, Ppyg = *P. pygmaeus*, Nlei = *Nyctalus leisleri*, Nnoc = *N. noctula*.

3.5 Discussion

In studies dealing with the vertical stratification of temperate bat communities, sampled woodlands differ in structure and tree species, and have led to ambiguous or contrasting results even in Europe under similar climatic conditions and with comparable bat species assemblages (Plank et al. 2012, Mueller et al. 2013, Froidevaux et al. 2014). In accordance with our hypotheses, our study demonstrates differential guild-and species-dependent height use by insectivorous bats in a lowland temperate old-growth forest. We show that restricting acoustic bat sampling to the ground layer leads to a strong bias in most of the species' activities and to wrong conclusions considering their habitat needs. Moreover, we identified a generally higher activity during the postlactation period for all species groups except *Myotis* spec. and *Myotis nattereri* and found species-specific seasonal activity differences in height and canopy structure use.

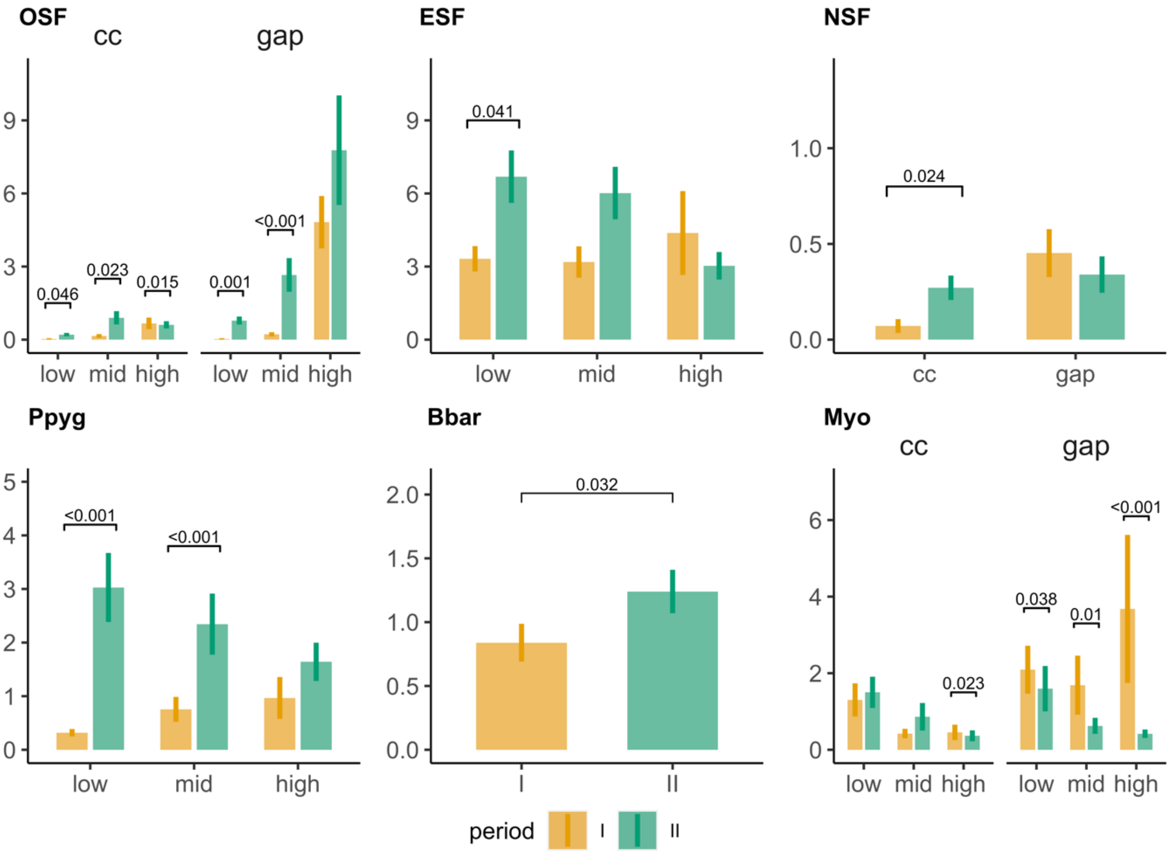

FIGURE 3.6 Seasonal mean night-time activity changes in bat guilds and dominating ESF species with error bars indicating standard errors. Significant effects were fitted in GLMMs with negative-binomial distributions and corrected for multiple comparisons using Tukey´s post-hoc test. OSF: open-space forager, ESF: edge-space forager, NSF: narrow-space forager, Ppyg: *Pipistrellus pygmaeus*, Bbar: *Barbastella barbastellus*, Myo: *Myotis* spec.

Acoustic surveys have shortcomings that need to be addressed. We synchronously sampled canopy gaps largely void of vegetation and the forest interior, where vegetation clutter creates a completely different habitat type. This induces differences in detection probability of bat calls within the same species. However, we paid attention to place batcorders in a way that their omnidirectional ultrasonic microphones were completely surrounded by free space on a hypothetical sphere of 10 m diameter with the microphone at its centre. This is important since Yates and Muzika (2006) and Bender et al. (2015) found vegetation clutter to be more important than detection probability for bat occupancy. We are therefore confident that differences in detection probability are only a minor factor influencing our results.

As expected, vertical stratification in bat activity was most pronounced in the forest interior. In forest gaps, the absence of physical constraints such as vegetation clutter caused a vertically more uniform height use pattern. Our findings corroborate studies from Adams et al. (2009) and Tiago Marques et al. (2016) who found stronger stratification in bat activity in the forest interior compared to forest edges. This edge-interior gradient in vertical height stratification was also found for saproxylic beetles (Vodka and Cizek 2013). Indeed, bat activity in the forest interior is mainly determined by the interaction of habitat accessibility and prey availability, whereas in open spaces such as forest gaps prey availability is the major factor driving bat activity (Adams et al. 2009, Tiago Marques et al. 2016). In contrast to Adams et al. (2009) who found generally higher activity levels in the subcanopy and canopy of the forest interior, we recorded guild-and species-mediated activity patterns. Our study further indicates habitat-dependent differences in activity levels, which highlights the role of plant species assemblages for the identification of animal–habitat relationships. This is in line with a study by Adams and Matthews (2019) on forest birds, where the influence of plant species on bird assemblages was stronger than the influence of vegetation structure. Penone et al. (2019) found that forests with a higher proportion of oak trees were more species-rich considering forest bats than forests with a high proportion of coniferous trees. These studies show that plant species composition can integrate aspects of structural vegetation features, potential prey availability, and roosting opportunities. Therefore, plant species composition should be considered alongside structural vegetation heterogeneity when studying bat–habitat interactions.

Our results confirm that the free space above the forest canopy is used by *OSF* species (Kalcounis et al. 1999, Adams et al. 2009, Mueller et al. 2012, 2013). This habitat is especially exploited by large *nyctaloid*s independent of the canopy structure or habitat type below them (Fukui et al. 2011, Erasmy et al. 2021). Free space within forest gaps, which is restricted in size and differs in microclimatic conditions from the aerosphere above the canopy, may represent adequate foraging habitats for smaller *nyctaloid*s like *E. nilssonii* or *P. nathusii* diving into them especially at high and mid heights.

Species from the *ESF* group clearly differed in their vertical height use concurrent with results from Plank et al. (2012) and Mueller et al. (2013), while Adams et al. (2009) did not detect profound differences in stratification pattern between *ESF* species. This finding shows the limitations of the guild concept masking species-specific habitat preferences. Barbastelle bats preferred the upper layers in the canopy gaps. Gap edge structures along tree crowns and the free space in gaps at mid and high heights probably offered highly profitable occurrences in lepidopteran prey (Rydell et al. 1996, Sierro and Arlettaz 1997). Burford et al. (1999) and Carr et al. (2020), however, found moth species richness, occurrence, and abundance to be positively related to vegetation clutter, but Barbastelle bats—as large and rather fast flying *ESF*s—are precluded from cluttered vegetation. In the forest interior, their activity was four times lower compared to canopy gaps and restricted to the lower two layers where limited hunting possibilities were available. P. *pygmaeus* was virtually absent from mixed coniferous habitats, and conclusions on their height use were thus deduced from their activity recorded in broadleaved forests. In the forest interior, soprano pipistrelles were mainly active near the ground with comparable activity levels at gap ground levels. Since these bats are known to forage within the vegetation, we think that this forest layer offered the highest amount of their preferred dipteran prey (Bartonicka et al. 2008). In gaps, these bats were able to fully use the edge and open gap space over the whole vertical height spectrum, with a preference for the tree crowns as highly lucrative microhabitat. We consider the *Myotis* spec. group as consisting mostly of *Myotis brandtii* (Rachwald et al. 2001, 2021, Dombrovski et al. 2017, Dietz et al. 2018, Erasmy et al. 2021). Brandt's bats were generally confined to the lowest layer with the highest activity levels in broadleaved gaps. Near the ground, their activity levels in gaps were nearly twice the activity levels in the forest interior. Their diet consists to a large extent of lepidopterans (Vesterinen et al. 2018), but dipterans and spiders, an indication for their gleaning foraging mode, have also been identified as main prey items (Taake 1992). Their predominant activity at low heights in the absence of vegetation clutter in gaps may be mainly mediated by prey availability.

A similar confinement to the ground layer in gaps was found for the *NSF* guild, namely *M. nattereri*. In contrast to *M. brandtii*, however, *M. nattereri* also hunted in mixed coniferous stands. These results contrast findings by Smith and Racey (2008) and Erasmy et al. (2021) who identified a strong preference for broadleaved forests for this species, but are in accordance with Siemers et al. (1999) who found Natterer's bats hunting indifferently in different habitat types. This contradiction might be caused by ephemeral accumulations of suitable prey in the coniferous stands. Gleaning is the main foraging strategy of Natterer's bats (Swift and Racey 2002). They are able to hunt close to vegetation and to very efficiently localize silent prey sitting on leaves and branches (Arlettaz 1996, Siemers and Schnitzler 2000, Siemers and Swift 2006). We therefore think that Natterer's bats in our study used low vegetation structures such as regenerating trees and low shrub vegetation in the forest interior to hunt on largely immobile prey (Siemers and Swift 2006).

Seasonal activity patterns in temperate bats are shaped by two different mechanisms. The first mechanism is directly linked to the bats' lifecycles. Energy demands especially of reproductive females change from pregnancy over lactation to weaning with a peak during lactation (Shiel et al. 1999). Newly volant young generally lead to an increase in the number of hunting bats in July and August (Russ et al. 2003). In early autumn, mating behaviour influences nightly spatial and temporal activity patterns, while the need to accumulate fat reserves for hibernation increases the energy demands (Ciechanowski et al. 2010). Secondly, arthropod lifecycles and their temperature dependency cause variations in prey occurrences and abundances and this way influence bat seasonal activity (Wang et al. 2010, Höhne and Dietz 2012, Mueller et al. 2012, Roeleke et al. 2018, Salvarina et al. 2018).

In concurrence with our results, Shiel et al. (1999), Russ et al. (2003), Bartonicka et al. (2008), Ciechanowski et al. (2010) and Lucan and Radil (2010) also found higher activity levels during the postlactation period. In our study, soprano pipistrelles and Brandt's bats were the only bats with seasonal height or canopy use shifts. P. *pygmaeus* increased their activity during postlactation especially near the ground. Bartonicka et al. (2008) found the occurrence of certain prey groups (Neuroptera and Simulidae) to positively influence soprano pipistrelle activity increases in forest sites during postlactation. Staton and Poulton (2012) in contrary found P. *pygmaeus* activity during postlactation to be precluded to the forest canopy. Interspecific competition especially with the very similar P. *Pipistrellus* is one further factor possibly influencing habitat use and therefore also height use (Davidson-Watts et al. 2006, Roeleke et al. 2018).

For *Myotis brandtii*, higher activity levels were recorded during pregnancy and lactation, a seasonal pattern opposite to the other bat species considered. Activity peaks in gaps changed from the highest canopy layer during lactation to the ground layer during postlactation. Moreover, Brandt's bats' high activity levels in forest gaps during lactation decreased during postlactation. This decrease in gaps was accompanied by a slight activity increase in the forest interior. A seasonal preference for the forest interior was also found for *NSF* species. *Myotis* species are adapted to aerial hawking or gleaning in cluttered vegetation. Their activity shifts to the forest interior during postlactation could be in accordance with the arguments of Plank et al. (2012) that lactating (and postlactating) females are more agile and better able to exploit cluttered habitats than pregnant females.

3.6 Conclusions

The need to incorporate three-dimensional structural heterogeneity in habitat–animal diversity studies has been acknowledged for different organisms (Vodka and Cizek 2013, Carrasco et al. 2019, Langridge et al. 2019, Penone et al. 2019, Heidrich et al. 2020). Even though many studies have dealt with the role of forest structure on bat species or species groups, no clear image has yet emerged. Our study tries to complement the present picture with a focus on vertical (height in tree) and horizontal (forest interior vs. forest gaps) aspects of structural diversity. Species-dependent differences in height and structure use become evident. Our study clearly shows that for a thorough understanding of the way bats are using forests, it is essential (i) to include the upper forest strata in the analysis, (ii) to consider seasonal changes in microhabitat use, and (iii) to focus on bat species, rather than considering bat guilds.

Recent rapid changes in European forests due to climate warming-related stress and vitality loss will expose forest biota to enormous challenges and intensify the need for the adaptation of silvicultural concepts. In addition, wind turbines are increasingly built in Europe's forests, which will alter the space that can be exploited by forest bat communities. A thorough understanding of the interaction between bats, forest structure, and tree species composition is essential for predicting future changes in forest bat populations and bat communities and for advising related conservation efforts.

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3.8 Conflict of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

3.9 Author contribution

Maude Erasmy: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Christoph Leuschner**: Funding acquisition (supporting); Supervision (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Niko Balkenhol**: Supervision (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Markus Dietz**: Conceptualization (supporting); Project administration (lead); Resources (supporting); Supervision (equal); Writing-original draft (supporting); Writing-review & editing (supporting).

3.10 Data availability statement

Labeled raw data for all analyses are made publicly available in the Dryad Digital repository https://doi.org/10.5061/dryad.cjsxk sn6m.

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3.12 Appendix

Table A 3.1 Sampling effort for the two time periods considered for each habitat, canopy structure and canopy height. N subplots refers to the number of subplots sampled for each habitat category.

Habitat	Structure	Height	Period I	n subplots period I	Period II	n subplots period II
Broadleaved	Closed canopy	Low	17	4	16	3
		Mid	17	4	17	3
		High	17	4	15	3
	Gap	Low	17	4	16	3
		Mid	17	4	14	3
		high	13	3	16	3
Mixed coniferous	Closed canopy	Low	16	4	18	3
		Mid	16	4	12	3
		High	16	4	18	3
	Gap	Low	16	4	21	3
		Mid	15	4	18	3
		high	15	4	15	3
SUM			192		198	

Table A 3.2 Differences in AICc-values for the candidate model sets. Final models chosen are shown in bold.

	Candidate model	OSF	ESF	NSF	Ppyg	Bbar	Myo
1	~ height*period + struc + hab + mean	12.5	30.5	5.8	37.9	9.3	3.4
2	~ height*struc + period + hab + mean	29.7	8.6	7.8	14.2	0.8	8.6
3	~ height*hab + struc + period + mean	14.5	29.4	8.6	36.2	9.8	7.7
4	~ structure*hab + period + height + mean	40.7	38.3	7.6	50.2	8.9	8.3
5	~ struc*period + hab + height + mean	39.6	33.3	0.6	42.3	3.2	2.9
6	~ height + hab + struc + period + mean	39.2	37.1	6.5	48.3	6.8	6.2
7	~ height:period + struc:height + struc + height + period + hab + mean	3	1.6	7.6	2.0	2.9	5.9
8	~ height:period + struc:height + struc:period + struc + height + period + hab + mean	0	0	3.0	0	0	2.8
9	~ height:period + period:struc + period + struc + hab + mean	13.3	28.5	0	55.7	6.1	0
	conditional R^2	0.802	0.740	0.482	0.744	0.668	0.638
	marginal R^2	0.543	0.503	0.266	0.644	0.405	0.403

Note: Conditional and marginal R^2-values calculated using the Nakagawa-equation from the performance package (Nakagawa and Schielzeth 2013, Lüdecke et al. 2021). All models with subplot (n=16) as random effect, and n=388 observations. Height=batcorder-position (low/mid/high), period=sampling season, (I=pregnancy/lactation, II=postlactation), struc=canopy structure (gap/closed canopy), hab=habitat (broadleaved/mixed coniferous), mean=mean night-time temperature.

TABLE A 3.3 Summary statistics for minute-intervals activity per night for all bat guilds and dominant *ESF* bat species.

