

Article

Distribution, Dominance Structure, Species Richness, and Diversity of Bats in Disturbed and Undisturbed Temperate Mountain Forests

Krzysztof Piksa ^{1,*}, Tomasz Brzuszkowski ¹ and Tomasz Zwijacz-Kozica ² 

¹ Department of Zoology, Institute of Biology, Pedagogical University of Cracow, Podchorążych 2, 30-084 Krakow, Poland; tomasz.brzuszkowski@student.up.krakow.pl

² Tatra National Park, Kuźnice 1, 34-500 Zakopane, Poland; tzwijacz@tpn.pl

* Correspondence: krzysztof.piksa@up.krakow.pl

Abstract: The increase in mean annual temperature and reduction in summer rainfall from climate change seem to increase the frequency of natural and human-made disturbances to forest vegetation. This type of rapid vegetation change also significantly affects bat diversity. The aim of our study was to document differences in the ecological parameters of bat assemblages in different types of temperate mountain forests, particularly between disturbed and undisturbed coniferous and deciduous forests. Additionally, these issues were considered along an elevation gradient. We mist netted bats on 73 sites, between 931 and 1453 m elevation, in the forests of the Tatra Mountains in southern Poland. During 2016–2020, 745 bats, representing 15 species, were caught. The most abundant were *Myotis mystacinus* (Kuhl, 1817) (53.0%) and *M. brandtii* (Eversmann, 1845) (21.5%). We observed differences in species diversity, elevational distribution, and dominance between different types of forests and forest zones. Species richness peaked at around 1000–1100 m elevation. The highest species richness and other indices were observed in undisturbed beech stands, although they constituted only about 2.7% of the forest area. The lowest species diversity was observed in disturbed coniferous forests, in both the lower and upper forest zone. The species richness and dominance structure of bat assemblages were also found to depend on the location above sea level. In some bat species, the sex ratio was higher at higher elevations, and differences in the sex ratio in a few bat species, between different types of forests, were observed. Our findings suggest that disturbed, beetle-killed spruce forests are an unsuitable environment for some bat species.

Keywords: elevational distribution; bark beetle outbreaks; Chiroptera; disturbance; *Myotis brandtii*; *Myotis mystacinus*; sex ratio



Citation: Piksa, K.; Brzuszkowski, T.; Zwijacz-Kozica, T. Distribution, Dominance Structure, Species Richness, and Diversity of Bats in Disturbed and Undisturbed Temperate Mountain Forests. *Forests* **2022**, *13*, 56. <https://doi.org/10.3390/f13010056>

Academic Editors: Susan C. Loeb and Roger W. Perry

Received: 28 November 2021

Accepted: 25 December 2021

Published: 3 January 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Bats are excellent indicators of measurable responses to environmental stressors that reflect the health of an entire ecosystem [1,2]. They are sensitive to human-induced changes to ecosystems, habitat degradation, and climatic changes [3–8].

The majority of Central European bat species are partially or entirely confined to forest ecosystems [9,10]. Forests serve as foraging areas [11,12] and provide roosts for bats [13–15].

The main tree species covering large mountain areas of Central Europe are European beech *Fagus sylvatica* L. and Norway spruce *Picea abies* (L.) Karst. The latter naturally prefer higher elevations, where spruce-dominated high-mountain forests occur [16,17]. By comparison, forests at lower elevations, dominated by deciduous species, have historically been much more intensively exploited. These changes have particularly affected stands comprising beech. In the case of this species, the area and age of beech stands have decreased significantly, and coniferous stands have often been planted in their place. However, in recent years, the proportion of beech in forests has increased in many European regions [18].

Norway spruce grows naturally on many substrates, especially on poor acidic soils and in high elevation areas, but it is also commonly planted in fast-growing, pure, and dense even-aged plantations. Due to its flat root system, spruce is not drought resistant and can be easily felled by wind [19]. When weakened by drought, storms, and fungal pathogens, the spruce stands, especially those that are pure and dense, become subject to bark beetle *Ips typographus* L. outbreaks [20]. Thus, cyclic natural disturbances on a fine and large scale are shaping the landscape of Central European mountain forests [21].

In managed or actively protected forests, natural disturbances are usually followed by salvage logging. Recent climate changes, such as the growth in mean annual temperature, reduction in summer rainfall, and more frequent large storms, seem to increase the frequency of natural and human-made disturbances to forest vegetation [22,23].

This type of rapid vegetation change significantly affects biodiversity [24,25]. In the case of bats, forest disturbances can lead to changes in bat species richness, community structure (increase in the share of non-clutter adapted bat species), activity [26–28], and summer roost availability in tree cavities and under bark [29,30], as well as probably sex and age structure and local migration routes. Elevation is also a factor that influences the local bat community [31,32]. Bat activity, species richness, and mist-netting efficiency are typically higher in lowlands than in the mountains [33,34]. The abundance of most bat species decreases with elevation, whereby the proportion of adult males to adult females increases, resulting in males being much more frequent at higher elevations [35–37].

The aim of our study was to analyze various ecological parameters relative to bats in different types of forests, particularly between the disturbed and undisturbed coniferous and deciduous forests. Additionally, these issues were considered in terms of elevation.

We tested the following hypotheses. (i) Assuming that the climatic conditions and food resources in the mountains lessen or change with increasing elevation: first, species richness would decrease with increasing elevation, and greater species diversity would be recorded at lower elevations; secondly, at higher elevations, the sex ratio would be strongly male-biased. (ii) In forests where bark beetle outbreaks produce open canopies, the number of open and edge-space bat foragers would be higher, species richness would be lower, and the sex ratio would be more male-biased. (iii) Due to a greater diversity of forest stands at lower elevations, bat species diversity is higher at lower elevations (and in deciduous stands) than at higher elevations, where stands comprising only coniferous species are predominant.

2. Materials and Methods

2.1. Study Area

Our study was conducted in the southern part of Poland in the Tatra Mountains. The Tatra Mountains, spanning southern Poland and northern Slovakia, form the highest range of the Carpathian massif, which is the highest point between the Alps and the Caucasus, and the highest between Scandinavia and the Balkan Peninsula. The elevation range is approximately 900–2650 m. Although the Tatra Mountains are much lower than the Alps, sufficient elevation and the high latitude allow for a large boreal/alpine landscape [38].

The largest number of high-mountain fauna and flora species in the region are found here, and the mountains are the northernmost center of endemism in Europe. The mountains are, therefore, an important area in the context of biodiversity protection, which is ensured by two national parks: Tatrzański Park Narodowy (TPN) in Poland, and Tatranský Národný Park (TANAP) in Slovakia.

The vegetation of the Tatra Mountains is very diverse in terms of elevation gradient. Five climatic–vegetation belts (lower montane, upper montane, subalpine, alpine, and subnival), as well as many floral and vegetation units, have been described [39].

The forest area of the TPN covers 137 km² (65% of the TPN area), but 13% is currently deforested (TPN, unpublished data). During the last four centuries, these forests have been greatly transformed by human activity. The most significant changes were caused by mining and metallurgy, poor forest management, pastoralism, air pollution, and to a lesser

extent, tourism [40]. In the last few decades, despite the protection of the Tatra Mountains in the form of national parks, the forests, especially spruce-dominated stands, have been subjected to further dynamic changes and large-scale disturbances [41–43].

The forest communities reach an elevation of approximately 1500 m above sea level (tree line) and are located within the lower and upper montane zone. The largest areas of the forest zone are covered with spruce, this being the most common tree species in the upper montane. The forest species composition of the lower montane zone (up to 1250 m a.s.l.) has been heavily transformed, mainly by past forest management. In many parts, the uneven-aged beech *Fagus sylvatica* L. and fir *Abies alba* Mill. stands of this zone were transformed into even-aged pure spruce plantations [42].

We selected 93 sites, between 931 and 1453 m a.s.l., situated in the forests of the Tatra Mountains. Bats were caught in 73 locations (Figure 1). Of these, 13 sites were situated in beech forests and 60 in coniferous forests. Among the latter, 37 were situated in the lower zone and 23 in the upper zone, and 29 and 31 in disturbed and undisturbed spruce forests, respectively.