		ALL			OSF			ESF			NSF		
	height	mean	CI	sum	mean	CI	sum	mean	CI	sum	mean	CI	sum
broadleaved closed canopy	high	1.7	0.9	54	0.4	0.4	14	1.2	0.6	39	0.0	0.1	1
	mid	4.1	2.2	141	0.0	0.1	1	4.0	2.2	137	0.1	0.1	3
	low	9.8	3.7	322	0.1	0.1	2	9.3	3.7	308	0.4	0.3	12
broadleaved gap	high	20.6	10.2	597	7.7	5.1	223	12.6	6.8	365	0.3	0.2	9
	mid	10.0	3.6	309	0.3	0.2	9	9.6	3.6	297	0.1	0.1	3
	low	10.4	2.4	342	0.2	0.2	5	9.1	2.4	299	1.2	0.7	38
coniferous closed canopy	high	1.2	0.5	40	0.8	0.4	28	0.3	0.2	10	0.1	0.1	2
	mid	1.6	0.8	45	1.1	0.6	30	0.4	0.3	12	0.1	0.1	3
	low	1.4	0.6	46	0.2	0.1	6	0.8	0.4	28	0.4	0.3	12
coniferous gap	high	6.9	2.0	206	5.1	1.6	153	1.6	0.7	47	0.2	0.2	6
	mid	6.5	2.7	216	2.5	1.4	83	3.9	1.7	128	0.2	0.2	5
	low	2.7	1.0	99	0.7	0.3	25	1.6	0.7	59	0.4	0.4	15

		Bbar			Ppyg			Myotis		
	height	mean	CI	sum	mean	CI	sum	mean	CI	sum
broadleaved closed canopy	high	0	0	0	0.3	0.2	9	0.8	0.5	26
	mid	1.1	1.0	37	1.2	0.8	42	1.1	0.6	36
	low	0.7	0.5	22	4.2	2.5	139	2.5	1.1	84
broadleaved gap	high	2.1	1.1	60	4.7	1.8	137	3.8	3.8	111
	mid	1.9	0.8	58	4.4	2.0	137	2.0	1.6	63
	low	1.4	0.9	45	2.8	1.2	94	3.5	1.7	114
coniferous closed canopy	high	0.1	0.1	5	0.1	0.1	4	0.0	0.1	1
	mid	0.3	0.2	7	0.0	0.1	1	0.1	0.1	3
	low	0.4	0.3	13	0.0	0.0	0	0.3	0.2	10
coniferous gap	high	0.6	0.4	19	0.5	0.3	14	0.2	0.1	5
	mid	3.0	1.5	99	0.4	0.2	12	0.3	0.2	11
	low	1.1	0.7	39	0.1	0.1	3	0.4	0.2	14

Note: *OSF* = open-space forager, *ESF* = edge-space forager, *NSF* = narrow-space forager. Bbar = *B. barbastellus*, Ppyg = *P. pygmaeus*, *Myotis* = *Myotis* spec. except *M. nattereri*.

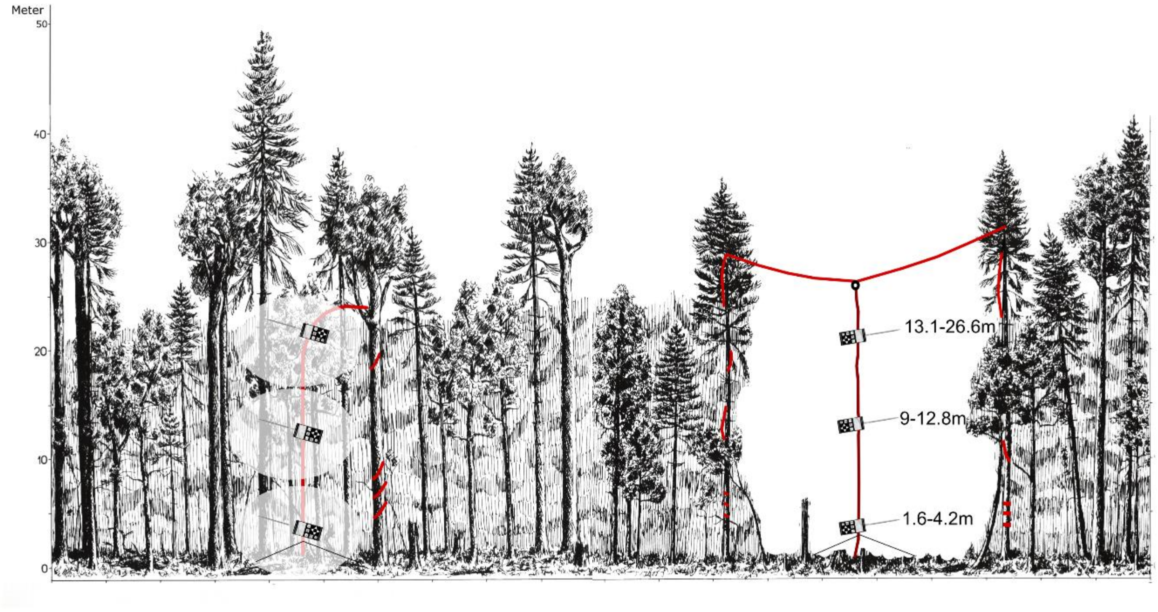

Figure A 3.1 Batcorder chain setup in canopy gaps and in the forest interior, exemplary for a broadleaved plot. Figure changed after Falinski (1986). In canopy gaps, batcorder were mostly hung up using a line spanning between two trees on each side of the gap. Batcorders were pulled up using a pulley. In the forest interior, mostly only one tree branch was necessary to pull up the batcorders attached to a string. Side strings fixed to tent pegs prevented the batcorder chain from moving around.

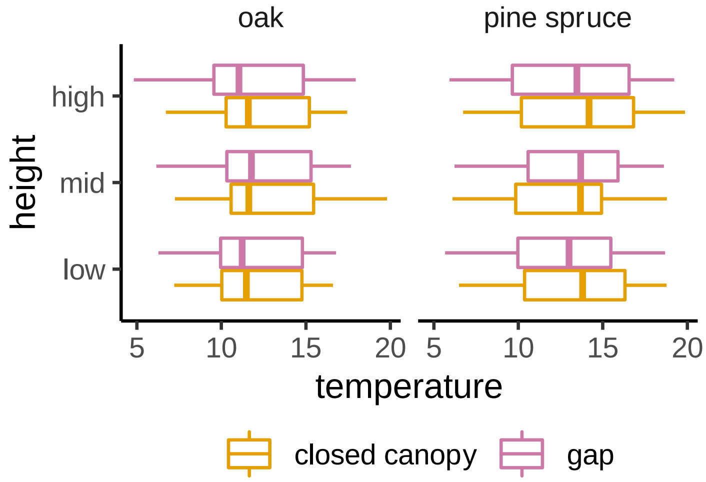

Figure A 3.2 Mean night-time temperatures for the two habitat types, two canopy structures and for the three canopy strata sampled.

CHAPTER 4

4 Bat diversity in a temperate lowland forest reserve: the importance of unmanaged stands for hunting and roosting

4.1 Abstract

Intact forest ecosystems play an essential role not only for protecting biodiversity, but also for mitigating climate change through storage of carbon in biomass and soil. However, globally increasing demands for timber as a raw material in industry and construction and for replacing fossil fuels as a renewable energy source increase the pressure on intact forests worldwide. In order to conserve forest biodiversity while sustaining timber yield, we need a better understanding of forest management effects on forest structure and function. A characteristic element of temperate forest biodiversity are bats, who rely on forests both for hunting and roosting. However, it is not well known how changes in forest structure are influencing their habitat use and roosting availabilities.

We analysed differences in forest bat diversity between managed and unmanaged forest stands of the Belovezhskaya Pushcha natural forest complex in Belarus using Rényi-diversity profiles. Further, we compared acoustically recorded activities of the four most abundant strict forest species *Barbastella barbastellus*, *Myotis brandtii*, *M. nattereri* and *Pipistrellus pygmaeus* between management types. Finally, we extracted species-specific roosting associations to tree-related microhabitats in a meta-analytical framework for these four forest bat species.

Bat diversity was more strongly influenced by management type than by forest habitat type, while the opposite was true for the four bat species' activity patterns. Habitat homogenization in managed forests led to lower evenness compared to unmanaged stands. We found narrow roosting niches for *B. barbastellus* and *M. nattereri*. *B. barbastellus* preferred roosting behind the loose bark of snags, while *M. nattereri* was predominantly roosting in cavities or crevices of vital broadleaved trees.

Our study supports the hypothesis that forest structural heterogeneity increases bat diversity in temperate forests. Apart from maintaining forest structural heterogeneity, the retention of snags and large old trees provides a variety of microhabitats essential for the roosting needs of a diverse forest bat community.

4.2 Introduction

The increasing demand for forest products has led to a dramatic loss and the fragmentation of forested ecosystems worldwide (FAO and UNEP 2020). However, ecosystem service provisioning is supported by, and partly dependent on, biodiversity and intact communities (Kaňuch et al. 2008, Thompson et al. 2011, Duncker et al. 2012b, Harrison et al. 2014, Krumm et al. 2020). In the face of recorded declines in forest biodiversity and continuing threat through climate change, there is a vital debate on the introduction of climate-smart forestry and close-to-nature forest management to address these challenges (Brang et al. 2014, Aggestam et al. 2020, Verkerk et al. 2020). Besides the adoption of a more biodiversity-friendly forest management such as the retention forestry approach (Lindenmeier et al. 2012), the preservation of unmanaged forests in protected areas e.g. as forest national parks is of primary importance, where natural processes and dynamics can take place on a large area untouched by man (Rivard et al. 2000, Gurd et al. 2001, Gaston et al. 2008, Ma et al. 2020, Häkkilä et al. 2021).

Forest management in Europe encompasses a variety of harvesting systems and rotation periods (Duncker et al. 2012a, Cardellini et al. 2018, Härkönen et al. 2019). Management practices often induce severe changes in biodiversity, since vertical and horizontal forest structures are simplified and natural processes and dynamics are disrupted (e.g. Paillet et al. 2010, Lelli et al. 2019). Most European bat species are considered to be specialised on forested habitats for at least one part of their life cycle (Meschede and Heller 2000, Dietz et al. 2009, Russo et al. 2016). In the last few years, impacts of forest management on insectivorous bats in Europe have been brought to the focus of research interest. Bouvet et al. (2016) found a general increase in bat species richness of edge-space foragers with increasing deadwood volumes in French forests. Renner et al. (2018) detected higher bat species richness in vertically and horizontally heterogeneously structured forests, and forest structural parameters differently influenced species richness within different functional groups considered. Similarly, in the study of Starik et al. (2018), bat species richness and bat diversity were highest in structurally complex coniferous and mixed forests. Singer et al. (2021) observed that tree-dwelling Bechstein´s bat *Myotis bechsteinii* and woodpecker species selected forest patches with above-average quantities of old-growth-related habitat structures. Alder et al. (2020) found bat species richness to be highest in irregular high forest stands compared to coppice and limited intervention forests. According to Carr et al. (2020a) species richness and activity levels of common and adaptable bat species are higher in thinned woodlands, but negative effects of thinning prevail on rarer and wood-dwelling species such as the Western barbastelle *Barbastella barbastellus*. A direct comparison of these studies is however difficult due to the wide spectrum of management treatments and forest types considered.

A number of studies, especially from the United States, identified positive effects of management activities such as thinning or clear-cutting on bats (Patriquin and Barclay 2003, Silvis et al. 2016, Brooks et al. 2017, Bender et al. 2021, Wright et al. 2021). However, even while some thinning practices prove to be beneficial in the short term for e.g. open-space or edge-space foragers by increasing free foraging space and edge structures, two issues have to be addressed. Firstly, most studies dealing with bats and management practices solely rely on activity or species richness differences. However, species richness does not capture functional diversity, the role of dominant or characteristic species or changes in community structure (Lelli et al. 2019). For example, Kirkpatrick et al. (2017) report a marked positive influence of clear-cuts in non-native pine plantations only on open-space *Nyctalus* species, but not on other species. Secondly, most studies considering the influence of forest management on bats do not consider how management activities change tree roost availability. Tree cavities, crevices and loose bark as tree-related microhabitats (TreMs) constitute essential resources for tree-roosting bats. These TreMs are known to be affected both in density and diversity by management practices (Kozak et al. 2018, Asbeck et al. 2019, Paillet et al. 2019, Asbeck and Kozák 2021, Courbaud et al. 2021). Effects of TreMs on bat activity and diversity can be direct by providing more roosting opportunities. Indirectly, insect abundance and diversity may increase, and the more diversely structured habitats thus offer more foraging niches. Consequently, TreMs have been shown to be connected to bat diversity (Regnery et al. 2013, Paillet et al. 2018, Singer et al. 2021). The concept of functional guilds segregating bats according to their ecomorphological adaptations is frequently used in bat research especially in studies relying on acoustic data (Denzinger and Schnitzler 2013). A separation of bats into functional roosting guilds would create an additional tool to consider bat needs both in relation to hunting and roosting (Drake et al. 2020).

We studied the impact of forest management on bat diversity in one of the last remaining large and unfragmented temperate lowland old-growth forests, the Belovezhskaya Pushcha National Park (*BPNP*) in Belarus. We compared uneven-aged heterogeneously structured unmanaged forest stands with mature (>50 years) even-aged thinned coniferous stands. We utilised Rényi-diversity-profiles to compare habitats. We furthermore focused on four tree roosting and forest hunting species especially abundant in the Belovezhskaya Pushcha (*BP*), but with a European-wide range: *Barbastella barbastellus*, *Pipistrellus pygmaeus*, *Myotis brandtii* and *Myotis nattereri*. *B. barbastellus* is thought to have its distribution centre in this forest complex (Dietz et al. 2018, Erasmy et al. 2021a, Rachwald et al. 2022). To reveal the effects of forest management on strict forest bats, we compared bat activity in relation to forest structural parameters in nearby managed and unmanaged forest sites. We completed our analyses with a meta-analysis, combining own data with literature data in order to elucidate differences in tree roost requirements for the four bat species considered. We expected

i) generally reduced biodiversity metrics in managed forests due to a homogenization of stand structure

ii) ii) higher activity levels with higher stand structural heterogeneity

iii) iii) species-related activity differences to depend on forest structure variables

iv) iv) species-specific niche differentiation in tree roost characteristics.

4.3 Methods

4.3.1 Site description

The study took place in the Belovezhskaya Pushcha National Park (*BPNP*), Belarus. *BPNP* is part of a large forest complex (~150,000 ha) that stretches beyond the Polish-Belarussian border and is considered to be one of the last and largest remaining old-growth forests of the Central European lowlands (Sabatini et al. 2018, Jaroszewicz et al. 2019, but see Mikusinski et al. (2018) for recent conservation issues and Bobiec (2012) for an evaluation of anthropogenic impacts on the Polish side of the forest complex). The forest lies at the intersection of boreal and nemoral influences at the South-western extension of the oak-hornbeam dark-coniferous forests of the Eurasian taiga zone (Tsvirko and Grummo 2020). Its forest communities are thus marked by boreal influences, such as the presence of *Picea abies* (L.) H. Karst. (Norway spruce) at the Southwestern border of its continuous boreal distribution range (Caudullo et al. 2016), as well as by nemoral influences represented by the deciduous forest associations present (Grummo et al. 2019). Forest communities of *BPNP* are dominated by Scots pine (*Pinus sylvestri*s L.) in the vegetation class Vaccinio-Piceetea (64.4% of the *BPNP* area), including the Querco-Pinetum association (Falinski 1986, Tsvirko and Grummo 2020). These forests are characterized by a complex vertical structure (Tsvirko and Grummo 2020). Besides alder-forests on moist sites, the Tilio-Carpinetum association is the dominating broad-leaved forest community in *BPNP* with

12.2% of the area (Tsvirko and Grummo 2020). *Acer platanoides* L. (Norway Maple), *Carpinus betulus* L. (Common hornbeam), *Quercus robur* L. (Common oak) and *Tilia cordata* Mill. (small-leaved lime) are the tree species dominating the tree layer in this association. The woodland complex of the Belovezhskaya Pushcha (*BP*) is located 134-202 m above sea level (Jaroszewicz et al. 2019) and is characterized by a subcontinental climate with mean annual temperatures of 7.3°C and 625 mm precipitation per year (Boczoń et al. 2018) (period 1985-2015).