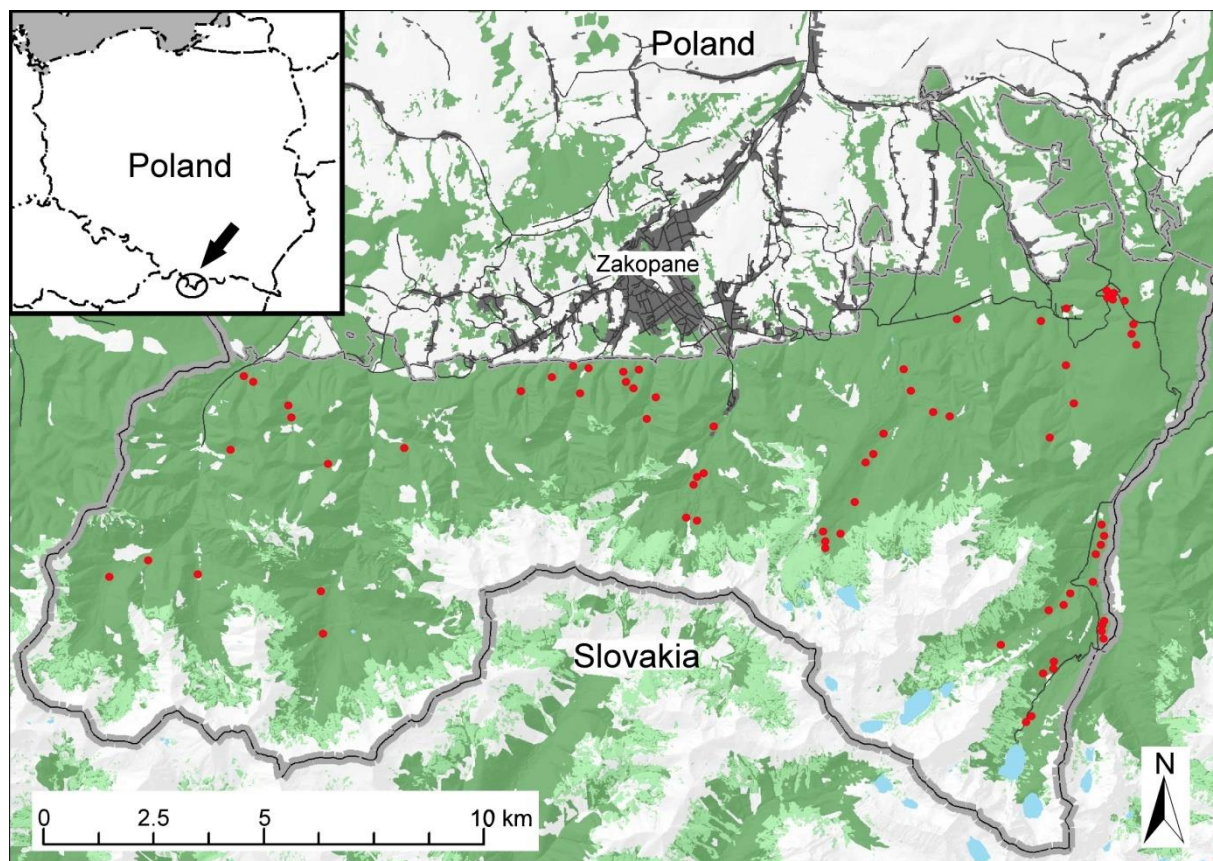


Figure 1. Location of the study area in Poland (top left) and location of 73 mist-netting sites (filled red circles) in the Polish Tatra Mountains (bottom) in the years 2016–2020.

The spruce stands found in the lower zone of the Tatra Mountains (both undisturbed and disturbed) are either artificial stands planted in the place of deciduous stands or natural spruce stands occurring on poor soils of crystalmoraines. Within these stands, bats were caught in both relatively young stands, as well as mature stands over 150 years old. In the upper forest zone, bats were mainly caught in mature, uneven-aged natural spruce stands, with individual trees exceeding 300 years of age.

In the beech stands, which constitute only 2.7% of the forest area of the Tatra Mountains, mist-netting was carried out, both in the best-preserved, uneven-aged old stands, and in young, reconstructed, 40–50-year-old stands.

Within disturbed forests, we chose sites affected by bark beetle outbreaks that resulted in severe beetle-kill ($\geq 50\%$ dead trees within 50 m of the trapping site), with empty or open canopies and trees felled by winds. Within undisturbed forests, we caught bats in sites with no beetle-killed trees, mainly with closed and sometimes with open canopies. Finally, in the beech forests, we only sampled bats in sites with closed canopies.

2.2. Capture of Bats

Bats were caught over 143 nights in 2016–2020. Between 2017 and 2019, the number of trapping sites was similar (33–38). In 2016 and 2020, surveys were conducted at 14 and 23 sites, respectively (Table S1). Most of the sites where bats were caught were located far away from landscape elements known to influence bat activity, such as wide roads, buildings, rivers, lakes, and caves [44,45]. Captures were made between June or July and the end of August or September each year. Bats were caught using one to ten mist-nets (3, 6, or 9 m long and 3 m high, Ecotone, Poland). We employed more nets per area surveyed in the disturbed coniferous stands, upper montane forests, and young beech stands to improve the efficiency of bat capture or detection probability. Mist netting started before dusk and continued until dawn or 2:00 a.m. and, less frequently, until midnight.

Captured bats were identified by species and sex and marked with different nontoxic alcohol-based color marks. They were also aged as juveniles (born that year) or adults (born the previous year or earlier), and the reproduction status of females was determined. Time of capture was also noted. Afterward, bats were released at the capture site.

2.3. Data Analysis

The species diversity was determined based on Hill numbers [46–48], in the following order of the diversity index:

- At $q = 0$, species richness; the abundances of individual species are not taken into account, so the value is simply the species richness of a given area.
- At $q = 1$, Shannon diversity index, according to the Hill formula; very abundant and less abundant or rare species all have the same weight, i.e., the value obtained is the most neutral and indicates 'true species diversity'.
- At $q = 2$, the reverse of Simpson's index; Hill's formula gives greater weight to more numerous and common species and less to rare species. Lower values at $q = 2$ indicate the strong dominance of two or three species in the assemblage.

The diversity profile curves for each belt and type of forest were plotted based on the Hill numbers. The three fixed dots on each graph indicate Hill numbers for $q = 0, 1$, and 2 . The slope of the curve reflects the unevenness of the relative species abundances.

Based on a Monte Carlo null model, the rarefaction method was used to determine the species richness for each forest type. This method makes it possible to compare sites differing in the number of species and sample size.

To assess relationships between elevation, bat abundance, and richness, we used a generalized additive model (GAM) with the Poisson error distribution and log link, where the number of species in each site was the response variable and the elevation was the explanatory variable. The elevation was modeled as a covariate fitted with penalized cubic regression splines. Chi-square statistics or Fisher's exact tests were used to test differences in the sex ratio. Spearman's correlation analysis was used to explore the association between the elevation and sex ratio. Richness and diversity analyses were performed in PAST 4.04 [49], modeling (GAM) was performed with the help of the 'mgcv' package [50] in the R program v. 2.14.0 (R Foundation for Statistical Computing, Vienna, Austria), and other analyses were conducted in STATISTICA 13.2 for Windows (Statsoft©, Inc., Tulsa, OK, USA).

3. Results

During 2016–2020 we caught 745 bats, representing 15 species and 7 genera (Tables 1 and S1).

The most numerous species, recorded at very high numbers in all types of forests, was *Myotis mystacinus*, comprising 53.0% of the captured bats. Relatively large numbers of *M. brandtii* (21.5% of the total), *Plecotus auritus* (Linnaeus, 1758) (11.1%), and *M. myotis* (Borkhausen, 1797) (6.8%) were noted. The remaining species were found in small numbers (<2%).

Table 1. Numbers of bats of each species caught in the forests of the Polish Tatra Mountains, 2016–2020. The sex ratio (proportion of males in total) is provided in brackets. Used symbols: * sex ratio significantly different from unity ($p \leq 0.05$), ^{NS} sex ratio not significantly different from unity ($p > 0.05$), + evidence of breeding (presence of adult lactating females and/or juveniles), – lack of evidence, empty—lack of species.

No.	Species	Female	Male	Total (Sex Ratio)	Status (Zone)	
					Lower	Upper
1	<i>Myotis myotis</i>	25	26	51 (0.51) ^{NS}	+	
2	<i>M. bechsteinii</i>	1	7	8 (0.88)	+	+
3	<i>M. nattereri</i>		4	4 (1)	–	
4	<i>M. emarginatus</i>		2	2 (1)	–	
5	<i>M. brandtii</i>	45	115	161 (0.71) *	+	+
6	<i>M. mystacinus</i>	126	269	351 (0.77) *	+	+
7	<i>M. alcaethoe</i>		2	2 (1)	–	
8	<i>M. daubentonii</i>		4	4 (1)	+	–
9	<i>Eptesicus nilssonii</i>	4	8	12 (0.67)	+	+
10	<i>Vespertilio murinus</i>		6	6 (1)	–	–
11	<i>Nyctalus noctula</i>	6	4	10 (0.4) ^{NS}	+	–
12	<i>Pipistrellus pipistrellus</i>	3	3	6 (0.5)	+	
13	<i>Pipistrellus nathusii</i>	1		1 (0)	–	
14	<i>Plecotus auritus</i>	13	69	83 (0.83) *	+	+
15	<i>Barbastella barbastellus</i>		1	1 (1)		–
Total		224	520	745		

Note: In one individual of *P. auritus*, the sex was not determined.

3.1. Species Richness and Elevation

Species differed from each other in their elevational range and abundance (Figure 2, Table S2). The GAM model, using elevation as an explanatory variable, showed a significant nonlinear pattern in the species richness of bat assemblages along the elevational gradient (Figure 3, Table S3). The effect of elevation fitted with the spline was highly significant ($df = 8.11$, $p < 0.001$), suggesting the highest richness around 1000–1100 m a.s.l. The adjusted determination coefficient for the model denoted 45%. Empirical and interpolated data showed a similar pattern: with the low elevational peak in species richness at 1000–1100 m a.s.l. (empirical data) and at 1000–1300 m a.s.l. (interpolated data), respectively (Figure 3, inner subplot).

3.2. Species Diversity and Dominance Structures of Bat Assemblages in Different Types of Forests

In undisturbed and disturbed spruce forests, the bat species richness was 12 vs. 7 (${}^0D = 12$ vs. ${}^0D = 7$), while the diversity at the 1D and 2D levels did not differ (Figure 4). The superdominant species in both types of forests was *M. mystacinus* (65.4% vs. 53.2%). However, its frequency was higher in undisturbed forests (Figure 5).

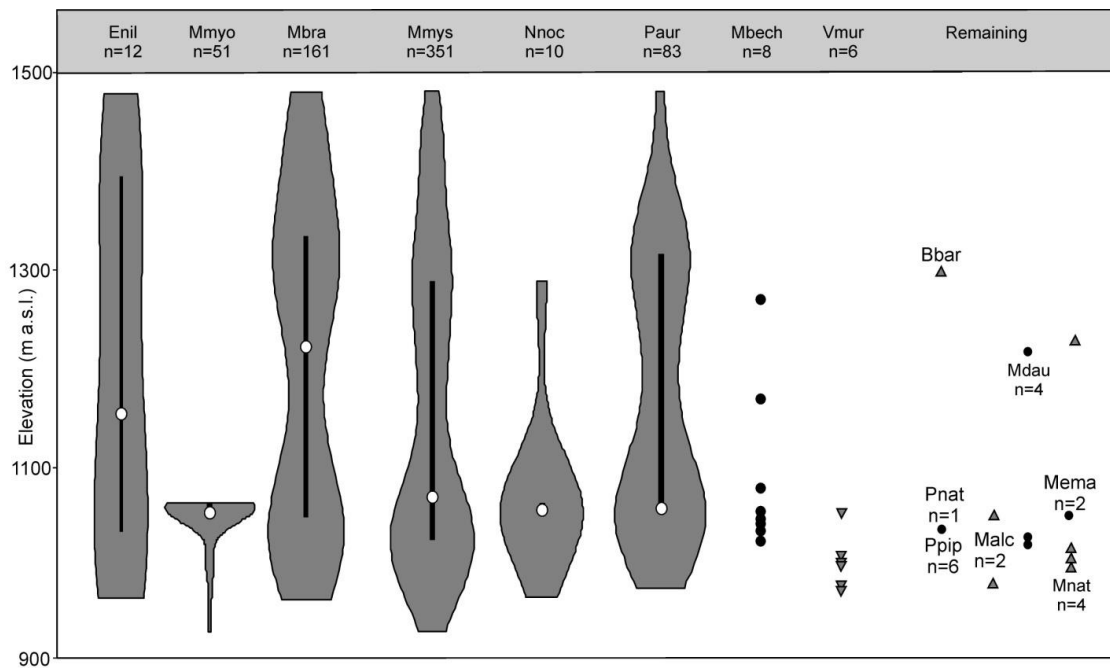


Figure 2. Distribution pattern of bats in forests of the Polish Tatra Mountains, 2016–2020 along the elevation gradient expressed with kernel density estimators and boxplots. Violin plots were used when the bat number was ≥ 10 . Total abundance of each species is given below its abbreviated name: Enil—*E. nilssonii*, Mmyo—*Myotis myotis*, Mbra—*M. brandtii*, Mmys—*M. mystacinus*, Nnoc—*Nyctalus noctula*, Paur—*Plecotus auritus*, Mbech—*M. bechsteinii*, Vmur—*Vespertilio murinus*, Ppip—*Pipistrellus pipistrellus*, Pnat—*P. nathusii*, Bbar—*Barbastella barbastellus*, Malc—*M. alcaethoe*, Mdau—*M. daubentonii*, Mnat—*M. nattereri*, Mema—*M. emarginatus*.

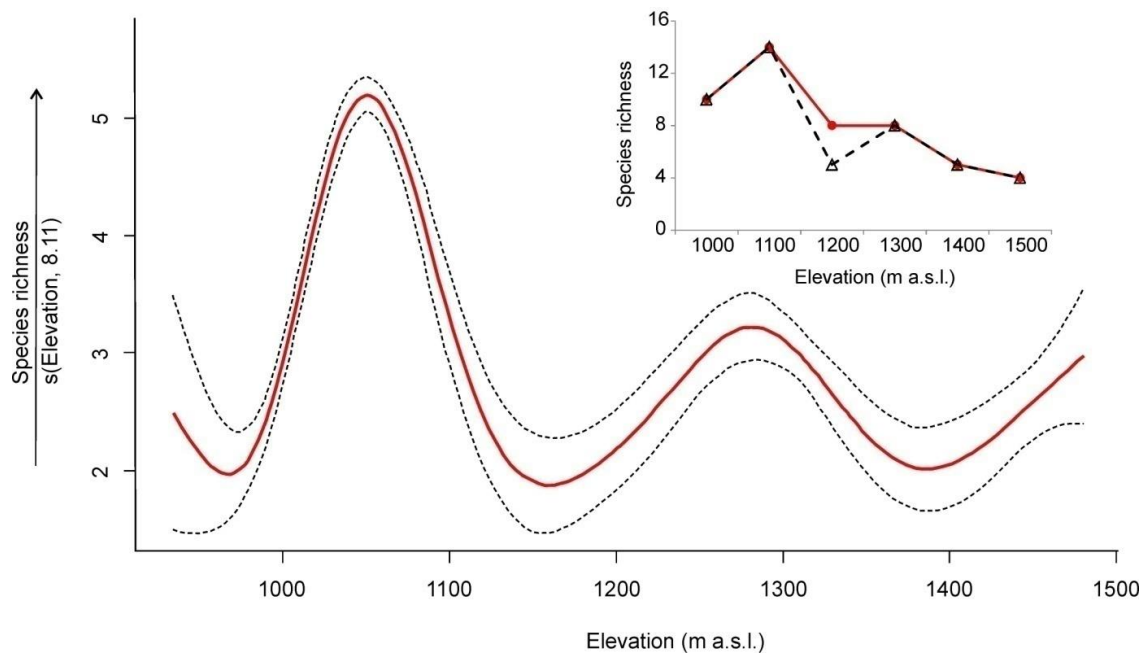


Figure 3. The variability in the species richness of bat assemblages captured in the forest of the Polish Tatra Mountains between 2016 and 2020 as a function of elevation (GAM: species richness, intercept+s(elevation)). In the inner subplot, empirical (dashed black line and empty black triangles; number of recorded species on every 100 m vertical band) and interpolated (solid red line and red circles; species were recorded in a range between the highest and the lowest records) species richness are presented.