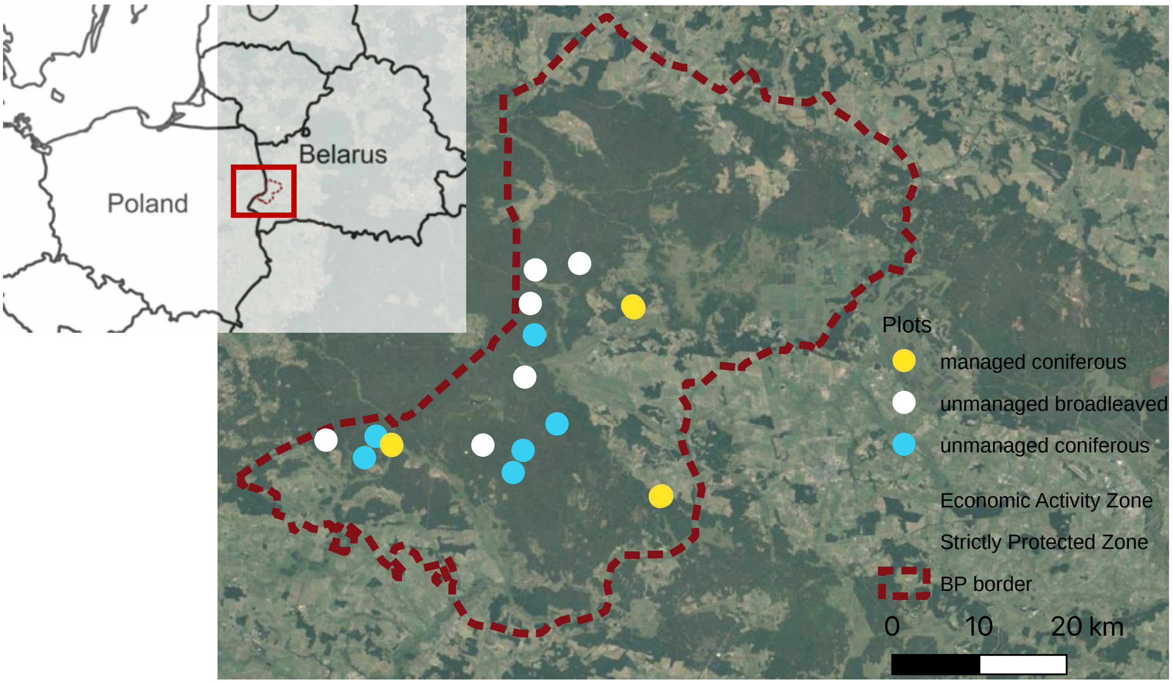

FIGURE 4.1 Location of Belovezhskaya Pushcha Nationalpark (*BP*) on the Southwestern border of Belarus, and location of the paired study plots within *BP*. Black line: country border.

The National Park is divided into five zones of differing protection status (Nikiforov and Bambiza 2008). We chose six unmanaged broadleaved plots (Tilio-Carpinetum) and six unmanaged coniferous plots (Querco-Pinetum or Tilio-Carpinetum with its *Pinus sylvestris* facies following Tsvirko and Grummo (2020)), all situated in the Strictly Protected Zone (~31,000 ha, Figure 4.1, Figure 4.2). Six managed coniferous plots (Peucedano-Pinetum) situated in the *Economic Activity Zone* (~57,000 ha) and the buffer zone of *BPNP* where management is taking place were chosen for comparison (Figure 4.1, Figure 4.2).

Since managed broadleaved plots are not present in the surroundings of *BPNP*, it was not possible to fully balance the study design. All plots were located at least 1.8 km distant from each other. To minimize edge effects and the influence of anthropogenic infrastructure, all unmanaged plots were located at least 1 km from settlements and 300 m from forest trails. The managed plots were located at least 400 m away from the next outer forest edge. Water bodies or courses were kept at a minimum distance of 500 m from our study plots. Plots were established in a paired design. In unmanaged plots, forest interior subplots were studied synchronously with adjacent naturally created gap subplots (located 159 ± 68 m from each other). This way, the structural heterogeneity of old-growth forests including small canopy gaps created by old fallen trees was considered. In managed stands, natural gaps were not present, and we restricted our analyses to two adjacent forest interior subplots (located 212 ± 63 m from each other).

Figure 4.2 Forest structure in A) unmanaged broadleaved (Tilio-Carpinetum), B) unmanaged coniferous (Querco-Pinetum/Tilio-Carpinetum facies *Pinus sylvestris*) and C) managed coniferous (Peucedano-Pinetum) plots in Belovezhskaya Pushcha National Park (*BPNP*).

4.3.2 Bat species identification

We used batcorders (EcoObs GmbH Nuremberg) to automatically record bat calls during nighttime. Batcorders were installed at 2 m from the ground with their omnidirectional ultrasonic microphones slightly angled upwards and away from vegetation, following recommendations from Weller and Zabel (2002) and Britzke et al. (2013). The internal recording mode "Auto-Timer" and the following recording settings were used during all recording nights: quality=20, threshold=-27dB, posttrigger = 400 ms, critical frequency = 16 kHz. In 2014, recordings took place from June 3 until September 10 and lasted from half an hour after sunset until half an hour before sunrise in the morning. In 2015, all-night recording sessions lasted from May 31 until September 3, and we recorded from sunset until one hour after sunrise. Due to a restricted number of batcorders, managed plots were only studied between July 26 and August 14, 2014. We used the automatic pre-identification process performed by the software BatIdent (EcoObs GmbH Nuremberg) to sort the recordings into species groups. All bat calls were manually verified using the software bcAnalyze 2 (EcoObs GmbH Nuremberg), since the combination of automatic and human identification processes has revealed to be a successful approach (López-Baucells et al. 2019). We used the manual parameters described in Erasmy et al. (2021a) (Appendix) to identify bat species.

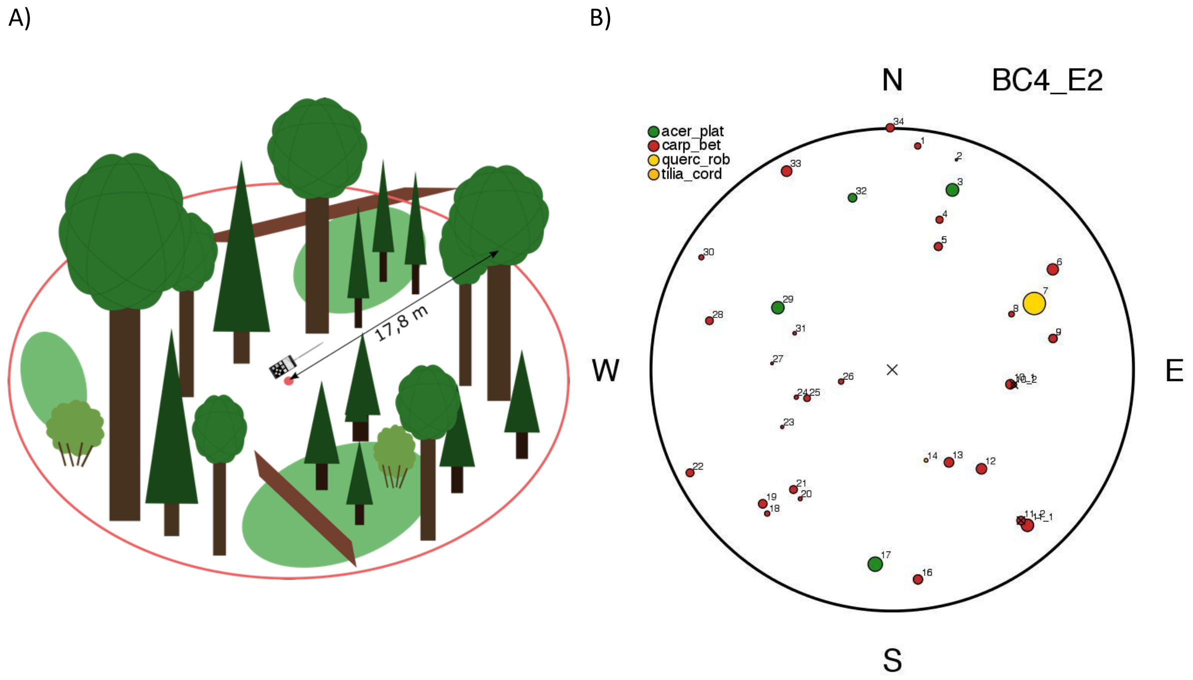

Figure 4.3 A) On 0.1 ha circular plots with the batcorders in the plot centre (red dot), forest structural variables were collected such as diameter at breast height (dbh) and tree species, B) as illustrated in an exemplary plotmap of one unmanaged broadleaved plot. The cross marks the batcorder position. The circle size of trees is proportional to their dbh and different colours represent different species. acer_plat: *Acer platanoides*, carp_bet: *Carpinus betulus*, querc_rob: *Quercus robur*, tilia_cord: *Tilia cordata*.

We restricted our analyses on species activity to calls from *P. pygmaeus*, *B. barbastellus*, *M. nattereri* and *M. brandtii*. In the forest interior, these species are mostly active near the ground (Erasmy et al. 2021b) and restricting our analyses to the ground is thus not biased. *P. pygmaeus* and *B. barbastellus* calls are easily recognizable and can hardly be confounded with other bat species. Because of their extreme long bandwidth and high frequency of maximum energy, *M. nattereri* calls were as well identifiable. We were not able to distinguish between the remaining *Myotis*-species. However, besides *M. nattereri*, only *M. alcathoe*, *M. daubentonii* and *M. dasycneme* are known to occur within the *BP* territory. *M. daubentonii* and *M. dasycneme* only rarely occur in forested areas away from water bodies (Dietz et al. 2009). For *M. alcathoe*, the few calls recorded within *BPNP* have to be verified by mist-netting. We therefore argue that not further specified *Myotis* recordings within the forest most probably belong to *M. brandtii*, a species known to occur within the territory studied (Dietz et al. 2018, Rachwald et al. 2021). All unidentified *Myotis* calls were therefore unified with *M. brandtii* calls automatically assigned to this species.

4.3.3 Stand structural data

To analyse the influence of forest structural parameters on bat activity and diversity, we measured structural parameters on plot level to be able to directly associate the present vegetation structures to the bat activity measured.

We established circular 0.1 ha plots with the batcorder in the centre (Figure 4.3). Within these plots, all trees were identified to species, their diameter at breast height (dbh) >7cm and the height of 5-14 trees/plot were measured using a Vertex III height meter (Haglöf Sweden AB). We used the non-linear regression equation reported by Petterson (1955) to predict the height of all trees not measured. The vitality of trees was assessed, and the number of cavities in each tree within the plot radius was counted. We estimated the amount of lying coarse woody debris using two perpendicular transects crossing at the plot centre (71.2 m) and by measuring the dbh of every lying stem >7cm dbh crossing these transects. The amount of coarse woody debris was estimated using the equation

$$V = \frac{\pi^2}{8L}\sum_{i=1}^{N} d_i^2 \text{ (van Wagner 1968)} \qquad (1)$$

We estimated canopy density using a concave spherical densiometer and by averaging values taken from 4 cardinal points at a distance of 1 m around the plot centre.

4.3.4 Statistical analyses

All statistical analyses were run in the R Environment 4.0.3 (R Development Core Team 2019).

4.3.5 Diversity analyses

We calculated Rényi-diversity profiles with Hill numbers using the function renyicomp within the package BiodiversityR with 100 permutations for each of the three habitat types unmanaged broadleaved, unmanaged coniferous and managed coniferous (Kindt and Coe 2005). Rényi-diversity profiles D_α belong to the diversity ordering techniques and allow for a direct comparison of habitats. These diversity profiles are based on Rényi´s generalized entropy theory (Rényi 1961), which was picked up and extended by Hill (1973) in a general class of measures known as the Hill numbers (H_α), with $H_\alpha = \exp(D_\alpha)$.

$$D_\alpha = \frac{\log \sum_i^S p^\alpha}{1-\alpha} \tag{2}$$

In this equation, S is the total number of species, α is called the “order” of the diversity measure and p_i denotes the relative abundance of the i^{th} species (Jost 2006, 2007, Chao et al. 2014). The Rényi diversity represents the absolute diversity of a community over a series of values for the diversity order α. The value of α represents the sensitivity of the community towards abundant species (Jost 2006, 2007). For α=0, the Rényi-profile value corresponds to species richness. For α=1, the diversity is equivalent to the Shannon-Wiener-diversity, α=2 corresponds to the Simpson diversity, and α=inf gives insight on the proportion of the most abundant species (Kindt and Coe 2005, Jost 2006, 2007, Chao et al. 2014). We included only species with occurrences >20 in the total dataset and the dataset included twelve species, respectively species groups (Table 4.1). Indeed, not further identified *Pipistrellus* species and *nyctaloid*s were included as species groups. *Plecotus spec.* most probably is *P. auritus* since *P. austriacus* has not been identified in *BP* for more than 30 years (Ruprecht 2004). To further investigate community differences between the three habitats considered, we calculated rank-abundance curves using average bat activity values per plot for each habitat type. Rank-abundance curves illustrate the contribution of species and species groups to the community. Moreover, evenness values of the habitats can be compared using rank-abundance curves (Kindt and Coe 2005).

4.3.6 Bat species activity models

Bat species activity models were calculated for the four forest bats *B. barbastellus*, *P. pygmaeus*, *M. brandtii* and *M. nattereri.* We used minute-intervals per night as an activity index (Erasmy et al. 2021a). We conducted two model sets. First of all, we fitted bat species activities to the habitat categories unmanaged broadleaved, unmanaged coniferous and managed coniferous to define differences between management types. Activity data for this model set included all plots sampled (n=30). Plot and Julian date were included as random intercepts. In a second step, bat species activity models were calculated only for forest interior plots where stand structural data were measured (n=15). We fitted bat species activities to forest structural variables to identify those parameters responsible for the activity differences between habitat types. Plot structural variables were checked for correlations, and the number of cavities per tree and canopy density (positively correlated to the proportion of broadleaved trees per plot) as well as the relative deviation in dbh (correlated to height standard deviation) were excluded. Thus, the base model included height standard deviation, basal area per plot, the proportion of broadleaved trees per plot, coarse woody debris volume and the number of tree species per plot. We included year as

TABLE 4.1 Mean activity (min.-intervals/night) with standard error and minimum and maximum activity values per night for the bat species considered in diversity analyses for the three habitat categories.

Habitat	Unmanaged broadleaf (n=235)	Unmanaged coniferous (n=202)	Managed coniferous (n=54)
Bbar	2.4 ± 0.3 (0-25)	0.4 ± 0.08 (0-7)	5.9 ± 1.5 (0-40)
Enil	0.02 ± 0.008 (0-1)	0.1 ± 0.05 (0-8)	0.4 ± 0.1 (0-3)
Mdau	0.09 ± 0.02 (0-2)	0.03 ± 0.01 (0-1)	0
Mnat	0.8 ± 0.09 (0-8)	0.2 ± 0.05 (0-7)	0.1 ± 0.04 (0-1)
Mbra	4.1 ± 0.4 (0-40)	0.3 ± 0.04 (0-4)	0.6 ± 0.1 (0-4)
Nnoc	0.08 ± 0.03 (0-3)	0.04 ± 0.02 (0-2)	0.1 ± 0.04 (0-1)
Nyctaloid	0.6 ± 0.1 (0-16)	0.6 ± 0.1 (0-17)	3.0 ± 0.5 (0-16)
Pipistrellus	1.3 ± 0.3 (0-38)	0.02 ± 0.01 (0-2)	0.04 ± 0.03 (0-1)
Plecotus	0.05 ± 0.02 (0-2)	0.01 ± 0.007 (0-1)	0.09 ± 0.05 (0-2)
Pnat	0.2 ± 0.05 (0-7)	0	0.1 ± 0.04 (0-1)
Ppip	0.3 ± 0.08 (0-13)	0	0
Ppyg	3.0 ± 0.5 (0-74)	0.05 ± 0.02 (0-2)	0.3 ± 0.08 (0-2)

Note: Bbar = *B. barbastellus*, Enil = *E. nilssonii*, Mdau = *M. daubentonii*, Mnat = *M. nattereri*, Mbra = *M. brandtii*, Nnoc = *Nyctalus* noctula, Pnat = *Pipistrellus nathusii*, Ppip = *P. pipistrellus*, Ppyg =*P. pygmaeus*.

a fixed effect to account for inter-annual activity differences. All models furthermore contained mean night-time temperature as a fixed effect, since temperature is known to influence bat activity (Mueller et al. 2012, Wolbert et al. 2014, Froidevaux et al. 2021). The plot ID (n=15) was added as a random intercept. The final model was fitted with restricted maximum likelihood. We fitted a candidate set of 28 Generalized linear mixed effects models (GLMMs) with assumed negative-binomial distributions including all possible combinations of our parameters and chose the most parsimonious model within Akaike´s Information Criterion corrected for small sample size (AICc) differences below 2 (Burnham and Anderson 2004, Burnham et al. 2011, Brewer et al. 2016). We furthermore checked whether including a zero-inflation intercept enhanced model fit by comparing AICc values with and without zero-inflation. We estimated model variances using marginal R^2-values (Nakagawa and Schielzeth 2013) using the performance package (Lüdecke et al. 2021). We used the DHARMa-package to validate our models (Hartig 2021).