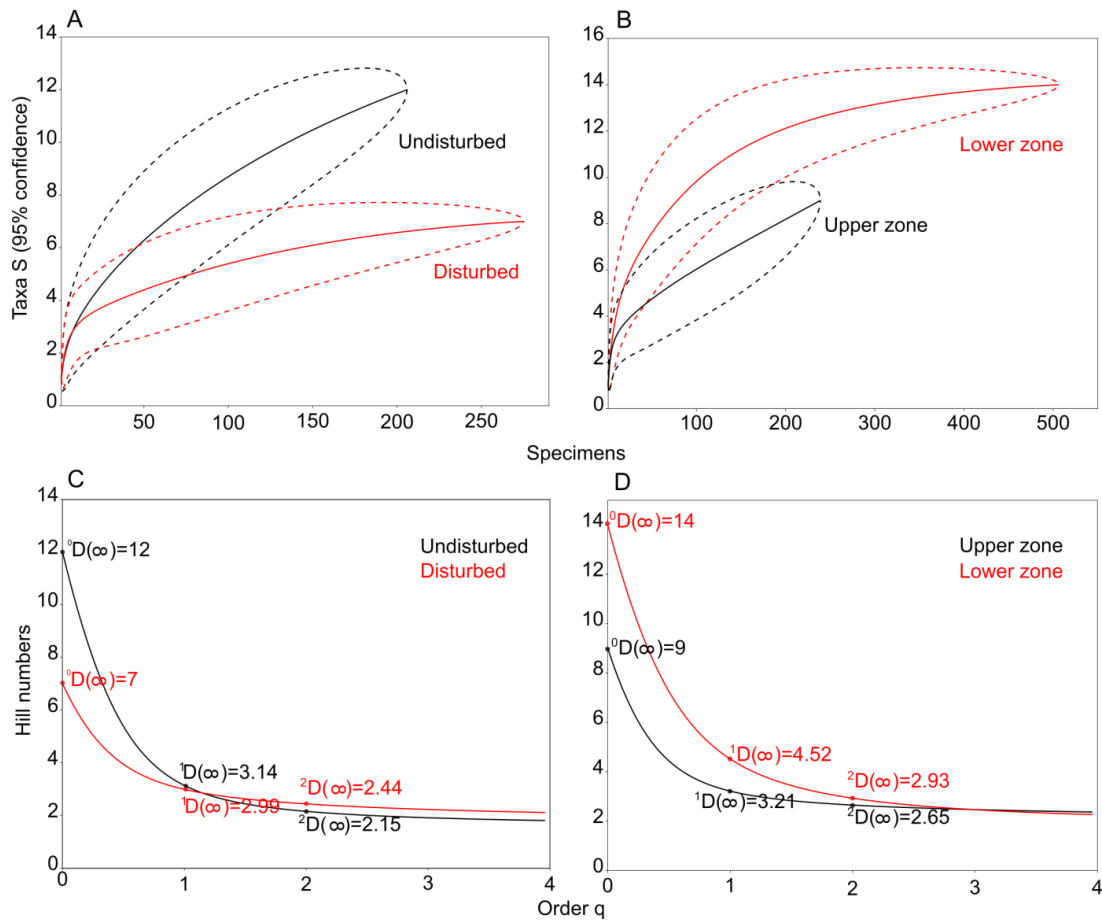


Figure 4. Rarefaction curves with 95% confidence intervals for species richness of bats (A,B) and diversity profile curve plotting Hill numbers (C,D) for the undisturbed and disturbed coniferous forests and the forests of the upper and lower zone in the Polish Tatra Mountains, 2016–2020.

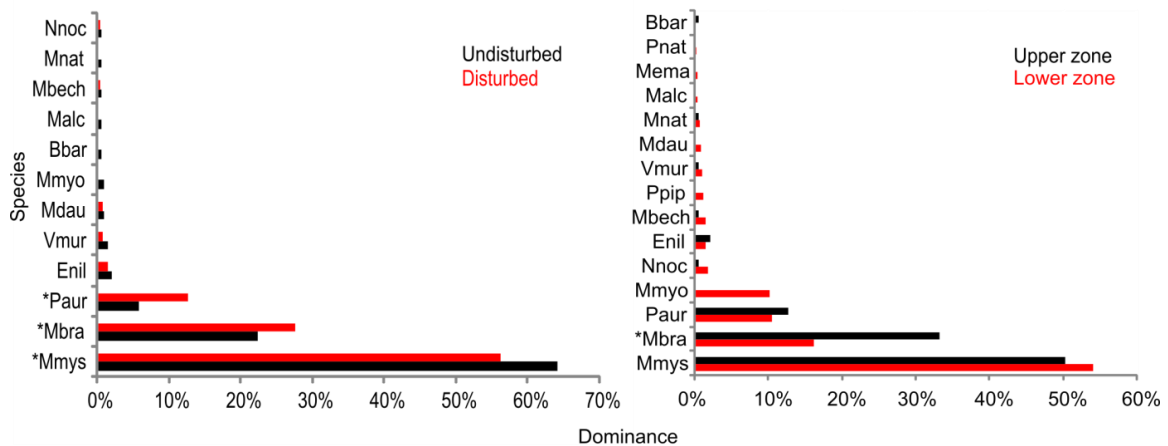


Figure 5. Dominance structure of bat assemblages recorded in the undisturbed and disturbed coniferous forests and the forests of the lower and upper zone in the Polish Tatra Mountains, 2016–2020. Used symbols: * frequency of species significantly differing between forests ($p \leq 0.05$). For species abbreviations see description of Figure 2.

Between the lower and upper forest zone, differences in the bat species diversity (with the exception of diversity at 2D) were observed (Figure 4). However, in the upper forest zone, the species richness was underestimated. The superdominant species in both forest

zones was *M. mystacinus* (54.2% vs. 50.4%) (Figure 5). The frequency of *M. brandtii* was higher in the upper forest zone, and *M. myotis* was absent in the forest of this zone.

The bat species richness was lower in disturbed spruce forests, both in the lower and upper forest zone, than in undisturbed forests of these zones, 6 vs. 9 species (lower zone ${}^0D = 6$ vs. ${}^0D = 9$) and 4 vs. 8 species (upper zone ${}^0D = 4$ vs. ${}^0D = 8$), respectively. Diversity at the 1D and 2D levels were higher in the upper forest zone (Figure 6). The superdominant species in all types of spruce forests was *M. mystacinus* (Figure 7).

No differences in bat species richness were found between the beech and spruce forest of the lower zone (data from the upper forest zone were excluded from analysis due to lack of deciduous forest in this belt). However, differences were observed in other indices of diversity (Figure 8). The superdominant species in both types of forests was *M. mystacinus* (40.6% vs. 69.9%); however, the frequency of this species was higher in coniferous forests. The frequency of gleaning species *M. bechsteinii* (Kuhl, 1817), *M. myotis*, *M. nattereri* (Kuhl, 1817), and *P. auritus* was higher in the deciduous forest than in the coniferous (36.9% vs. 21.4%; $\chi^2 = 13.92$, $df = 1$, $p < 0.001$). The frequency of *M. myotis* and *M. brandtii* was also higher in deciduous forests than in coniferous forests (Figure 9).

Between the spruce forests of the lower and upper zones, both the bat species richness and other diversity indices did not differ (Figure 8). The superdominant species in both types of forests was *M. mystacinus*; however, the frequency of this species was higher in coniferous forests of the lower zone (69.1% vs. 50.5%). The frequency of *M. brandtii* and *P. auritus* was higher in the spruce forests of the upper zone than in the lower zone (Figure 9).

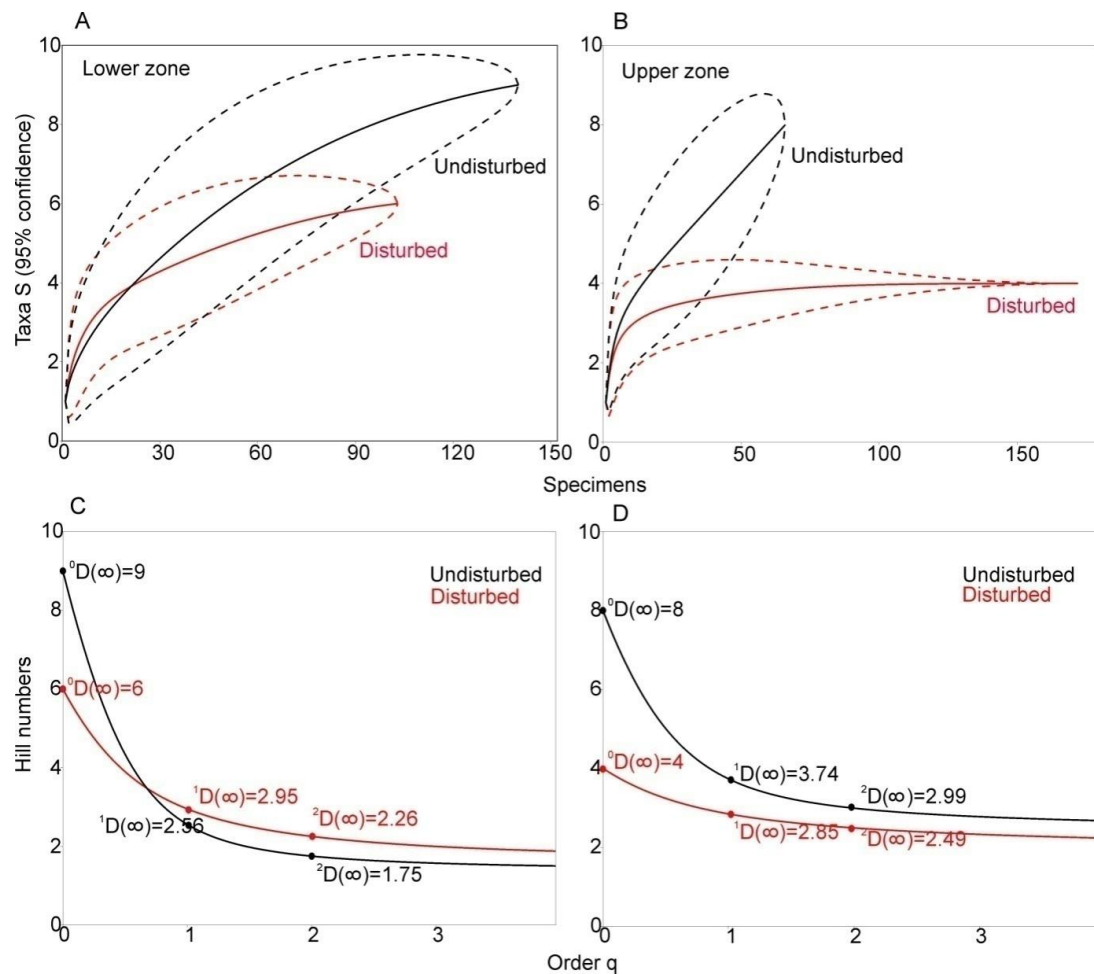


Figure 6. Rarefaction curves with 95% confidence intervals for species richness of bats (A,B) and diversity profile curve plotting Hill numbers (C,D) for the undisturbed and disturbed coniferous forests of the lower and upper forest zone in the Polish Tatra Mountains, 2016–2020.

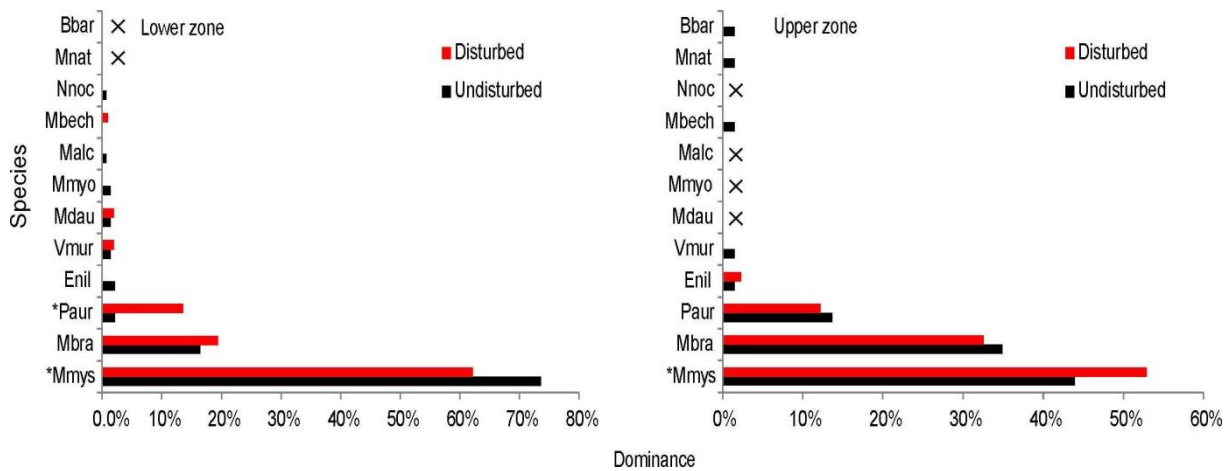


Figure 7. Dominance structure of bat assemblages recorded in the undisturbed and disturbed coniferous forests of the lower and upper zone in the Polish Tatra Mountains, 2016–2020. Used symbols: * species frequency significantly differed between forests $p \leq 0.05$, X—lack of species. For species abbreviations see description of Figure 2.

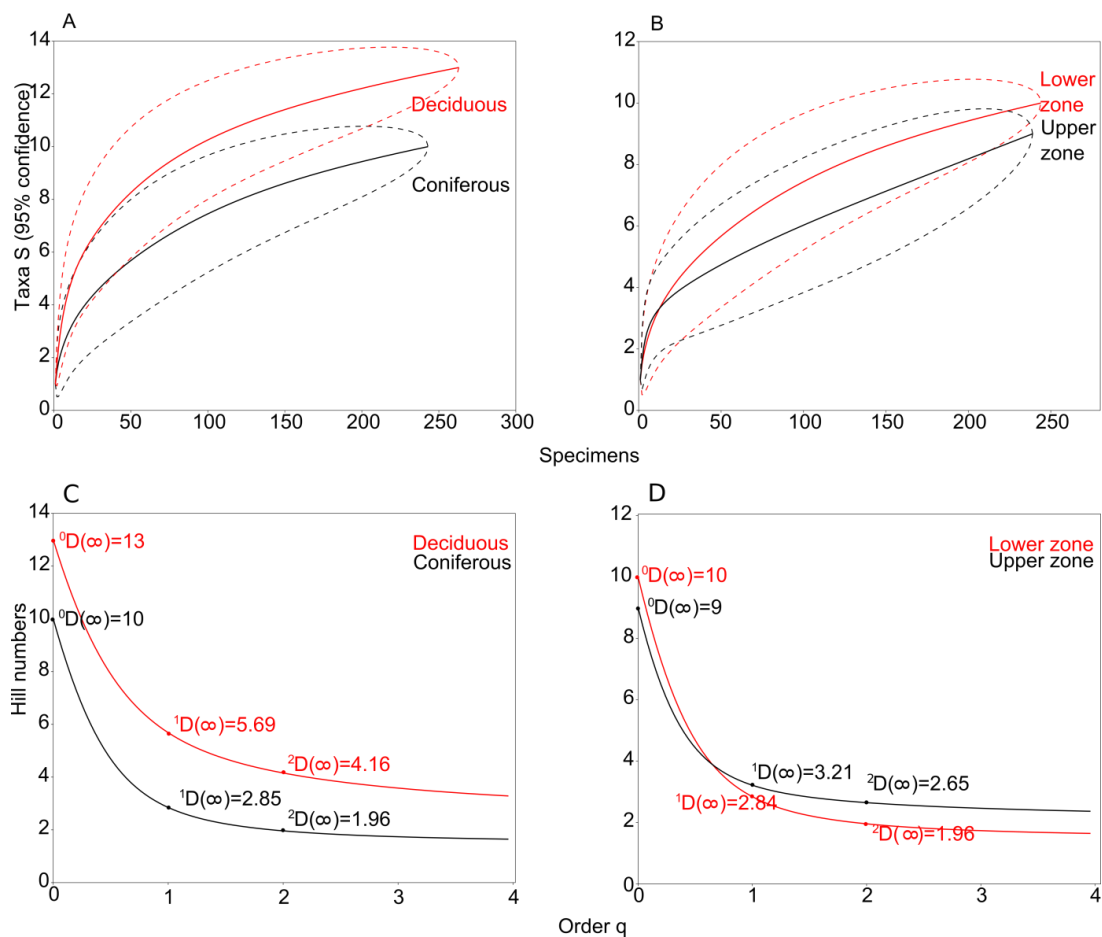


Figure 8. Rarefaction curves with 95% confidence intervals for species richness of bats (A,B) and diversity profile curve plotting Hill numbers (C,D) for the deciduous and coniferous forests of lower forest zone (data from upper forest zone were excluded from analysis due to lack of deciduous forest in this belt) and undisturbed coniferous forests of lower and upper forest zone in the Polish Tatra Mountains, 2016–2020.

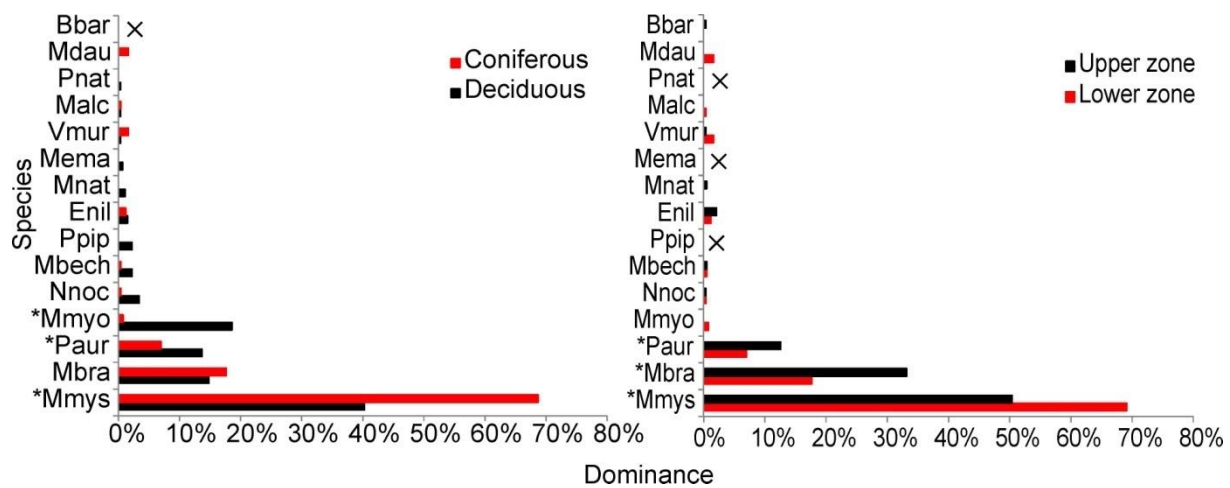


Figure 9. Dominance structure of bat assemblages recorded in the deciduous and coniferous forests and coniferous forests of the upper and lower zone in the Polish Tatra Mountains, 2016–2020. Used symbols: * frequency of species significantly differed between forests $p \leq 0.05$, X—lack of species. For species abbreviations see description of Figure 2.