4.3.7 Meta-analysis on tree roost preferences

In order to define tree roost preferences of the four tree-dwelling bat species *B. barbastellus*, *P. pygmaeus*, *M. brandtii* and *M. nattereri*, we conducted a meta-analysis following the guides of Wang (2018) and Harrer et al. (2021). We restricted our literature search to studies that contained information on roost tree species, roost tree vitality and roost type. We did not a priori select a geographic region since the species assemblage considered defined the geographic range. The distribution ranges of tree species do not necessarily overlap over the range of studies selected and we grouped tree species into the categories “broadleaved” (BL) and “coniferous” (C). For roost tree vitality, we considered the categories “vital” and “dead”. If roosts were explicitly described as located in a dead limb of a tree, the whole tree was considered as “dead”. We included the roost types loose bark, crevice and cavity (including hollows of differing origins such as woodpecker holes or branch breakoffs).

4.3.7.1 Search and selection of published studies

We searched the electronic databases ISI Web of Knowledge and Science Direct using the search terms “Scientific bat species name” AND “roost*”. Furthermore, we conducted an internet search using the meta-search engine Google Scholar. Google Scholar searches resulted in a very high amount of hits. Since the relevance of the results exponentially diminished, we only considered the first hundred hits for Google Scholar searches. We moreover consulted the species section in Dietz et al. (2009) for non-English literature on species roosts. We successively refined our search by screening titles, abstracts and finally entire articles. Our search resulted in a set of 25 datasets for the four species considered. We enlarged this dataset with own unpublished data (54 datasets) on tree roost use from Belarus and Germany (Figure 4.4). These datasets were collected in the frame of ecological intervention or conservation research and published in ecological reports. Including unpublished or so-called “grey literature” into

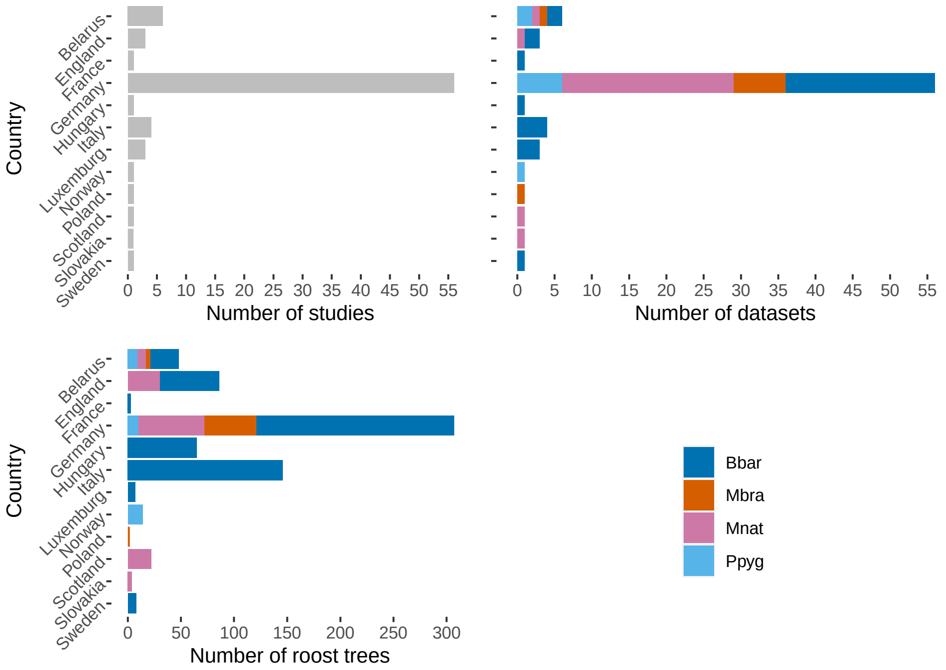

FIGURE 4.4 Association of studies, datasets and roost trees used for meta-analysis to species and countries.

systematic reviews can reduce the effects of publication bias by introducing otherwise unrepresented samples of unpublished studies (McKenzie et al. 2021).

4.3.7.2 Data extraction

Finally, 67 studies matched our eligibility criteria, from which 79 datasets were extracted. 712 tree roosts were described within the dataset and 66.4% of tree roost (473 tree roosts) resulted from published literature. 34 datasets reported on *B. barbastella*, 27 on *M. nattereri*, 9 on *M. brandtii* and 9 on *P. pygmaeus* roost preferences. The datasets included either raw data or data on proportions and were used to calculate effect sizes (proportions in our case), as requested for meta-analysis. Different subsets of the original dataset were used to evaluate roost preferences on tree type, tree vitality and the type of roost used, respectively.

4.3.7.3 Metaregression

We used the function *mprop* within the meta package to calculate overall logit-transformed proportions for studies reporting single proportions (Harrer et al. 2021, Schwarzer 2021). Publication bias is one of the major threats in meta-analyses. Small studies are more frequently submitted and published the stronger the effects they report. Publication bias in studies dealing with proportions, i.e. in non-comparative and observational studies, is unlikely to be an issue since there is no “positive” or “desirable” result that influences publication probability (Wang 2018). Moreover, the use of visually assessing publication bias in funnel plots, especially in meta-analyses on proportions, is questionable (Hunter et al. 2014, Wang 2018). All traditional approaches estimating publication bias are based on the assumptions that the publication probability of a study depends on its size, on its statistical significance or the direction of its results (Coburn and Vevea 2015). Since none of these assumptions is relevant for the studies we included, we refrained from assessing publication bias.

We subsequently conducted subgroup analyses with the bat species as fixed categorical predictors and study ID as a random effect within subgroups following Wang (2018) and Harrer et al. (2021). We visually inspected Baujat´s plots for the detection of influential studies (i.e. studies present in the top-right corner of the Baujat plot) contributing to heterogeneity in our meta-analytic data (Baujat et al. 2002, Wang 2018, Harrer et al. 2021). If influential studies were detected, we recalculated our subgroup analysis without the identified studies and checked for differences in estimates and heterogeneity. In all cases, the influential studies only had minor influence on estimates and heterogeneity values, and we stayed with the original datasets. The effect sizes used were

i) Proportion broadleaved trees (660 tree roosts from 74 datasets)

ii) Proportion dead trees (532 tree roosts from 68 datasets)

iii) Proportion roost type (543 tree roosts from 70 datasets)

For the estimation of our meta-analytical effects, we used a continuity correction of 0.5 in studies with 0-cell-frequency. Effects were pooled using the inverse variance method and weighted using least squares. Variance was estimated using maximum likelihood and between-subgroup heterogeneity was allowed to differ. We used Knapp-Hartung adjustments (Hartung and Knapp 2003) for the random effects part of the mixed model and confidence intervals were calculated using the Clopper-Pearson method. To work out roost preferences we predefined our null hypothesis at 0.5 in a way that a proportion of 50% represents a tendency towards the preference of this roost tree/type.

4.4 Results

4.4.1 Bat diversity

Bat diversity in managed coniferous forests was equivalent to unmanaged broadleaf forests for α=0 (corresponding to species richness) in the Rényi-diversity profile (Figure 4.5). For all values of α>0, diversity in unmanaged forests was higher compared to managed coniferous stands (Figure 4.5). Moreover, the steep curve for managed coniferous forests indicates a lower evenness in managed forests, whereas evenness in both unmanaged forest types was equal (parallel lines in Figure 4.5). We thus cannot attest generally higher bat diversity in unmanaged plots in *BPNP*. Confidence intervals indicate that bat diversity between unmanaged broadleaved and unmanaged coniferous forests was not significantly different. For the managed plots, no confidence intervals were calculated due to the randomization process.

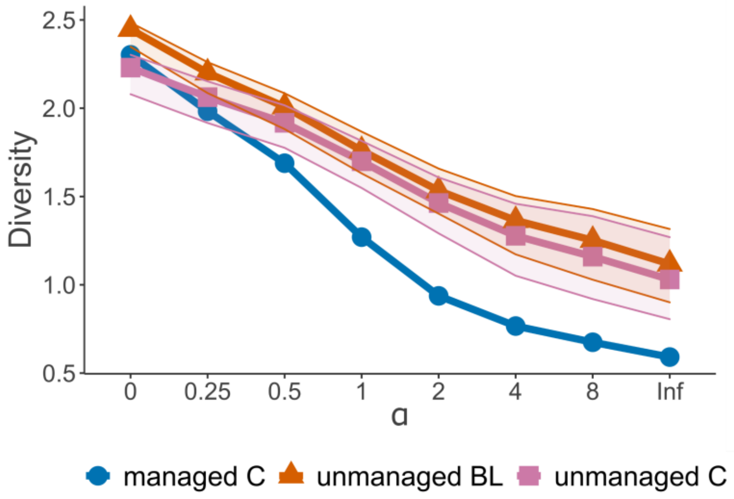

FIGURE 4.5 Rényi-diversity profiles for the three habitat types considered. C = coniferous, BL = broadleaved. α gives different aspects of the Rényi diversity, with α =0 being equivalent to species richness, α=1 to the Shannon index, α=2 to the Simpson index and α=Inf showing the proportion of the most abundant species.

In unmanaged broadleaved plots, the three most abundant species were *M. brandtii*, *P. pygmaeus* and *B. barbastellus* (Figure 4.6). In unmanaged coniferous plots, *nyctaloid* bats, *B. barbastellus* and *M. brandtii* dominated with low general activity levels, while *B. barbastellus*, *nyctaloid* bats and *M. brandtii* were the species with highest activity levels in managed coniferous plots (Figure 4.6). The high activity levels of *B. barbastellus* in the managed stands were concentrated in two neighbouring plots similar in structure (mean 18.5 ± 3.3 min.-intervals/night), whereas the remaining four managed plots had much lower activity levels of *B. barbastellus* (mean 1.3 ± 0.1 min.-intervals/night, Figure 4.6).

4.4.2 Influence of forest management and forest structural variables on bat species activity

The forest structure variables measured differed between habitats (Table 4.2). Especially, the number of cavities and coarse woody debris in unmanaged broadleaf stands was higher compared to coniferous stands in general (Table 4.2). Unmanaged plots of both broadleaved and coniferous forest types had higher variations in dbh- and height-values (Table 4.2). Unmanaged coniferous plots reached very high basal area values (Table 4.2).

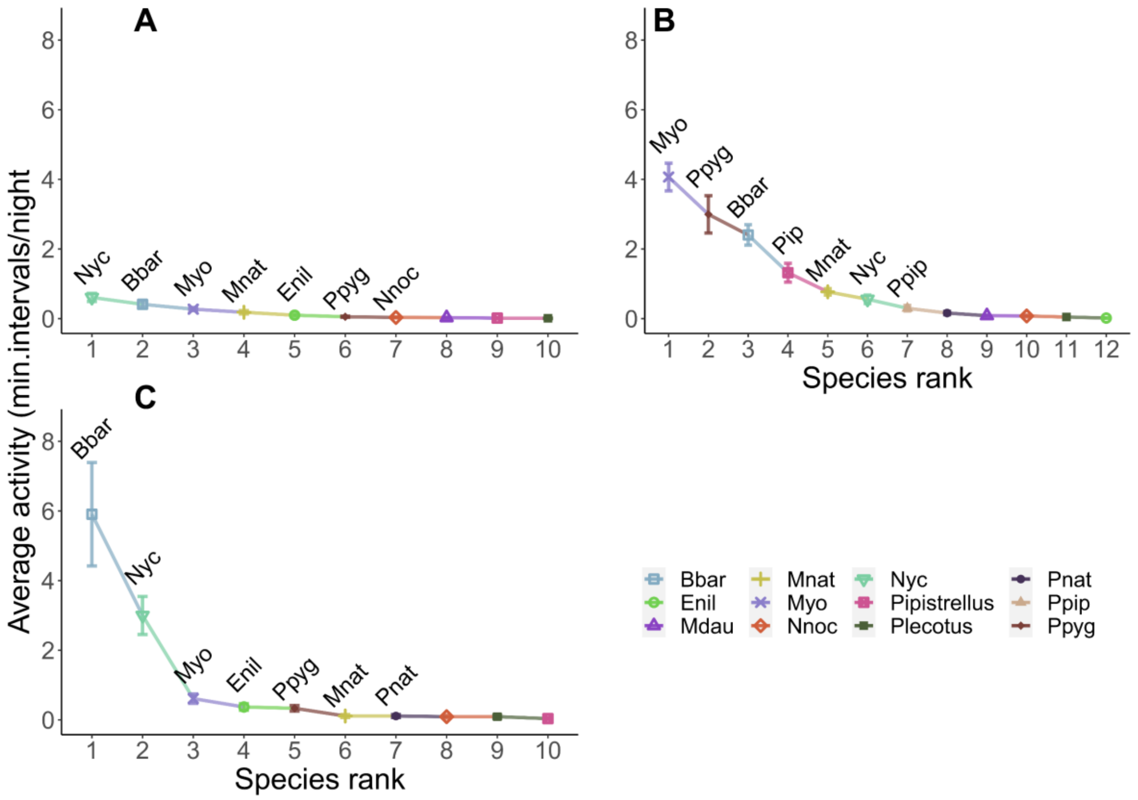

Figure 4.6 Rank-abundance curves (RAC) for A) unmanaged coniferous B) unmanaged broadleaf and C) managed coniferous forest stands. Mean activity levels/habitat are represented as symbols with errorbars showing the standard error (min.-intervals/night). Bbar = *Barbastella barbastellus*, Enil = *Eptesicus nilssonii*, Mdau = *Myotis* daubentonii, Mnat = *Myotis nattereri*, Myo = undefined *Myotis* spec., Nnoc = *Nyctalus noctula*, Nyc = *Nyctaloid*, *Pipistrellus* = undefined *Pipistrellus* spec, *Plecotus* = *Plecotus auritus*, Pnat = *Pipistrellus nathusii*, Ppip = *Pipistrellus pipistrellus*, Ppyg = *Pipistrellus pygmaeus*.

Western barbastelles were equally active in unmanaged broadleaved and in unmanaged stands (Figure 4.7, Table A 4.1). Tree basal area best explained activity differences in this species since their activity levels decreased with increasing plot basal area (Table A 4.2, Figure 4.7). Soprano pipistrelles, Brandt´s bats and Natterer´s bats were all most active in broadleaved unmanaged forests (Figure 4.7, Table A 4.1).

TABLE 4.2 Structural parameters on plot level for the different management categories considered.

	Cavities	cwd (m^3/ha)	BA (m^2)	Dbh (cm)	Rel. sd dbh	Height (m)	Sd height	Tree species richness	Prop. BL trees (%)
Unmanaged broadleaf	(n=6)								
mean ± SE	10.2 ± 7.9	296.7 ± 393.3	41.9 ± 8.3	275.6 ± 43.3	67.5 ± 11.2	23.4 ± 2.2	7.4 ± 1.0	3.8 ± 0.8	80.7 ± 16.5
min	1	29.3	29.7	214.4	48.3	19.1	6.1	3	62.7
max	22	988.6	53.6	339.9	78.6	25.1	8.3	5	100
Unmanaged coniferous	(n=6)								
mean ± SE	1.8 ± 2.0	52.5 ± 8.8	195.5 ± 178.2	275.8 ± 41.4	57.8 ± 7.1	23.4 ± 2.2	7.9 ± 0.8	4.2 ± 1.2	17.5 ± 12.9
min	1	39.7	20.5	223.6	49.4	20	6.7	2	0
max	6	61.2	435.2	324.5	69.3	26.2	9	5	39
Managed coniferous	(n=3)								
mean ± SE	1.0 ± 1.7	4.4 ± 7.6	30.8 ± 16.7	308.5 ± 104.8	36 ± 18.2	26.1 ± 3.0	4.5 ± 1.5	1 ± 0.0	0 ± 0
min	0	0	11.7	240.3	22.2	24	3.6	1	0
max	3	13.1	42.9	429.2	56.6	29.6	6.2	1	0

Note: Cwd = coarse woody debris, BA = basal area, dbh = diameter at breast height, sd height = height standard deviation, rel. sd dbh = dbh standard deviation/mean dbh.

Brandt´s bats activity levels were best explained by decreasing basal area and increasing proportion of broadleaved trees (Figure 4.8, Table A 4.2). Soprano pipistrelles´ activities deceased with increasing basal area and showed higher activity levels with increasing proportions of broadleaved trees (Figure 4.8, Table A 4.2). Their activity slightly decreased with higher volumes of coarse woody debris (Figure 4.8, Table A 4.2). Natterer´s bats’ activity was positively influenced by the numbers of broadleaved trees per plot (Figure 4.8, Table A 4.2).