3.3. Sex Ratio

The sex ratio was highly male-biased for *M. mystacinus*, *M. brandtii*, and *P. auritus* (Table 1). In the case of *M. mystacinus* and *M. brandtii*, the value of the sex ratio increased with elevation (Figure 10). It was higher in the upper forest zone than in the lower zone (0.82 vs. 0.62 and 0.85 vs. 0.60, respectively). In the case of *P. auritus*, this pattern was not observed (0.83 vs. 0.87, respectively). In *M. myotis*, the proportion of males to females was almost equal (Table 1). Between the different types of forests, statistically significant differences in sex ratio in *M. mystacinus* and *M. brandtii* were also observed (Table S4). In *M. mystacinus*, the proportion of females was higher in coniferous forests of the lower zone than in the upper zone and, similarly, higher in disturbed coniferous forests of the lower zone than in the upper forest zone. There are more differences in the case of *M. brandtii*. Differences in sex ratio in this species were observed between coniferous forests of the lower and upper zone, disturbed and undisturbed coniferous forests, disturbed forests of the lower and upper zone, and undisturbed and disturbed coniferous forests in the upper zone (Table S3).

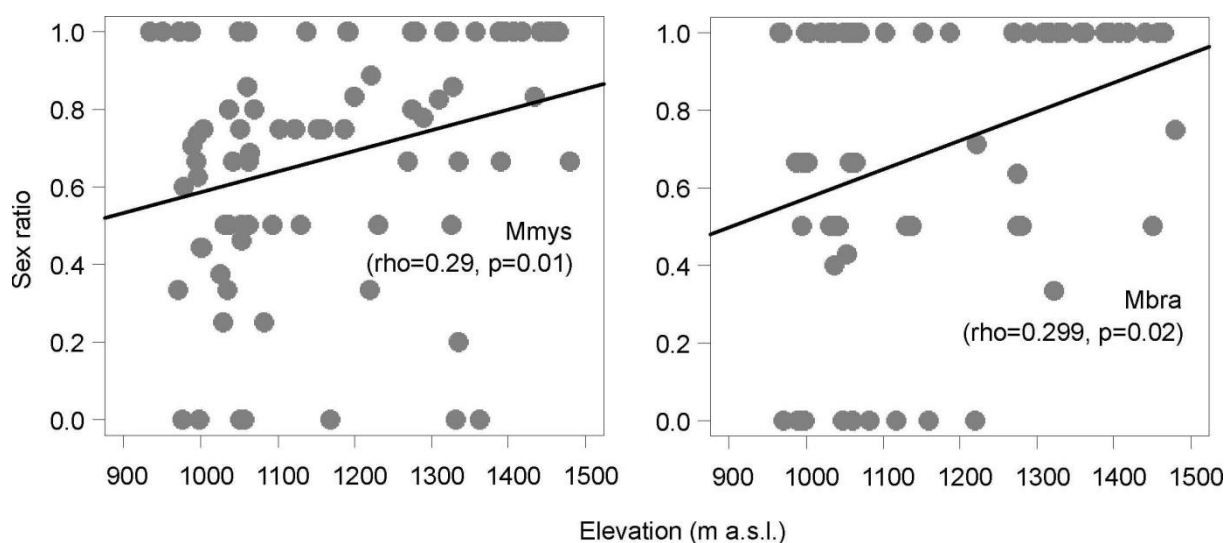


Figure 10. Changes in the sex ratio of *M. mystacinus* (Mmys) and *M. brandtii* (Mbra) along the elevation gradient in the forest of the Polish Tatra Mountains, 2016–2020.

4. Discussion

The dominance of bats from the *Myotis mystacinus* group is a common (indeed, the most characteristic) feature of the summer bat assemblage of these forests. It is also one of the most characteristic features distinguishing them from most other forest areas in Europe. This species is usually less numerous in the forests of European mountain areas [10,51,52]. However, it is abundant within the coniferous forests of northern Europe [53]. The large presence of the former in the forests of the Tatra Mountains is, therefore, not surprising. This species is also the most abundant in the caves of the Tatra Mountains during swarming and hibernation [54,55]. The dominance of *M. mystacinus* in all types of tree stands of the Tatra Mountains, as well as observations from different types of forests in Slovakia [10], coniferous forest in Finland [53], and mixed woodland of Ireland [56], seem to indicate that this species is usually a woodland generalist and not associated with a particular forest type. This species is also adapted for foraging along riverside and riparian habitats [10,56–59], preferring small woodlands, groves, and tree clusters in fields [59]. It is a species that usually avoids open landscapes [59], although, in Westphalia, its activity was observed in this type of habitat [57]. Therefore, it is a species with a relatively high adaptation capacity, in terms of its choice of feeding sites.

M. brandtii is considered a species more associated with forests [57], compared to *M. mystacinus*. Important habitats of this species also include watercourses and water reservoirs [51,57]. In the Tatra Mountains, this species was found in all types of tree stands. However, this species was more abundant in deciduous stands and upper montane stands (mainly intact stands). Its higher abundance in the forests of the upper montane region, which have retained their primeval character to a much greater extent [40], as well as in the mixed stands, which are the remains of the extensive beech and fir stands of the lower montane region, suggests that this species is associated with primeval mountain forests. Surprisingly, we found a particularly high frequency of this species in forests of the upper montane zone, compared to the lower montane region. To date, all observations in the Tatra Mountains and Polish Carpathian Mountains—of the summer activity, swarming, and the hibernation period—indicate that this species prefers lower montane regions compared to *M. mystacinus* [54,55,60]. It seems that, with respect to this particular species, tree stand quality may be the decisive factor behind the higher frequency of this species in the forests of the upper mountainous region of the Tatra Mountains. The forests of this montane zone have retained their primeval character to a much greater extent, and a smaller acreage is affected [40]. During the so-called Holocene ‘forest optimum’, this species was more numerous than *M. mystacinus* [61], which corroborates the hypothesis that this species is associated with primeval mountain forests. The period was also a geological epoch when the range and area of deciduous and coniferous forests were the largest in the Tatra Mountains.

Eptesicus nilssonii (Keyserling & Blasius, 1839) is surprisingly sparse in the forests of the Tatra Mountains, especially in the upper mountain belt. In Central Europe, this species is mainly adapted to the hemiboreal coniferous forest [62]. It is also considered by Jaberg and Guisan [31] to be a unique, high-elevation species. Similarly, in Bulgaria, where the Mediterranean species dominate, this northern species occurred only at the highest elevations [63]. The low abundance of this species in the forests of the Tatra Mountains may be due to several factors. Perhaps it is related to the slightly different preferences of this species in this area. Preliminary observations indicate that, in the Tatra Mountains, this species is the most active along watercourses and riverside areas and in open spaces [58]. Perhaps it is also due to the open-space foraging strategy of this species and the limited possibility of capturing it in the nets. *E. nilssonii* is an extremely psychrophilic boreal species and, therefore, particularly susceptible to climate change [64]. Perhaps the large-scale disturbances of spruce stands and the climatic change, which is manifested by the appearance in the Tatra Mountains of previously absent thermophilous species [55], can have an impact on their abundance. A decline in those species seemed to be confirmed by the observations from its swarming sites in the Tatra Mountains, especially

in the hibernation period, which confirms the decline in the number of these species (Piksa, Brzuszkowski, and Nowak, unpublished data). A dramatic decline in northern bat numbers, probably caused by climatic changes, was also observed over a 30-year period in Sweden [65].

We observed differences between the elevational ranges of bat species. In the forests of the Tatra Mountains, it seems that *M. mystacinus*, *M. brandtii*, *P. auritus*, and *E. nilssonii* are elevational generalist species. The remaining species, taking into account both the abundance and the elevational range spectrum, are species that prefer rather lower elevations. It is also possible that the population abundance is too small to correctly assess their preferences in this regard. Similar patterns regarding elevational ranges, concerning the species mentioned above, are consistent with observations from the summer period from many mountain ranges of Europe, including the Alps [35], the Pyrenees [66], and the Slovak and Czech part of the Carpathians [10,36,67]. A very similar valence, in terms of elevational range, was observed in the Polish part of the Carpathians from the hibernation and swarming periods [54,60].

We found that the species richness of bat assemblages was not evenly distributed with elevation, reaching the highest values between approximately 1000 and 1100 (or 1000–1300 m a.s.l.). This peak in bat species richness in this elevational range seems to be the effect of more heterogeneous forest landscapes in this area, characterized by the presence of both coniferous and deciduous stands. The presence of the latter is significant, and activity and species richness are known to be exceptionally high in deciduous-dominated stands [28,68]. At higher elevations in the Tatra Mountains, almost solely coniferous stands are found, which represent generally poorer-quality habitats for bats, compared with deciduous and mixed forests [69].

On the other hand, this picture of bat species richness may have been influenced by significant differences in the number of individuals captured at different elevations. The rarefaction curves from different elevation ranges indicate that this picture of species richness was not significantly affected by significant differences in bat numbers. Only in the elevation range between 1200 and 1300 would greater species richness be expected (see Figure S1).

Natural disturbances occurring in forest ecosystems increase habitat heterogeneity. These, in many cases, lead to an increase in species richness in various taxa, including vertebrates, e.g., woodpeckers [70,71], the presence of tree cavities for bird cavity-nesters [26,30,72], and also bats [26,70]. In the case of bats in this type of forest stand, an increase in the number of available roosts [29,30], number of bats, and species richness [26,27] are observed, which also leads to an increase in the feeding activity of bats, especially those hunting in open spaces [73]. However, sometimes, differences in species richness or activity of bats are not observed [74,75].

In the case of the Tatra Mountains, the opposite is observed in terms of species richness, both in the upper and lower montane forests in the state of advanced bark beetle outbreaks. The bat species richness was lower in relation to those parts of the stands that had not yet been subjected to disturbance and not covered with bark beetle gradation. In the Tatra Mountains, almost 90% of the caught bats, regardless of the elevation or the type of tree stand, were bats of the genus *Myotis* and *Plecotus*. Many studies have indicated that most bat species of these genera found in Europe forage in highly cluttered or background-cluttered spaces, within tree stands and on their edges [76–79]. In the case of the Tatra Mountains, the lower species richness in the disturbed forests seems to be related to the deterioration of the habitat conditions. When the natural protection in the form of canopy cover is lost, the area becomes more open and less optimal, thereby causing a decrease in the relative activity [68,80].

On the other hand, the open spaces created may increase the availability of prey for bats unable to hunt in cluttered spaces, e.g., *Nyctalus* spp., *Pipistrellus* spp., and *E. nilssonii*, [62,81] and, consequently, increase the activity of this specific group of bats. Based on the bats caught in the nets, these observations could not be confirmed in the Tatra

Mountains forests. Weather conditions may also affect the lower richness of bat species in disturbed stands. The harsher weather conditions occurring at higher elevations in the mountains are an important factor limiting the presence of bats [32]. On the edge of the forest and in open areas, weather conditions (temperature, wind speed) are more unstable than in the tree stands [82].

In mountainous conditions, where the lability of weather conditions is greater, forest stands with dense canopy cover (compared to canopy openness stands in an advanced stage of disturbance) seem to provide bats of the genus *Myotis* and *Plecotus* with more stable conditions. They also likely offer protection against unfavorable weather conditions, strong winds, and other extreme weather events [83]. Additionally, this can also help bats avoid aerial predators by reducing light [84]. Our observations confirmed those hypotheses. No bats were caught almost twice as often in disturbed stands. More often, due to weather conditions, catching was abandoned in these areas (most often due to gusty winds and heavy fog). However, bats were caught during gusty winds in dense spruce stands and, especially, in beech stands. Interestingly, bats of the genus *Pipistrellus* hunting in the beech tree stand were only caught successfully during gusty (high) winds.

It cannot be ruled out that the activity of bats hunting at higher elevations, e.g., of the genera *Nyctalus*, *Pipistrellus*, and *E. nilssonii*, may be increasing in that location. Moreover, the lack of these species during mist-netting may be a result of the disadvantages of the method used in this study [85]. The mist-netting was performed in a small area, up to a height of approx. 3–4 m. This could have resulted in limiting the bats caught from these particular sites.

Considering age–sex structure, two categories of species can be distinguished among bats caught in the forest areas of the Tatra Mountains. In most of the bat species (with relatively small home range) [59,77] caught in the Tatra Mountains, males were more numerous. The prevalence of males at a higher elevation is typical for the mountain bat populations [33,86,87]. This spatial segregation is the result of the different energy requirements of both sexes. Living at higher elevations with lower average temperatures seems to be beneficial for adult males. Inactivity during the day allows bats to effectively save fat reserves. Breeding and lactating females must maintain homeothermy, in order to maintain fetal development and subsequent lactation. This leads to higher female abundance at lower elevations, where they can find warmer summer roosts and where more-productive feeding grounds are available [33,37,86,88].

The second group, in which no male predominance was found, consists of the species *M. myotis* and *N. noctula* (Schreber, 1774). Unlike the previous group, these species can hunt at a considerable distance from their summer roosts [89–91], sometimes even over 20 km away. They presumably penetrate the Tatra forests from the lower situated summer roosts and feed in the most abundant feeding areas (in this case, deciduous forests). In the case of the thermophilous species *M. myotis*, the roosts are presumably located in the attics of buildings at the foot of the Tatra Mountains (where the thermal conditions in the roosts are certainly more favorable and the number of potential roosts is greater). This species has no summer roosts found within the Tatra Mountains [58]. Similarly, in the case of *N. noctula* in the Tatra Mountains, only one known roost of this species is located at a low elevation [92].

In this study, the highest value of the species richness parameter in bat communities (and a more balanced structure) was found in the beech stands, even though the area of these stands in the Polish part of the Tatra Mountains is exceptionally small (beech constitutes 2.7% and 6.6% of tree volume or 4% and 3.9% of tree number, respectively [42]). Most deciduous forests in the Tatra Mountains have been destroyed due to overharvesting and intensive forest management [40]. In contrast to spruce stands, in beech forest bat assemblages in the Tatra Mountains, a frequency of gleaning from the ground and leaves species (*M. bechsteinii*, *M. myotis*, *M. nattereri*, and *P. auritus*), are higher (36.9% vs. 21.4%). Open-space species, such as *N. noctule*, and species of the genus *Pipistrellus* are also present. With the dominant structure of bat communities, these forests are mainly similar to the deciduous forests of Central Europe and the Carpathians [36]. The presence of bats with

different hunting strategies in those forests is a result of their structure. The typical beech forests of the Carpathians usually have a more open structure compared to, e.g., spruce forests [36]. The large space between the tree canopy and the ground favors a high bat activity [11,36,93]. Due to the very poor understory zone in the beech forests of the Tatra Mountains, it is easier for bats to access prey inhabiting the ground or staying on the leaf surfaces, compared to coniferous stands.

5. Conclusions

This study is one of few in Europe to analyze bat diversity in undisturbed and disturbed forests of temperate mountains. Disturbances in spruce stands, related to bark beetle outbreaks and winds, have a significant impact on reducing the occurrence of bats and causing a decline in their species diversity. Our results highlight the vital role of broadleaved forests in bat species diversity. They also confirm elevation as a factor influencing species diversity and limiting the elevational range of bats in mountain areas. In recent decades, highly dynamic changes have been observed in the stands of the Tatra Mountains. The most visible effect of this is a very rapid natural decay of spruce stands covering huge areas and, at the same time, their renewal in some areas of mixed coniferous and broadleaved forests. Due to these changes of tree stands, a change in bat species diversity and the structure of bat communities in the Tatra Mountains can be expected. This issue requires further research in this area. Understanding this process will be of considerable value for knowledge about the impact of natural disturbances on animal populations in the forest ecosystem.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f13010056/s1>. Table S1: Numbers of bats of each species caught between 2016 and 2020 during particular years in the forests of the Polish Tatra Mountains. Table S2: Numbers of bats of each species caught on every 100 m vertical band in the forests of the Polish Tatra Mountains. Table S3. Summary of generalized additive models (GAM) explaining the number of bat species in the forests of the Polish Tatra Mountains on the basis of elevation. Table S4. Comparison of frequency of sex in *Myotis mystacinus* and *M. brandtii* between different types of forests in the Polish Tatra Mountains. Figure S1: Rarefaction curves for species richness of bats caught on every 100 m vertical band in the forests of the Polish Tatra Mountains.

Author Contributions: Conceptualization, K.P. and T.Z.-K.; methodology, K.P.; validation, K.P. and T.B.; formal analysis, K.P. and T.B.; investigation, K.P. and T.B.; resources, K.P., T.Z.-K. and T.B.; data curation, K.P. and T.Z.-K.; writing—original draft preparation, K.P.; writing—review and editing, K.P. and T.Z.-K.; visualization, K.P., T.Z.-K. and T.B.; supervision, K.P.; project administration, K.P. All authors have read and agreed to the published version of the manuscript.

Funding: This project was supported by the resources of the Polish State Forests Fund transferred to the Tatra National Park by State Forest National Holding in 2016–2019, and in 2020–2021, it was supported by the Institute of Biology Cracow Pedagogical University (WPBU/2020/05/00403).