4.4.3 Roost preferences

For the subgroup analysis on tree type (broadleaf versus coniferous) preferences, we found high heterogeneity between studies only for Western Barbastelles. In this species, there was a tendency towards roosting in broadleaved trees, but the pattern was not as clear as for the other three species. Natterer´s bats, Brandt´s bats and soprano pipistrelles were significantly more often found roosting in broadleaved trees (Table 4.3, Figure A 4.4). Considering tree vitality, Western barbastelles significantly more often roosted in dead trees, while Natterer´s bats more frequently chose vital trees as dayroosts (Table 4.3, Figure A 4.5). Heterogeneity in the roost choice data for vital trees was moderate in Western barbastelles (I^2 = 54.2%, Table 4.3). Brandt´s bats and soprano pipistrelles did not show any tendency towards a certain tree vitality type (Table 4.3, Figure A 4.5). Western barbastelles were specialised in roosting behind loose bark, while soprano pipistrelles showed a tendency towards roosting more often in cavities (Table 4.3, Figure A 4.1, Figure A 4.2). We did not identify any other species-specific relation between a bat species and a certain cavity type (Table 4.3). Crevice roosts could not be associated to any bat species (Table 4.3, Figure A 4.3).

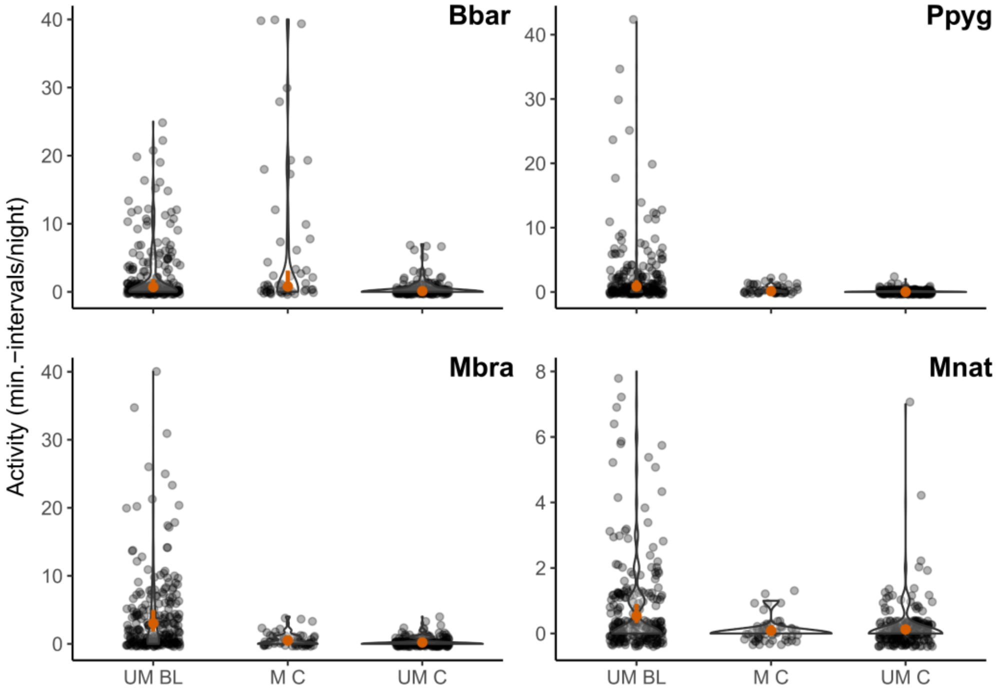

Figure 4.7 Activity data for the habitat categories unmanaged broadleaf (UM BL), unmanaged coniferous (UM C) and managed coniferous (M C). Raw data are plotted as semitransparent dots, while results from GLMMs with assumed negative-binomial distributions are plotted as orange estimated marginal means with standard errors as errorbars. Effects were fitted with plot (n=30) and Julian date (n=163) as random effects and habitat category as fixed effect. For better visualisation, the highest datapoint for *Pipistrellus pygmaeus* (60) was excluded. Bbar = *Barbastella barbastellus*, Ppyg = *Pipistrellus pygmaeus*, Mbra = *Myotis brandtii*, Mnat = *Myotis nattereri*.

Table 4.3 Results from metaregression models on the different tree roost characteristics tested. Significances of subgroup-effects (i.e. species) are only indicated as well as the overall subgroup effect. n = number of studies, I^2 = proportion of observed heterogeneity, $p_{subgroup}$ gives the results of the null hypothesis that all subgroup effect sizes are equal. p-value gives the treatment effect of subgroups (fixed effects) under the null-hypothesis 0.5. Bbar = *Barbastella barbastellus*, Mbra =*Myotis brandtii*, Mnat = *M. nattereri*, Ppyg = *Pipistrellus pygmaeus*.

Proportion broadleaf, $p_{subgroup}$ = 0.07					Proportion live trees, $p_{subgroup}$ **<0.001**				
	Estimate (CI %)	PI	I^2 (CI %)	p-value		Estimate (CI %)	PI	I^2 (CI %)	p-value
Bbar (n=29)	70.0 (50.8-84.1)	6.4-98.8	74.7 (63.6-82.3)	na	Bbar (n=27)	27.3 (18.3-38.6)	5.9-69.1	54.2 (29.2-70.4)	<0.001
Mbra (n=9)	89.5 (80.4-94.6)	80.1-94.7	0.0 (0.0-64.8)	na	Mbra (n=8)	41.1 (26.6-57.3)	26.2-57.9	0.0 (0.0-67.6)	0.29
Mnat (n=27)	82.5 (73.4-89.0)	73.3-89.0	0.0 (0.0-42.5)	na	Mnat (n=26)	83.7 (78.3-88.0)	78.3-88.0	0.0 (0.0-43.2)	<0.001
Ppyg (n=9)	76.6 (51.2-91.1)	50.5-91.3	0.9 (0.0-65.1)	na	Ppyg (n=7)	58.0 (29.2-82.2)	27.9-83.1	0.0 (0.0-70.8)	0.55

Proportion bark, $p_{subgroup}$ **<0.001**					Proportion cavity $p_{subgroup}$ **<0.001**				Proportion crevice, $p_{subgroup}$ = **0.002**			
	Estimate (CI %)	PI	I^2 (CI %)	p-value	Estimate (CI) (%)	PI	I^2 (CI %)	p-value	Estimate (CI) (%)	PI	I^2 (CI %)	p-value
Bbar (n=30)	84.3 (79.1-88.5)	79.1-88.5	0.0 (0.0-40.8)	<0.001	6.8 (4.5-10.1)	4.5-10.1	0.0 (0.0-40.8)	<0.001	15.2 (11.1-20.4)	11.1-20.4	0.0 (0.0-40.8)	<0.001
Mbra (n=8)	59.0 (36.5-78.3)	28.8-83.7	5.7 (0.0-69.4)	0.15	24.2 (10.9-45.7)	10.5-46.5	4.8 (0-69.1)	0.004	22.9 (11.2-41.1)	10.3-43.5	0.0 (0.0-67.6)	0.003
Mnat (n=24)	13.6 (9.8-18.4)	9.8-18.4	0.0 (0.0-44.6)	<0.001	65.6 (53.3-76.0)	53.3-76.1	0.0 (0.0-44.6)	0.01	34.4 (23.9-46.7)	23.9-46.7	0.0 (0.0-44.6)	0.01
Ppyg (n=8)	61.1 (32.5-83.7)	31.6-84.3	15.0 (0.0-57.9)	0.32	35.5 (12.7-67.6)	8.2-77.3	22.4 (0-65.1)	0.21	14.7 (8.5-24.2)	8.3-24.6	0.0 (0.0-67.6	<0.001

Non-metric multidimensional scaling resulted in linear R^2-values of 0.98, and a stress-value of 0.068 (k=2 dimensions). Western barbastelles were identified to occupy the roosting niche of loose bark from dead coniferous trees, while Natterer´s bats occupied the roosting niche of live broadleaved tree cavities and crevices (Figure 4.9). Brandt´s bats were able to use a wider range of tree roosts with no clearly identifiable preference for tree type, tree vitality or roost type (Figure 4.9). Soprano pipistrelles used crevices and bark roosts with no clear preference on tree vitality and tree type (Figure 4.9).

4.5 Discussion

Bat diversity in managed stands of the Belovezhskaya Pushcha National Park was not per se lower compared to unmanaged stands since species richness as one diversity measure was similar in both management types. However, all other diversity measures considered, especially evenness, were higher in unmanaged forest stands. Moreover, we used bat activity (own data) and tree roost preferences (meta-analytic data) to analyse the dependence of four abundant

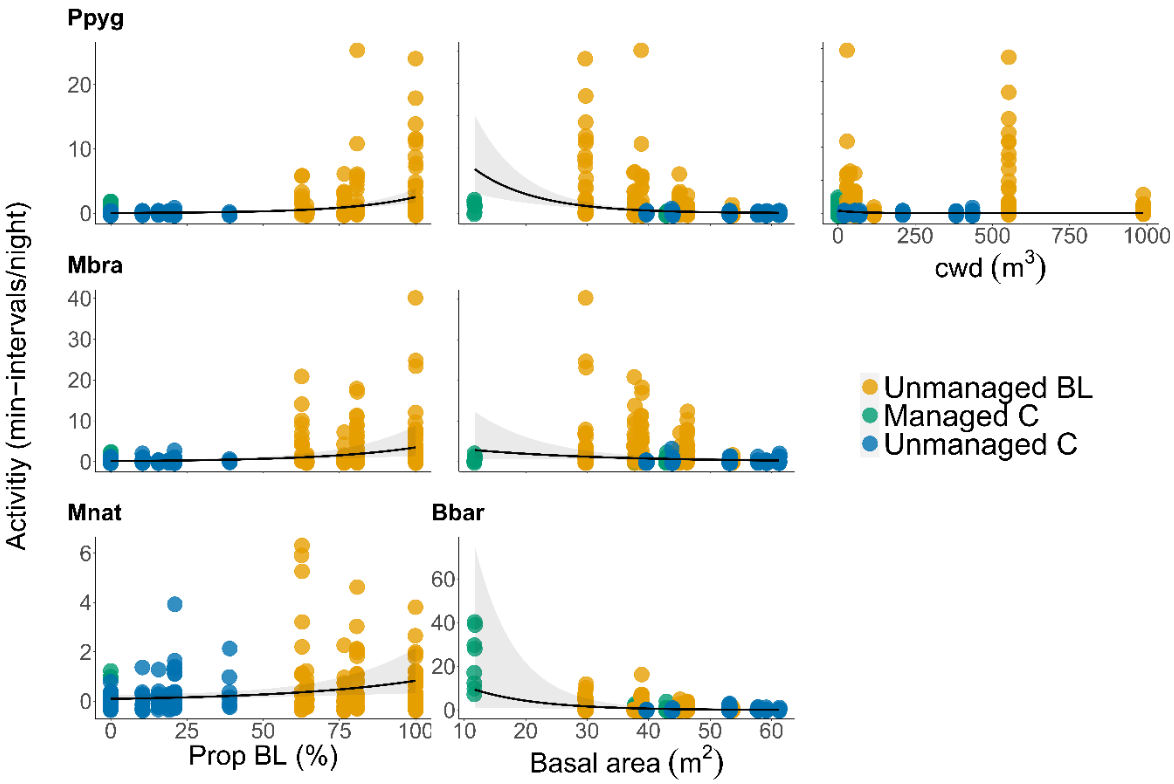

Figure 4.8 Significant effects from Generalized linear mixed effect models on the influence of forest structural variables on bat species activities. Jittered dots show the raw data, lines and shaded areas the estimated marginal means and their respective confidence intervals, Ppyg=*Pipistrellus pygmaeus*, Mbra=*Myotis brandtii*, Mnat=*M. nattereri*, Bbar=Barbastella barbastellus. Prop BL = proportion broadleaved trees per plot. UM BL = unmanged broadleaved, MAN C = managed coniferous, UM C = unmanaged coniferous.

strict forest bat species on old-growth structures. All species except Western barbastelles showed increasing activity levels in forests with a higher proportion of broadleaved trees and were most active in unmanaged broadleaved stands. Furthermore, basal area was an important structural variable influencing bat species activity in the forest.

4.5.1 Bat diversity in managed versus unmanaged forests

We chose Rényi-Diversity profiles for bat diversity analyses, since they integrate different diversity orders and allow for direct comparisons between habitats (Kindt and Coe 2005, Chao et al. 2014). Our results showed that management had a higher influence on bat diversity than forest type. Diversity measures in both broadleaved and mixed-coniferous unmanaged stands were similar. We think that the commonalities in unmanaged stands leading to these similar diversity values despite differences in activity levels between habitats are vertical and horizontal structural heterogeneity. Indeed, variability in tree height (mean tree height standard variation: 7.4 m and 8.3 m in both unmanaged versus 4.5 m in managed plots) and the mean relative deviation in dbh (67.5 mm and 57.8 mm in unmanaged versus 36.0 mm in managed plots) were similar in unmanaged plots and were deviating from managed stands. Structural heterogeneity is indeed known to positively influence bat activity, occurrence, and diversity (Jung et al. 2012, Froidevaux et al. 2016, Renner et al. 2018, Langridge et al. 2019, Alder et al.

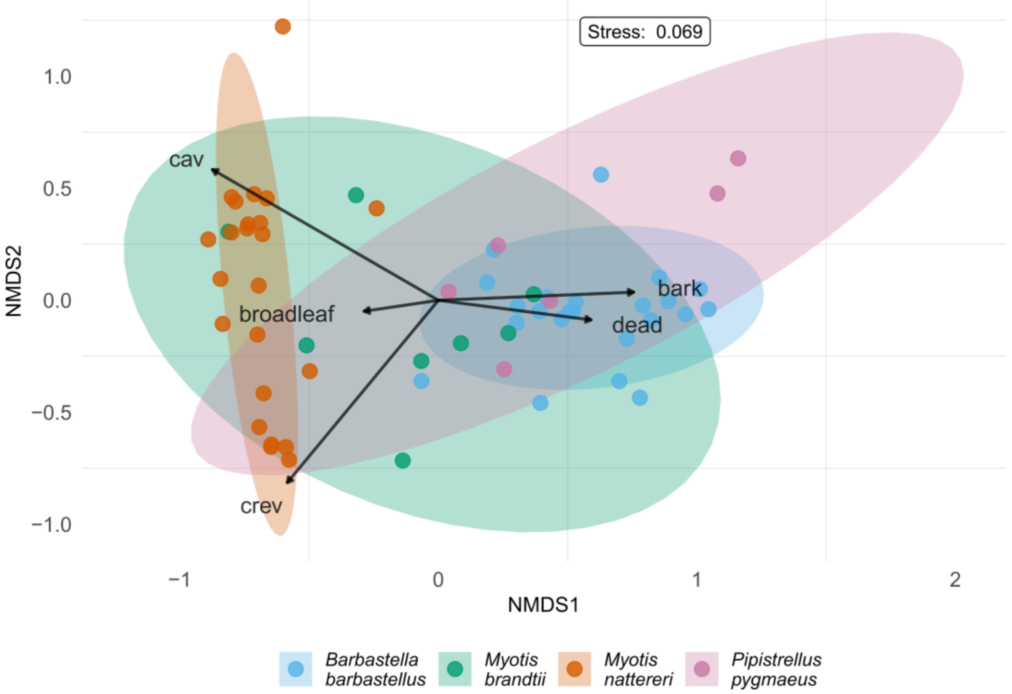

FIGURE 4.9 Nonmetric multidimensional scaling for roost tree preferences of *B. barbastellus*, P. *pygmaeus*, *M. nattereri* and *M. brandtii* considering tree roost species (coniferous versus broadleaved), roost type (bark, cavity, crevice) and roost tree vitality (dead versus vital). Cav = cavities, crev = crevices, bark = looose bark, dead = dead trees, broadleaf = broadleaved trees. Bbar = Barbastella barbastellus, Mbar = *Myotis brandtii*, Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*.

2020, Franke et al. 2020, Erasmy et al. 2021a). However, species richness as the simplest diversity measure did not differ between management types. Considering solely species richness as a diversity measure has been challenged, since it conveys limited information on structure and function of ecosystems (Fleishman et al. 2006, Hillebrand et al. 2008, Lelli et al. 2019). Managed study plots were located in the Economic Activity zone of *BPNP* and are thus part of the same forest complex as the unmanaged plots. We therefore anticipated an identical potential species pool for all study plots. Hillebrand et al. (2008) reviewed the influence of dominance structures in anthropogenically-altered habitats on the regional biodiversity. The fertilization of habitats leads to more homogeneous resources, which in turn decreases evenness and increases dominance structures in diversity (Hillebrand et al. 2007). In our study, we observed mainly Western barbastelles and *nyctaloid* species exploiting managed coniferous plots and the predominance of these species led to the low evenness values for unmanaged plots. In line with Hillebrand et al. (2007) and Lelli et al. (2019), we believe that the dominance pattern observed in managed coniferous stands was due to a homogenization in structural forest features (Dieler et al. 2017), resulting in a less diverse prey supply and fewer physical potential foraging niches (Renner et al. 2018, Langridge et al. 2019). Similarly, Celuch and Kropil (2008) found highest Shannon-diversity-index values for bats in the forest interior in the Carpathian Mountains compared to artificial forest edges or forest roads. Moreover, the species dominance patterns were best balanced in the forest interior (Celuch and Kropil 2008).

We are aware of the challenges and shortcomings of taxonomic diversity indices. Franke et al. (2020) found low phylogenetic diversity values for bats in forest habitats with high species richness in Bavaria, Germany. This was due to the fact that these habitats harbour many closely related species, for example species of the genus *Myotis*. However, these species with low phylogenetic diversity nevertheless belong to different functional guilds, as has been shown e.g. for *Myotis bechsteinii* and *Myotis nattereri* (Siemers and Swift 2006). Thus, we assume that for insectivorous bats, even closely related species occurring in the same habitat may occupy distinct ecological niches which would lead to a correlation of phylogenetic and taxonomic diversity values.

4.5.2 Bat activity in relation to old-growth structural attributes for strict forest dwellers

For all forest bat species in our study except *B. barbastellus*, the proportion of broadleaved trees at plot level was the most important structural parameter explaining activity levels, a finding supported by Froidevaux et al. (2021) for conifer-dominated landscapes. Basal area was as well influential and shaped bat activity levels in all species except for *M. nattereri,* a finding in accordance with Bender et al. (2021) and Froidevaux et al. (2021).

Western barbastelles preferred hunting in managed coniferous stands. However, these high activity levels were recorded in only two of the managed coniferous Peucedano-Pinetum plots with very high inter-tree distances and very low stem counts and basal areas. This finding supports Froidevaux et al. (2021) but contradicts Tillon et al. (2016) who found a positive relationship between Western barbastelle occurrences and basal area as well as findings from Sierro (1999), where these bats were predominantly hunting in the most productive sites. Western barbastelles are specialized in preying on Lepidopteran prey (Sierro and Arlettaz 1997, Sierro 1999). This narrow prey niche results from species-specific constraints rather than from habitat selection (Sierro 1999, Carr et al. 2020b). The open Peucedano-Pinetum stands probably had ephemerally very high prey abundances in adequate lepidopteran prey, as it is known to occur during cyclic mass outbreaks of so-called pest insects (Charbonnier et al. 2014, Auger-Rozenberg et al. 2015, Garin et al. 2019). When excluding those two plots from our analyses, Western barbastelles were most active in unmanaged broadleaved forests. We emphasize the important role the *BP* forests has for populations of the Western barbastelle (Rachwald et al. 2018, 2021, Erasmy et al. 2021a). They have been identified to be the second most abundant bat species in *BP* but are categorized as rare for Belarus and classified as near-threatened by the IUCN (Shpak 2014, Piraccini 2016).

Pipistrellus pygmaeus had highest activity levels in unmanaged broadleaved forests, which was best explained by the high share of broadleaved trees. This finding is in line with other studies which identified *P. pygmaeus* as preferentially hunting in broadleaved forests (Russ and Montgomery 2002, Davidson-Watts et al. 2006, Nicholls and Racey 2006b, 2006a). We cannot deduce from this result on the impact of management practices on soprano pipistrelles´ activity, since we were not able to include managed broadleaved forest plots into our study (see 4.3.1 Site description). Soprano pipistrelles had decreasing activity levels with increasing basal area, and as a typical edge-space forager thus showed an avoidance of very dense stands. This is in line with findings from Fuentes-Montemayor et al. (2013) and Froidevaux et al. (2021) but contradicts findings from Tillon et al. (2016) for *P. pygmaeus.* Moreover, Bouvet et al. (2016) and Tillon et al. (2016) detected a positive relationship between *P. pygmaeus* activity and lying deadwood volumes. However, the clear interrelation between deadwood and insectivorous bats has not been disentangled so far (Zehetmair et al. 2015, Tillon et al. 2016). Indeed, deadwood can directly influence bats through arthropod and roost abundance and diversity (Vuidot et al. 2011, Floren et al. 2014, Seibold et al. 2016, Kozak et al. 2018, Paillet et al. 2019), and may indirectly act as a proxy for the structural characteristics of a forest, such as openness and vertical or horizontal heterogeneity (Seibold et al. 2016, Paillet et al. 2018). We therefore do not have an explanation for the slight tendency of soprano pipistrelles to be less active with increasing deadwood volumes in our study.

M. nattereri, while preferring broadleaved stands, was as well hunting in unmanaged coniferous forests but to a lesser extent. The positive influence of the proportion of broadleaved trees on Natterer´s bats´ activity might be due to the fact that broadleaved trees, e.g. *Quercus* species, harbour a higher arthropod diversity and/or abundance (spiders: Floren et al. (2008), phytophagous beetles: Sprick and Floren (2008), Heteroptera: Gossner (2008)). Natterer´s bats as a mainly gleaning species rely on leaves and other plant surfaces that harbour potential prey Swift and Racey (2002). We think that Natterer´s bats mainly preying in the lowest forest layer (Erasmy et al. 2021) benefit from the diverse herb layer and the young regrowth providing prey present in the unmanaged forests.

Myotis spec. (*M. nattereri* excluded) are expected to be *M. brandtii* bats (4.3.2 Bat species identification). *M. brandtii* clearly preferred hunting in broadleaved forests, which probably offered a higher suitable prey availability (Taake 1992, Dense and Rahmel 2002, Mueller et al. 2018). As an edge-space forager like *P. pygmaeus*, these bats also showed decreasing activity levels with increasing basal area values. This finding again does not coincide with results from (Tillon et al. 2016) who identified a positive influence of increasing basal area on *M. brandtii* activity. However, Froidevaux et al. (2016) found a negative influence of tree density on the functional group “short-range echolocators” which included Brandt´s bats and McKay (2020) describe *M. brandtii* as relying on mature forests. These contrasting results lead us to the yet to be confirmed hypothesis that Brandt´s bats are able to hunt in forest stands up to a certain tree density threshold, above which stands become too dense to be efficiently exploited.

4.5.3 Species-specific roost preferences

During the literature search on tree roost preferences of four insectivorous forest dwelling bat species, we identified 25 studies meeting our eligibility criteria and completed the dataset with own unpublished data. This led to a bias in the geographical range of studies included, with a focus on datasets from Germany (Figure 4.4). However, datasets were collected in a variety of habitats and federal states, and we estimate that the importance of a larger sample size prevails. Moreover, we accounted for between-study heterogeneity by fitting a random-effects meta-analytical model.

One issue immanent in our observational systematic review consists in the habitat types the respective studies took place. Especially for tree type choice, i.e. the choice between broadleaved versus coniferous trees, data collected in a broadleaved dominated landscape tend to result in a roost preference for broadleaved trees. We utilised 79 datasets from 12 European countries containing 712 treeroosts and a variety of habitats from largely vegetation-free badlands (Ancillotto et al. 2015) to old-growth forests (Dietz et al. 2018). We estimate that we thereby reflect the true variability of possible natural roost type preferences throughout the distribution range of these four forest species.

For bats, the guild concept established by Denzinger and Schnitzler (2013) is frequently used to describe functional diversity. This framework acknowledges different aspect of bat feeding ecology by integrating physiological and morphological characteristics and establishes feeding guilds. Consequently, this guild concept can be used to describe habitat use in relation to habitat structure and prey availability. Considering roosting behaviour, many temperate bat species rely on trees as roosts and use tree hollows, crevices, or loose bark for solitary roosting or for the formation of maternity colonies (Dietz et al. 2009). Therefore, the availability of adequate roosting opportunities in forests can fundamentally influence bat habitat use (Regnery et al. 2013, Paillet et al. 2018, Basile et al. 2020). The structural description of tree roosts answers proximate questions on roost choice, but of course ignores its ultimate reasons, such as species-specific heterothermic behaviour, reproductive stage, sociability, or predation risk (Sedgeley 2001, Boyles 2007, Otto et al. 2016, Bergeson et al. 2021). Moreover, tree roost selection is strongly dependent on the availability of potential roosts: Monarchino et al. (2020) showed that in structurally diverse forests, bats selected their roosts on tree and stand level, while in anthropogenically more strongly influenced forests, they did not detect differences in roost characteristics. Moreover, regular roost switching has been shown to be an important adaptation to variable climatic conditions and a parasite minimisation strategy (Reckardt and Kerth 2007, Patriquin et al. 2016, Ruczynski and Barton 2020). Therefore, besides structural and climatic roost characteristics, the abundance and diversity of tree roosts are limiting factors for forest-dwelling bats. We think that identifying roosting guilds can be a useful tool for raising the awareness on the importance of TreMs for bats and for implementing bat conservation needs into forest management. These roosting guilds could be used in complement with the already described foraging guilds. Kalcounis-Ruppell et al. (2005) conducted a meta-analysis on tree roost selection in North American bats. They found that roost trees were generally larger and higher than random trees and were located in open stands with a high snag density. Nado and Kanuch (2015) conducted a global meta-analysis relating dbh of roost trees to dbh measures of trees surrounding the roost. At a global scale, tree roosts were 80% larger than surrounding trees. Drake et al. (2020) systematically revised literature on North American tree roost preferences and were able to differentiate roosting guilds for tree roosting bats.

We focussed on the four most abundant bat species in *BP* relying on forests both for hunting and roosting. We chose to analyse tree roost preferences according to tree type (coniferous versus broadleaved), tree vitality and microhabitat, since these characteristics can very easily be used to formulate forest management implementations. We were able to identify species-specific roosting needs relying on different TreMs.

Western barbastelles strictly relied on snags for roosting. This finding highlights the importance of standing deadwood and the important microhabitats occurring on these snags. A study by Rachwald et al. (2022) showed the importance of bark-beetle infested stands for *B. barbastellus* on the Polish side of *BP*. Deadwood is reported to experience more extreme temperatures and less stable temperatures than live trees (Wiebe 2001). Due to differences in temperature sensibility and species-specific differences in heterothermic behaviour, Western barbastelles seem well adapted to more extreme roosts considering microclimate. Indeed, they are treated as a cryophilic bat species since they prefer cold temperatures in their winter roosts (Jurczyszyn et al. 2003).

Myotis brandtii, *M. nattereri* and *P. pygmaeus* all relied on broadleaved forests for hunting. However, they segregated considering their roosting needs. Only *M. nattereri* showed a clear specialisation for live broadleaved trees with roosts either in cavities or crevices. *M. brandtii* and *P. pygmaeus* used a variety of roosting opportunities and did not seem to prefer a certain tree type, vitality or microhabitat.

Microhabitats need time to develop and have highest abundances and diversities in old-growth forests (Vuidot et al. 2011, Walankiewicz et al. 2014, Asbeck and Kozák 2021, Courbaud et al. 2021). We showed that a variety of microhabitats, including microhabitats on snags, are necessary to offer the diversity of roosts needed by a diverse bat community.

4.5.4 Conclusion

Our study supports the hypothesis that forest structural heterogeneity increases bat diversity. Especially evenness was higher in more heterogeneous forest stands. Hillebrand et al. (2008) describe the effects of altered evenness through human-induced dominance changes in species communities, which may, depending on the functional traits of the dominant species, decrease ecosystem resilience. In the light of rapidly changing climatic conditions and an increasing need for timber products, we ask for heterogeneity structures to be created or kept during forest management processes in order to maintain forest biodiversity and keep managed forests climate-smart (Verkerk et al. 2020). Besides structural heterogeneity, TreMs are of outstanding importance to support viable bat populations in forests (Regnery et al. 2013, Paillet et al. 2018, Basile et al. 2020). The retention of snags in adequate numbers as well as the persistence of live trees with large diameters, where a variety of microhabitats can develop, need to be implemented into forest management considerations to guarantee the survival of forest bat communities.

The size of forest patches and their degree of fragmentation have large impacts on biodiversity. Viljur et al. (2020) found that forest butterfly species richness was higher with larger proportions of forest cover surrounding the study sites, and that the full species spectrum was only reached in regionally heterogeneous forest stands. In the same line, Kozák et al. (2021) describe the importance of large and heterogeneous forested landscapes for saproxylic beetle assemblages. Thorn et al. (2020) analysed the proportion of naturally disturbed forest excluded from management (salvage logging in this case) necessary to conserve biodiversity. For bats, 90% unlogged forest area were necessary to maintain 90% species unique to unlogged naturally disturbed forest, and the retention of 50% unlogged area maintained 50% unique species to unlogged naturally disturbed forest.

Seventeen out of 19 bat species known to occur in Belarus have been detected in *BPNP* (Shpak 2014, Shpak and Larchenko 2016, Dombrovski et al. 2017b, 2017a). Of these 17 species, 13 have been recorded in the forest and are known to rely for at least some part of their life cycle on forest structures (Dietz et al. 2018, Erasmy et al. 2021a, Rachwald et al. 2021). We therefore emphasize the important role large and coherent forest complexes with unmanaged core areas like Belovezhskaya Pushcha are playing as refugia for species communities characteristic for natural forests and as a fundamental requirement for the persistence of diverse species assemblages with high resilience in response to disturbances (Nolet et al. 2018, Jaroszewicz et al. 2019). These aspects should be of primary importance especially in times of a rapidly changing climate and an ever increasing demand for timber.

4.6 References

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4.7 Appendix

TABLE A 4.1 N observations = 491. Habitat fitted against unmanaged broadleaved. Estimates fitted from a generalised linear mixed model with assumed negative binomial distribution.

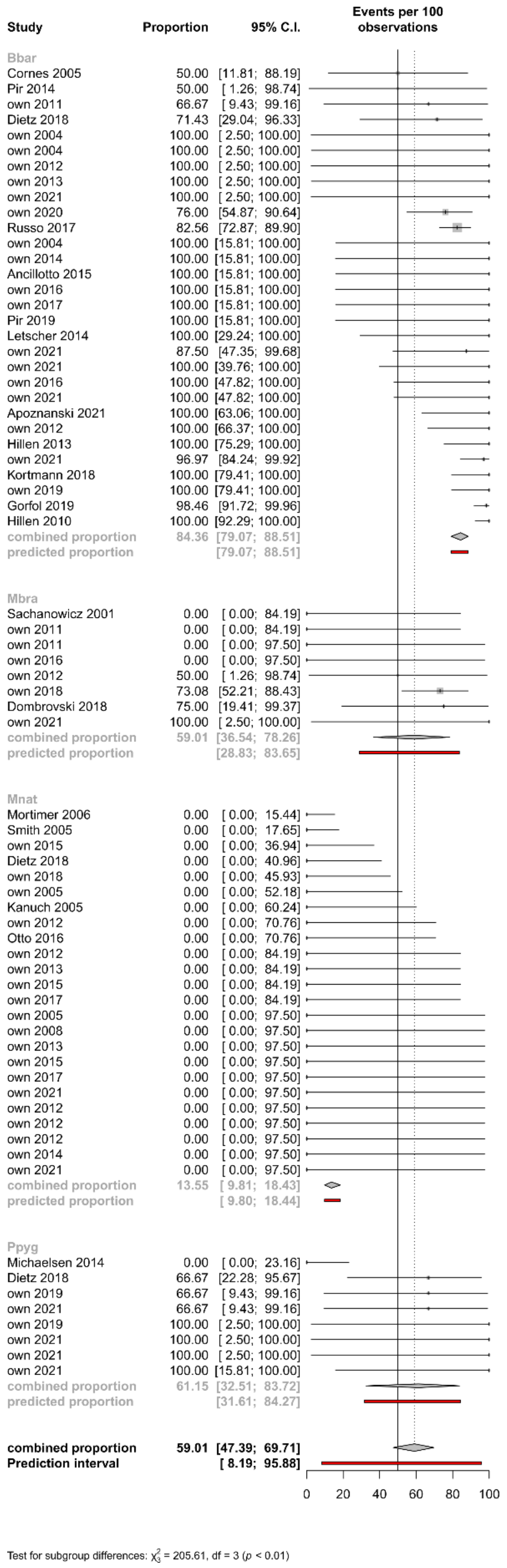
		Intercept	habitat [managed coniferous]	habitat [unmanaged coniferous]	Marginal R^2 / Conditional R^2
Bbar	IRR	0.72 ± 0.35	1.1 ± 0.92	0.15 ± 0.1	0.146 / 0.764
	CI	0.28 – 1.87	0.22 – 5.62	0.04 – 0.59	
	p	0.504	0.907	0.007	
Ppyg	IRR	0.87 ± 0.33	0.15 ± 0.11	0.03 ± 0.02	0.358 / 0.716
	CI	0.41 – 1.84	0.04 – 0.60	0.01 – 0.12	
	p	0.707	0.007	<0.001	
Mnat	IRR	0.54 ± 0.14	0.16 ± 0.1	0.23 ± 0.09	0.189 / 0.405
	CI	0.32 – 0.90	0.05 – 0.52	0.11 – 0.50	
	p	0.018	0.002	<0.001	
Myotot	IRR	1.75 ± 0.52	0.12 ± 0.07	0.07 ± 0.03	0.315 / 0.751
	CI	0.97 – 3.14	0.04 – 0.35	0.03 – 0.15	
	p	0.062	<0.001	<0.001	

Note: Results are shown on the response scale and models were estimated with restricted estimated maximum likelihood. IRR= incidence rate ratio, SE=standard error, CI=confidence interval. Bbar=*B. barbastella*, Ppyg=*P. pygmaeus*, Mnat=*Myotis nattereri*, Myotot=*Myotis brandtii*. Random effects plot n=30, date n=163. Significant results in bold.

TABLE A 4.2 Estimates fitted from species generalised linear mixed models with assumed negative-binomial distribution (n=244). For *B. barbastellus*, a zero-inflated Intercept was included.

		Proportion BL (%)	Basal area (m^2)	Coarse woody debris (m^3)	year [2015]	temperature	Zero-inflated Intercept	Marginal R^2
Mnat	IRR ± SE	1.02 ± 0.01			1.43 ± 0.5	1.13 ± 0.05		0.239
	p	0.004			0.303	0.005		
Mbra	IRR ± SE	1.03 ± 0.01	0.96 ± 0.02		0.9 ± 0.27	1.11 ± 0.04		0.512
	p	<0.001	0.036		0.737	0.006		
Bbar	IRR ± SE		0.91 ± 0.03		0.96 ± 0.34	1.19 ± 0.04	0.3 ± 0.12	0.226
	p		0.002		0.91	<0.001	0.002	
Ppyg	IRR ± SE	1.04 ± 0.01	0.9 ± 0.01	0.99 ± 0	2.99 ± 0.98	1.21 ± 0.06		0.695
	p	<0.001	<0.001	0.003	0.001	<0.001		

Note: Mnat=*M. nattereri*, *Myotis*=*M. brandtii*, Bbar=*B. barbastellus*, Ppyg=*P. pygmaeus*. Proportion BL= proportion broadleaved trees per plot, sd height=height standard deviation, IRR = incidence rate ratio, SE=standard error. Results from best models for each species are shown. Random effect: plot n=15. Significant results in bold.



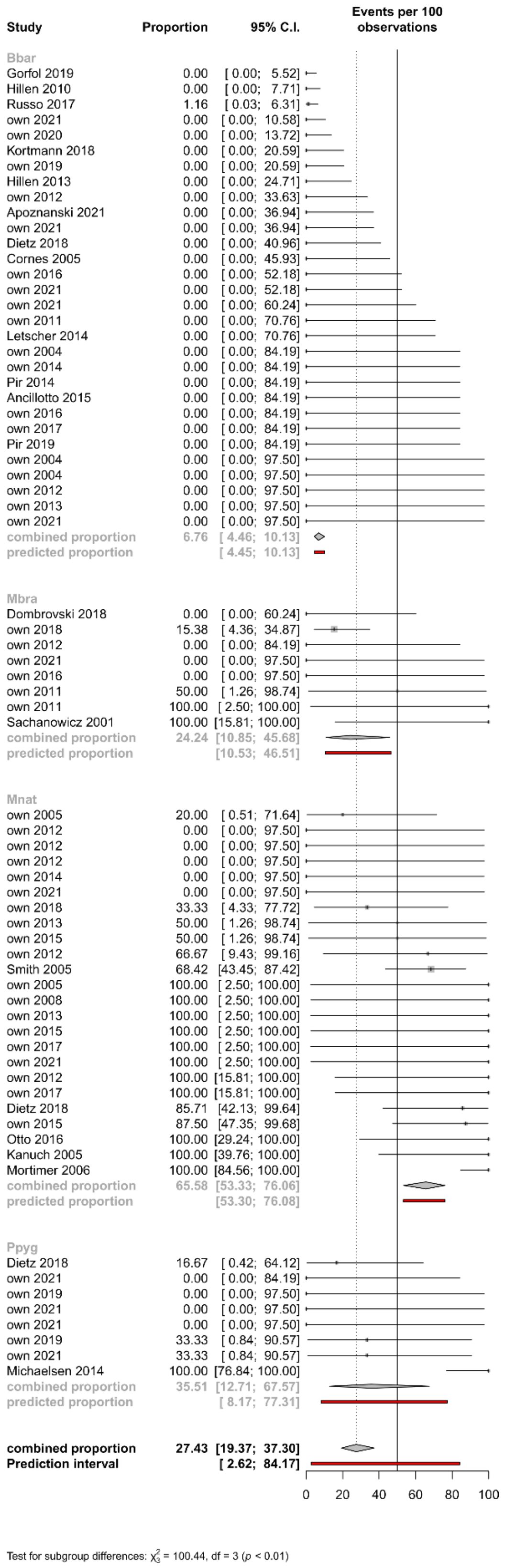


Figure A 4.1 Forest plot on the proportion of roosts behind loose bark for 4 forest bat species. Bbar = *Barbastella barbastellus*, Mbra = *Myotis brandtii*, Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*. Own marks own datasets from different regions in Germany and Belarus.

Figure A 4.2 Forest plot on the proportion of roosts in cavities for 4 forest bat species. Bbar = *Barbastella barbastellus*, Mbra = *Myotis brandtii*, Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*. Own marks own datasets from different regions in Germany and Belarus.

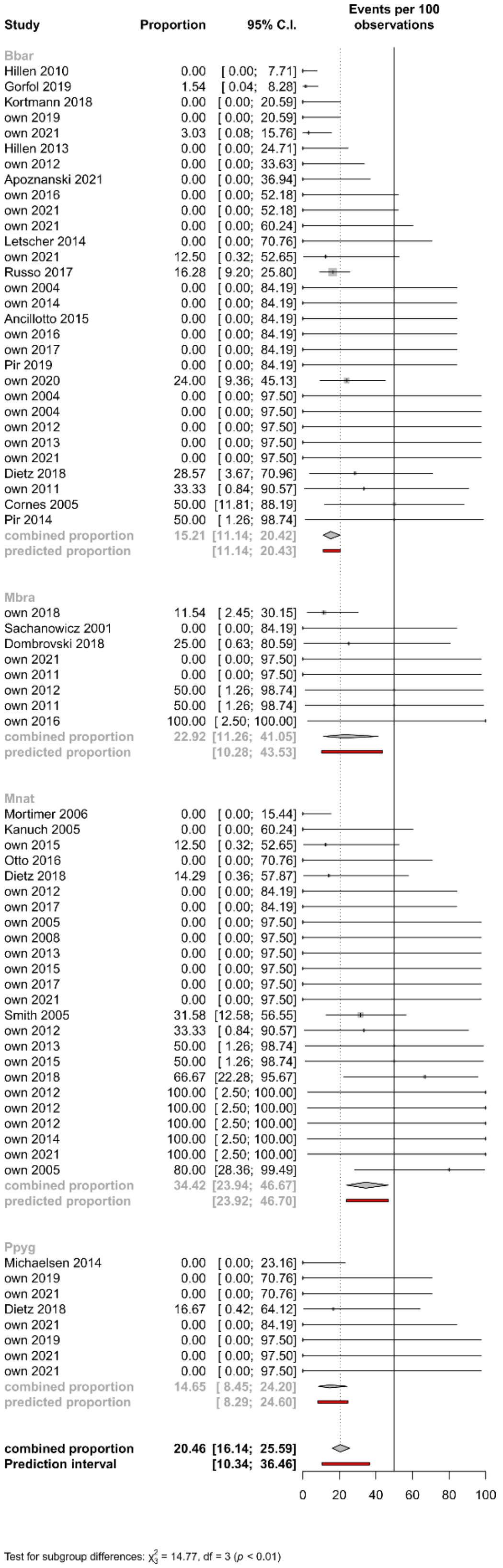


FIGURE A 4.3 Forest plot on the proportion of roosts in crevices for 4 forest bat species. Bbar = *Barbastella barbastellus*, Mbra = *Myotis brandtii*, Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*. Own marks own datasets from different regions in Germany and Belarus.

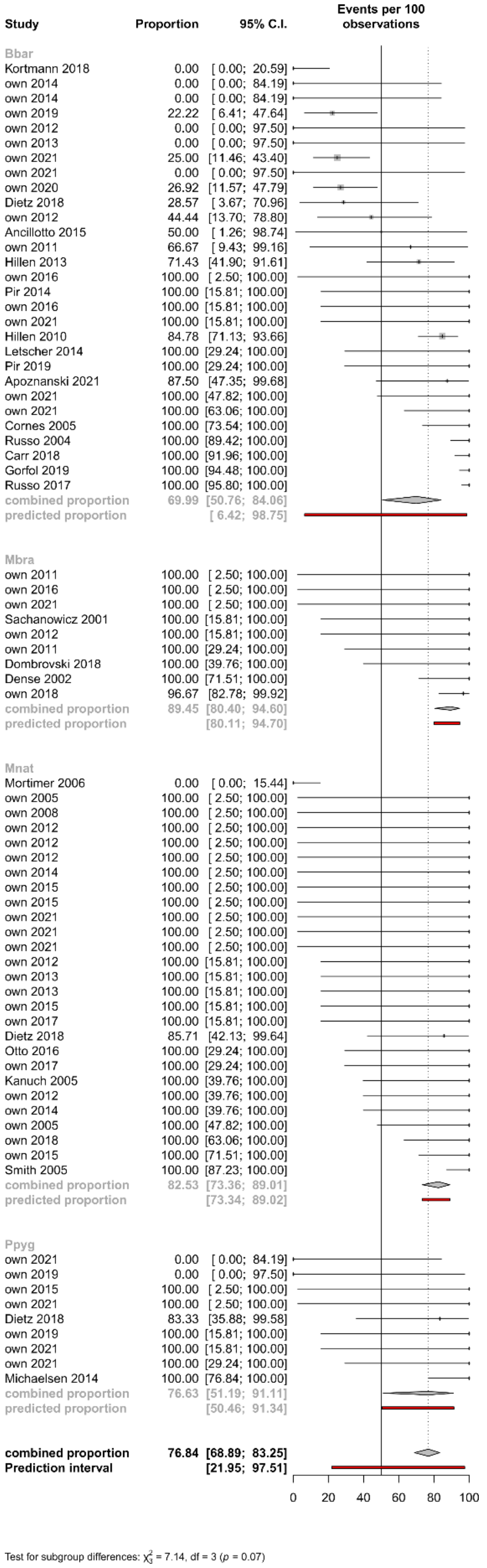


FIGURE A 4.4 Forest plot on the proportion of roosts in broadleaved trees for 4 forest bat species. Bbar = *Barbastella barbastellus*, Mbra = *Myotis brandtii*, Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*. Own marks own datasets from different regions in Germany and Belarus.

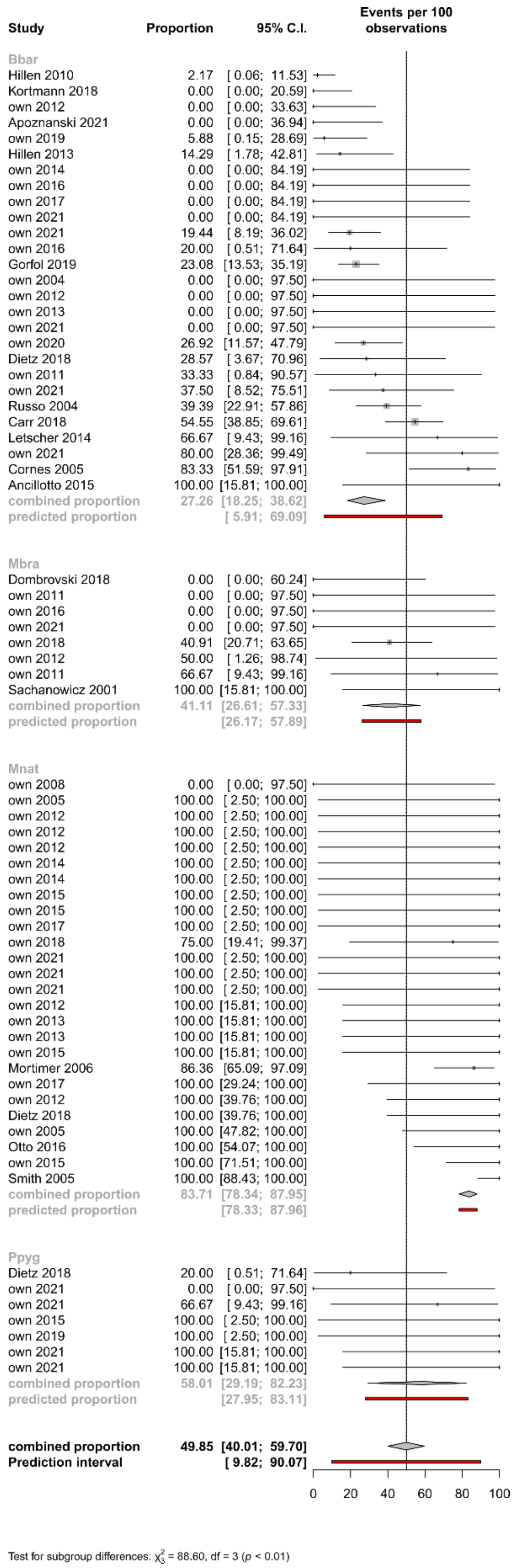


FIGURE A 4.5 Forest plot on the proportion of roosts in vital trees for 4 forest bat species. Bbar = *Barbastella barbastellus*, Mbra = *Myotis brandtii,* Mnat = *Myotis nattereri*, Ppyg = *Pipistrellus pygmaeus*. Own marks own datasets from different regions in Germany and Belarus

CHAPTER 5

5 Synopsis

Bats as highly mobile and flying mammals actively make use of all habitat dimensions for hunting and roosting. Alterations in habitat structure influence habitat use by bats directly or indirectly through changes in physical clutter, prey availability, roost availability or predation risk (e.g. Yates and Muzika 2006, Dodd et al. 2012, Bouvet et al. 2016, Renner et al. 2018, Langridge et al. 2019, Basile et al. 2020). In Europe, forests undisturbed by man only occupy 2.2% of the total forested area (Forest Europe 2020). Remnants of primary or old-growth forests can mainly be found in boreal Europe, European Russia or Eastern European mountainous regions (Sabatini et al. 2018). These remnants often suffer from fragmentation, isolation and an ever-increasing pressure for timber extraction (Sabatini et al. 2018). Therefore, large and coherent forest complexes like the Belovezhskaya Pushcha (*BP*) on the border between Poland and Belarus are important regions to study habitat-animal relationships of mobile species. Even though this vast woodland complex has suffered from a vivid history of man-made impacts (see 1.2), it still remains an important reservoir of untouched patches of natural or old-growth forests. I studied forest bats using different setups of automatic acoustic recording devices, while simultaneously investigating vegetation structural attributes in unmanaged broadleaved (Tilio-Carpinetum), unmanaged mixed-coniferous (Pino-Quercetum) and managed coniferous (Peucedano-Pinetum) plots. The following chapter aims to summarize, relate, and discuss the results of the three presented chapters on forest bat activity and diversity in the *BP* forest.

5.1 Natural forest gaps and bats

A key element of unmanaged forests is their demographic structure marked by the presence of trees from all age classes from seedlings to senescent trees. On stand level, this creates a mosaic of patches with trees in different age classes and with tree species assemblages depending on the successional status of the patch (Bengtsson et al. 2000). Natural succession includes tree mortality, which temporarily creates canopy gaps by dying or falling trees. Succession thus induces a form of natural disturbance. In canopy gaps, increased light incidences change local microclimate and biogeochemical nutrient cycling (Ritter 2005, Scharenbroch and Bockheim

2007, 2008, Ni et al. 2015, Thom et al. 2020). These abiotic parameters determine the fungal, plant and animal assemblages establishing in canopy gaps.

In Chapter 2, I studied the use of naturally created small canopy gaps by forest bats in the Strictly Protected Zone of the Belovezhskaya Pushcha National Park (*BPNP*). The presence of canopy gaps only had small effects on bat species activity levels, both for forest species and for species from the open space. Indeed, open-space foragers (*OSF*s) were not recorded more often in forest gaps independent of the gap size considered and their activity levels did not differ between forest types. The gaps I investigated were small-sized and not adapted for large and fast-flying *OSF* species to dive into them for hunting. Edge-space foragers (*ESF*s) were slightly more active in canopy gaps compared to the forest interior, whereas this effect disappeared on *ESF* species level. *ESF* activity declined in broadleaved stands with increasing gap area. Like narrow-space foragers (*NSF*s), they clearly preferred broadleaved forests. *NSF*s were equally active in canopy gaps and the forest interior independent of gap sizes. Bat richness was higher in canopy gaps only in mixed-coniferous plots. In the relatively species-poor mixed-coniferous forest stands, canopy openings constitute additional habitats which host different prey that can be exploited by species previously precluded from this habitat. Bat richness in broadleaved stands decreased with increasing gaps size, while the opposing trend was observed for mixed-coniferous stands. Bat richness and total bat activity were generally higher in broadleaved stands compared to mixed-coniferous stands, in line with Froidevaux et al. (2021) and Leidinger et al. (2021).

The biodiversity of intact ecosystems, i.e. ecosystems where natural processes and dynamics take place, has co-evolved and adapted to natural disturbances (Bengtsson et al. 2000). Pioneer seeds or pollen are present in seed banks, or disperse and colonise the newly created habitats, and succession begins. These ecosystems have a high resilience that allows them to recover from natural disturbances (Naeem 1998, Peterson et al. 1998). Forest management can be seen as a human-induced disturbance acting upon an ecosystem. Detailed knowledge on the impacts and frequencies of natural disturbances thus helps evaluating how forest management influences an ecosystem. However, there are important differences between natural and anthropogenic disturbances. Firstly, usually old or weakened trees are prone to create canopy gaps. Forest management however seeks to use trees still valuable for timber or woody fuel production, and therefore induces a different stand age structure. Secondly, unmanaged ecosystems have time to recover after the disturbance event, whereas management needs to take place on a more or less continuous time scale. Forest management systems emulating natural disturbances have been proposed as promising compromises between timber extraction and biodiversity conservation as part of a close-to-nature forest management (Kern et al. 2017, Weber-Blaschke and Muys 2020). Small-scaled canopy gaps mimicking natural disturbances slightly increase *ESF* activity and create attractive habitats increasing bat richness in species-poor stands.

The gaps analysed originated from single or small groups of trees dying of age or weakness. The restricted range of gap sizes limited the possibility to detect an influence of gap size on bat activity. Further research on naturally created gaps with a broader range of gap sizes would allow to define size thresholds above which canopy gaps are not used anymore by typical forest species. I focused my research on these inner forest edges without connections to other open structures. Differences between inner gap edges in the forest matrix to outer forest edges, i.e. the ecotones of forested habitats to e.g. agricultural or other open habitats are important open research questions. Furthermore, the size of edge-effects in bats is largely unknown. The determination of such an edge-effect would lead to answer the question on the importance of minimum forest patch sizes for forest bats.

5.2 Forest bats in four dimensions

In Chapter 3, I focused on seasonal vertical height use in unmanaged broadleaved and mixed-coniferous stands by temperate forest bats in the Strictly Protected Zone of *BPNP*. The vertical acoustic batcorder setup was installed simultaneously in forest gaps and in the forest interior.

Bat activity was more stratified in the forest interior than in forest gaps, in line with findings from Adams et al. (2009) and Tiago Marques et al. (2016) for bats and from Vodka and Cizek (2013) for saproxylic beetles. Bats choose their habitat according to vegetation clutter, prey diversity and abundance, seasonal energy requirements, local competitive interactions and predation (Russ et al. 2003, Lucan and Radil 2010, Andreas et al. 2012, Ruczynski et al. 2017, Roeleke et al. 2018, Salvarina et al. 2018, Vasko et al. 2020). Due to the size and the heterogeneity of the forest complex under study, I estimate that hunting and roosting resources are no limiting factors and local competition should only play a minor role in the bat assemblage (Walankiewicz et al. 2014, Ruczynski et al. 2017). Therefore and in the absence of physical constraints, flight height in gaps is mainly defined by species-dependent prey preferences. Indeed, species and guilds revealed differential vertical activity patterns which are in accordance with their preferential foraging mode or prey spectrum. Western barbastelles were most active at mid heights in canopy gaps, independent of the forest type. Soprano pipistrelles preferred foraging in the upper stratum in broadleaved forest gaps. Brandt´s bat was most often recorded near the ground in broadleaved plots both in canopy gaps and the forest interior.

Natterer´s bat as the most abundant *NSF* species preferred hunting in the lowest stratum in canopy gaps both in broadleaved and coniferous forests. Considering *OSF* species, highest activities were recorded at the highest height. However, none of the species considered was exclusively found in a certain height microhabitat, in contrast to studies in the Neotropics where the high diversity of foraging guilds, the height of canopy trees and the distinct vegetation strata leads to a more rigid stratification pattern in bat assemblages (e.g. Bernard 2001, Gregorin et al. 2017).

Seasonal variation in microhabitat choice in bats is driven by two mechanisms. The first driver is bat reproduction. Pregnant females are less agile, and lactating females have the highest energy demands (Shiel et al. 1999, Plank et al. 2012). Moreover, successful reproduction generates volant young bats which generally increase the number of hunting bats in late summer (Russ et al. 2003). Autumn is finally marked by mating behaviour and by the accumulation of fat reserves for hibernation or migration (Ciechanowski et al. 2010). The second driver is related to arthropod lifecycles and the temperature dependency of prey (Wang et al. 2010, Höhne and Dietz 2012, Mueller et al. 2012, Roeleke et al. 2018, Salvarina et al. 2018). For all species or species groups except for *Myotis* species, activity was higher during post-lactation then in early summer during pregnancy/lactation. A similar pattern was confirmed for *P. Pipistrellus* and *N. leisleri* by Russ et al. (2003), for *P. pygmaeus* by Bartonicka and Rehak (2004), for *M. daubentonii* by Bartonicka and Zukal (2003), and for *P. nathusii* by Furmankiewicz (2003). These increases in activity later in the season were related to young bats becoming volant or to mating behaviour. Moreover, I identified species-dependent shifts in horizontal and vertical microhabitat use between seasons for *P. pygmaeus* and *M. brandtii. P. pygmaeus* activity levels showed the steepest activity increase between seasons near the ground. In contrast to our results, Staton and Poulton (2012) found *P. pygmaeus* exclusively hunting in the forest canopy during post-lactation. In Bartonicka et al. (2008), the activity increase at forest sites for this species was correlated to the occurrence of certain prey groups. Possibly, both a higher agility of non-pregnant females able to exploit more cluttered habitats and changes in prey availability are responsible for the observed shifts towards lower vegetation levels during post-lactation in *P. pygmaeus* in my study. *M. brandtii* had higher activity levels during pregnancy/lactation compared to postlactation. Moreover, they were most active in the highest stratum in canopy gaps early in the season and shifted towards highest activity levels in the forest interior and near the ground later in the season. A similar tendency towards higher activity levels in the forest interior during postlactation was also observed for the narrow-space forager *M. nattereri* in our study. These shifts towards the forest interior can again be related to high agility levels of lactating and post-lactating females (Plank et al. 2012). This argument should indeed be especially relevant for gleaning *Myotis* species

Forest canopy research still leaves many questions unanswered. Bats as three-dimensionally moving animals exploit this microhabitat depending on their seasonal species-specific habitat and prey preferences. The results from Chapter 2 and 3 combined show that especially in forest gaps, bats exploit the three-dimensional space vertically. Studying bat assemblages solely from the forest floor leads to enormous underestimations in activity levels for *P. pygmaeus* and *B. barbastellus* species in forest gaps and generally for *OSF*s. Moreover, this study in a large and near-natural forest complex shows that natural canopy gaps probably were the hunting habitats of forest bats now focusing on man-made structures such as forest tracks and roads in human-altered habitats (e.g. *B. barbastellus:* Ancillotto et al. (2015), Rachwald et al. (2021)).

5.3 Bat diversity in managed and unmanaged forests: what tree-related microhabitats do forest bats prefer

In Chapter 4, I focused on diversity differences between managed and unmanaged stands in *BPNP*. Most temperate bat species are dependent on forests for some part of their life cycle. Strict forest species rely on woodlands both for roosting and hunting. I related bat activity for different management types to plot structural attributes for the four most abundant strict forest species in *BPNP*, namely *B. barbastellus*, *M. brandtii*, *M. nattereri* and *P. pygmaeus*. In a second step, I focused on tree roost selection by the four aforementioned species. To this end, I conducted a meta-analysis combining own tree roost datasets from *BPNP* and Germany with literature data from the species´ distribution ranges.

Generally, bat diversity in unmanaged stands was higher than in managed stands according to Rényi-diversity profiles, with the exception of species richness which was similar for all management types. Bat diversity was more strongly influenced by management type than by forest type. In unmanaged forests, the variability in tree height and the relative deviation in diameter at breast height (dbh) were much higher compared to the managed plots. These parameters describing vertical and horizontal structural heterogeneity have been positively associated to bat activity, occurrence or diversity (Jung et al. 2012, Froidevaux et al. 2016, Renner et al. 2018, Langridge et al. 2019, Alder et al. 2020, Franke et al. 2020). Evenness in unmanaged stands was higher independent of the forest type. Managed coniferous stands possessed a clear dominance pattern in activity for Western barbastelles and *nyctaloid* species. Species dominance patterns have been associated to homogeneous structural forest attributes (Dieler et al. 2017), which in turn lead to a less diverse prey supply and fewer structural foraging niches (Renner et al. 2018, Langridge et al. 2019). My results corroborate findings from Celuch and Kropil (2008) who found highest Shannon-diversity-index values in the forest interior, and lowest values for human-made structures such as forest edges and forest roads in a beech-oak forest in the Carpathian Mountains. Furthermore and in concordance with my results, the dominance of individual species was best balanced in the forest interior (Celuch and Kropil 2008).

Western barbastelles were most active in unmanaged broadleaved and managed coniferous forests. The remaining three forest species considered clearly preferred hunting in unmanaged broadleaved forests. Species-specific habitat preferences were best explained by low basal area (Western barbastelles, soprano pipistrelles and Brandt´s bats) and by the proportion of broadleaved trees for soprano pipistrelles, Brandt´s bats and Natterer´s bats. Indeed, the two managed plots inducing the extremely high Western barbastelles´ activity values had very evenly and widely spaced pine trees. Western barbastelles are more constrained by their very narrow trophic niche than by habitat type (Sierro 1999, Carr et al. 2020), which explains the higher diversity of habitats where this species can be found (e.g. Sierro 1999, Zeale et al. 2012, Ancillotto et al. 2015, Rachwald et al. 2018). Both *Myotis* species at least partly glean arthropods from vegetation surfaces (Swift and Racey 2002, Siemers and Swift 2006, Roswag et al. 2015, 2019). Broadleaved trees such as *Quercus* species harbour a higher arthropod diversity and/or abundance (spiders: Floren et al. (2008), phytophagous beetles: Sprick and Floren (2008), Heteroptera: Gossner (2008), and forests with a higher proportion of broadleaved trees may therefore be attractive hunting habitats for these species. For soprano pipistrelles, their preference for broadleaved forests in my study corroborates findings from Russ and Montgomery (2002), Davidson-Watts et al. (2006), Nicholls and Racey (2006) and Froidevaux et al. (2021). As edge-space foragers, both *M. brandtii* and *P. pygmaeus* preferred foraging in less dense stands. These findings are in line with Fuentes-Montemayor et al. (2013), Froidevaux et al. (2016), Froidevaux et al. (2021) and McKay (2020), but opposing results are also known from literature for both species (Tillon et al. 2016).

In this analysis, managed stands were represented with lower sample sizes than unmanaged stands. However, managed stands were sampled between 8-12 whole nights which is estimated as sufficient to register the species assemblage present. Moreover, I was not able to include broadleaved managed stands into the study design. This limits the interpretation on broadleaved stand preferences by *P. pygmaeus*, *M. nattereri* and *M. brandtii.*

In conclusion, bat diversity in *BPNP* is most influenced by management type, while bat activity is most influenced by habitat type. When analysing biodiversity changes in human-altered habitats, evenness should be taken into consideration as an important biodiversity measure.

Functional diversity in bats is frequently described with the foraging guild concept established by Denzinger and Schnitzler (2013). Physiological and morphological characteristics related to bat feeding ecology are used to establish these guilds. Within this framework, habitat use is mainly a function of habitat structure and prey availability and can be described using ecomorphological attributes. Many temperate bats rely on trees for roosting (Dietz et al. 2009). Tree cavities, crevices or loose bark are chosen depending on species-specific heterothermic behaviour, reproductive stage, sociability or predation risk (Sedgeley 2001, Boyles 2007, Otto et al. 2016, Bergeson et al. 2021). The occurrence and diversity of adequate tree roosts thus as well fundamentally influences bats´ habitat choice (Regnery et al. 2013, Paillet et al. 2018, Basile et al. 2020). The structural description of tree roosts answers proximate questions on roost choice, but of course ignores its ultimate reasons, such as species-specific heterothermic behaviour, reproductive stage, sociability or predation risk (Sedgeley 2001, Boyles 2007, Otto et al. 2016, Bergeson et al. 2021). Regular roost switching as an adaptation to variable climatic conditions and as a parasite minimisation strategy reinforce the need of a high diversity and abundance of tree roosts to meet these needs (Reckardt and Kerth 2007, Patriquin et al. 2016, Ruczynski and Barton 2020). I analysed datasets from 12 countries on tree roost preferences according to tree type (coniferous versus broadleaved), tree vitality and tree roost type using a meta-analytic framework. The analysis allowed to identify species-specific roosting needs.

I identified Western barbastelles and Natterers bats to be roost specialists, whereas Brandt´s bats and soprano pipistrelles used a broad variety of roost types. Western barbastelles almost exclusively relied on peeling bark on snags for roosting. The existence of dead standing trees is thus of fundamental importance for Western barbastelle conservation measures and salvage logging practices of bark-beetle infested stands negatively impact their roosting opportunities (Thorn et al. 2020). As a more cryophilic species, Western barbastelles seem well adapted to the more extreme temperatures and temperature variations reported from deadwood cavities (Wiebe 2001, Jurczyszyn et al. 2003). Natterer´s bats preferred roosting in cavities or crevices in vital broadleaved trees. Tree-related microhabitats (TreMs) are defined as “a distinct, well delineated structure occurring on living or standing dead trees that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed” (Larrieu et al. 2018), and thus include tree roosts used by forest bats. Unmanaged forests harbour a higher density and diversity in TreMs than managed stands (Walankiewicz et al. 2014, Asbeck and Kozák 2021, Courbaud et al. 2021). The formation of TreMs is driven by large tree diameters, altitude and the living status of trees (Asbeck et al. 2019, Paillet et al. 2019, Courbaud et al. 2021). Thus, the retention of large vital trees as so-called habitat trees is essential to allow for the development of tree-related microhabitats necessary for roosting of forest bats.

The identification of roosting guilds in addition and complementary to foraging guilds can be seen as a useful tool to identify essential TreMs-features that should be integrated into forest management practice. The meta-analytical approach used in Chapter 4 should be extended to a larger-scaled study integrating all European forest species to define bat roosting guilds.

5.4 Conclusions

Western barbastelle bats have a fragmented distribution throughout Europe and are categorized as rare for Belarus and classified as near-threatened by the IUCN (Shpak 2014, Piraccini 2016). In *BPNP*, Western barbastelles are the second most abundant species (Rachwald et al. 2018, 2021, 2022). Barbastelles are using a variety of habitats (Sierro and Arlettaz 1997, Sierro 1999, Zeale et al. 2012, Ancillotto et al. 2015, Carr et al. 2020, Froidevaux et al. 2021), while mainly preying on moths (Sierro and Arlettaz 1997, Carr et al. 2020). Besides specialization in habitat and roosts, prey specialization may also lead to higher extinction risks (Safi and Kerth 2004, Sagot and Chaverri 2015). Indeed, while conservation measures should focus on habitat heterogeneity and a high level of broadleaved trees for soprano pipistrelles or *Myotis* species, Western barbastelles benefit from amelioration measures focused on the larval host plants of moths consumed within the bats´ home range (Carr et al. 2020). Besides adequate available prey, Western barbastelle´s high abundance in *BPNP* is certainly due to the high availability of roosting opportunities behind the loose bark of dying spruce trees.

With its unique coherence and large size integrating a high number of untouched forest patches, the Belovezhskaya Pushcha National Park serves as a base line or study reference of a potential natural state of the forest bat assemblage. Small-scale natural disturbances creating canopy gaps are important foraging habitats for forest bats. Besides this horizontal heterogeneity, height in space creates a variety of microhabitats exploited by bats in species-specific and seasonally varying ways. This heterogeneity moreover favours the formation of a high number and variety of roosting opportunities, which in combination with the variety of hunting microhabitats increases biodiversity in unmanaged forests of the *BPNP* compared to managed forests especially considering evenness.

With my study, I underlined the value of unmanaged large and coherent forest complexes for bat diversity. On one hand, this reinforces the importance of forest national parks as large, forested areas with zones of no human intervention. These reserves are necessary for the maintenance of intact ecological networks and dynamics and can serve as species pools for other forest patches. On the other hand, forest management needs to combine ecosystem services and sustain biodiversity most effectively. An effective integration of small-scale disturbances, the creation of adequate roosting opportunities and a high local and regional heterogeneity should be integrated into near-natural forest management concepts.

5.5 References

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Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertation mit dem Titel

“Bat activity and diversity in a temperate old-growth lowland forest – Influence of horizontal and vertical structural heterogeneity on the bat assemblage of the Belovezhskaya Pushcha, Belarus”

selbstständig verfasst habe. Es wurden keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie alle wörtlich oder sinngemäß übernommenen Stellen in der Arbeit als solche und durch Angabe der Quelle gekennzeichnet. Dies gilt auch für Zeichnungen, Skizzen, bildliche Darstellungen sowie für Quellen aus dem Internet.

Falkenhagen, November 2021

Maude Erasmy