Institutional Review Board Statement: Our methodology fully complies with institutional, national, and international guidelines on wildlife research. All the activities were carried out under permits from the Polish Ministry of Environment and Tatra National Park.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We are grateful to friends who assisted with fieldwork, especially Justyna Ślęzak and Wojciech J. Gubała. We thank the Tatra National Park staff for enabling this research.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Wickramasinghe, L.P.; Harris, S.; Jones, G.; Vaughan, N. Bat activity and species richness on organic and conventional farms—Impact of agricultural intensification. *J. Appl. Ecol.* **2003**, *40*, 984–993. [[CrossRef](#)]
2. Jones, G.; Jacobs, D.S.; Kunz, T.H.; Willig, M.R.; Racey, P.A. Carpe noctem: The importance of bats as bioindicators. *Endanger. Species Res.* **2009**, *8*, 93–115. [[CrossRef](#)]
3. Fenton, M.B.; Acharya, L.; Audet, D.; Hickey, M.B.C.; Memiman, C.; Adkins, B. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the neotropics. *Biotropica* **1992**, *24*, 440–446. [[CrossRef](#)]
4. Medellín, R.A.; Equihua, M.; Amin, M.A. Bat diversity and abundance as indicators of disturbance in neotropical rainforest. *Conserv. Biol.* **2000**, *14*, 1666–1675. [[CrossRef](#)]
5. Moreno, C.E.; Halffter, G. Spatial and temporal analysis of α , β and γ diversities of bats in a fragmented landscape. *Biodivers. Conserv.* **2001**, *10*, 367–382. [[CrossRef](#)]
6. Clarke, F.M.; Rostant, L.V.; Racey, P.A. Life after logging: Post-logging recovery of a neotropical bat community. *J. Appl. Ecol.* **2005**, *42*, 409–420. [[CrossRef](#)]
7. Sherwin, H.A.; Montgomery, W.I.; Lundy, M.G. The impact and implications of climate change for bats. *Mamm. Rev.* **2013**, *43*, 171–182. [[CrossRef](#)]
8. Ramírez-Mejía, A.F.; Urbina-Cardona, J.N.; Sánchez, F. Functional diversity of phyllostomid bats in an urban–rural landscape: A scale-dependent analysis. *Biotropica* **2020**, *52*, 1168–1182. [[CrossRef](#)]
9. Meschede, A.; Heller, K.-G. *Ökologie und Schutz von Fledermäusen in Wäldern*; Bundesamt für Naturschutz: Bonn, Germany, 2000; ISBN 9783784336053.
10. Kaňuch, P.; Danko, Š.; Celuch, M.; Krištín, A.; Pjenčák, P.; Matis, Š.; Šmíd, J. Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). *Mamm. Biol.* **2008**, *73*, 147–155. [[CrossRef](#)]
11. Patriquin, K.J.; Barclay, R.M.R. Foraging by bats in cleared, thinned and unharvested boreal forest. *J. Appl. Ecol.* **2003**, *40*, 646–657. [[CrossRef](#)]
12. Lacki, M.J.; Baker, M.D. Foraging Ecology of Bats in Forests. In *Bats in Forests: Conservation and Management*; Lacki, M.J., Hayes, J.P., Kurta, A., Eds.; The Johns Hopkins University Press: Baltimore, MD, USA, 2007; pp. 83–127. ISBN 978-0801884993.
13. Ruczyński, I. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and eisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. *Can. J. Zool.* **2006**, *84*, 900–907. [[CrossRef](#)]
14. Dietz, M.; Brombacher, M.; Erasmy, M.; Fenchuk, V.; Simon, O. Bat community and roost site selection of tree-dwelling bats in a well-preserved European lowland forest. *Acta Chiropterol.* **2018**, *20*, 117–127. [[CrossRef](#)]
15. Vasko, V.; Blomberg, A.S.; Vesterinen, E.J.; Suominen, K.M.; Ruokolainen, L.; Brommer, J.E.; Norrdahl, K.; Niemelä, P.; Laine, V.N.; Selonen, V.; et al. Within-season changes in habitat use of forest-dwelling boreal bats. *Ecol. Evol.* **2020**, *10*, 4164–4174. [[CrossRef](#)] [[PubMed](#)]
16. Pretzsch, H.; Hilmers, T.; Biber, P.; Avdagić, A.; Binder, F.; Bončina, A.; Bosela, M.; Dobor, L.; Forrester, D.I.; Lévesque, M.; et al. Evidence of elevation-specific growth changes of spruce, fir, and beech in European mixed mountain forests during the last three centuries. *Can. J. For. Res.* **2020**, *50*, 689–703. [[CrossRef](#)]
17. Vacek, Z.; Prokúpková, A.; Vacek, S.; Bulušek, D.; Šimůnek, V.; Hájek, V.; Králíček, I. Mixed vs. monospecific mountain forests in response to climate change: Structural and growth perspectives of Norway spruce and European beech. *For. Ecol. Manag.* **2021**, *488*, 119019. [[CrossRef](#)]
18. Tudoran, G.-M.; Cicşa, A.; Boroeanu, M.; Dobre, A.-C.; Pascu, I.-S. Forest dynamics after five decades of management in the Romanian Carpathians. *Forests* **2021**, *12*, 783. [[CrossRef](#)]
19. Caudullo, G.; Tinner, W.; de Rigo, D. *Picea abies* in Europe: Distribution, habitat, usage and threats. In *European Atlas of Forest Tree Species*; Publication Office of the European Union: Luxembourg, 2016; pp. 114–116.
20. Wermelinger, B. Ecology and management of the spruce bark beetle *Ips typographus*—A review of recent research. *For. Ecol. Manag.* **2004**, *202*, 67–82. [[CrossRef](#)]
21. Synek, M.; Janda, P.; Mikoláš, M.; Nagel, T.A.; Schurman, J.S.; Pettit, J.L.; Trotsiuk, V.; Morrissey, R.C.; Bače, R.; Čada, V.; et al. Contrasting patterns of natural mortality in primary Picea forests of the Carpathian Mountains. *For. Ecol. Manag.* **2020**, *457*, 117734. [[CrossRef](#)]
22. Seidl, R.; Schelhaas, M.J.; Rammer, W.; Verkerk, P.J. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Chang.* **2014**, *4*, 806–810. [[CrossRef](#)]
23. Senf, C.; Seidl, R. Mapping the forest disturbance regimes of Europe. *Nat. Sustain.* **2021**, *4*, 63–70. [[CrossRef](#)]
24. Mikoláš, M.; Svitok, M.; Bollmann, K.; Reif, J.; Bače, R.; Janda, P.; Trotsiuk, V.; Čada, V.; Vítková, L.; Teodosiu, M.; et al. Mixed-severity natural disturbances promote the occurrence of an endangered umbrella species in primary forests. *For. Ecol. Manag.* **2017**, *405*, 210–218. [[CrossRef](#)]
25. Szwagrzyk, J.; Bodziarczyk, J.; Pielech, R. The impact of wind and bark beetle outbreaks and protective measures on the vegetation of spruce forests in the Tatra National Park. *Parki Nar. Rez. Przyn.* **2019**, *38*, 57–68.
26. Regnery, B.; Couvet, D.; Kubarek, L.; Julien, J.F.; Kerbirou, C. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecol. Indic.* **2013**, *34*, 221–230. [[CrossRef](#)]
27. Kotowska, D.; Zegarek, M.; Osojca, G.; Satory, A.; Pärt, T.; Żmihorski, M. Spatial patterns of bat diversity overlap with woodpecker abundance. *PeerJ* **2020**, *8*, 1–18. [[CrossRef](#)] [[PubMed](#)]

28. Rachwald, A.; Boratyński, J.S.; Krawczyk, J.; Szurlej, M.; Nowakowski, W.K. Natural and anthropogenic factors influencing the bat community in commercial tree stands in a temperate lowland forest of natural origin (Białowieża Forest). *For. Ecol. Manag.* **2021**, *479*, 118544. [[CrossRef](#)]
29. Barclay, R.M.R.; Kurta, A. Ecology and behavior of bats roosting in tree cavities and under bark. In *Bats in Forests: Conservation and Management*; Lacki, M.J., Hayes, J.P., Kurta, A., Eds.; The Johns Hopkins University Press: Baltimore, MD, USA, 2007; pp. 17–60; ISBN 978-0801884993.
30. Russo, D.; Cistrone, L.; Budinski, I.; Console, G.; Della Corte, M.; Milighetti, C.; Di Salvo, I.; Nardone, V.; Brigham, R.M.; Ancillotto, L. Sociality influences thermoregulation and roost switching in a forest bat using ephemeral roosts. *Ecol. Evol.* **2017**, *7*, 5310–5321. [[CrossRef](#)] [[PubMed](#)]
31. Jaberg, C.; Guisan, A. Modeling the distribution of bats in relation to landscape structure in a temperate mountain environment. *J. Appl. Ecol.* **2001**, *38*, 1169–1181. [[CrossRef](#)]
32. McCain, C.M. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Glob. Ecol. Biogeogr.* **2007**, *16*, 1–13. [[CrossRef](#)]
33. Grindal, S.D.; Morissette, J.L.; Brigham, R.M. Concentration of bat activity in riparian habitats over an elevational gradient. *Can. J. Zool.* **1999**, *77*, 972–977. [[CrossRef](#)]
34. Erickson, J.L.; Adams, M.J. A comparison of bat activity at low and high elevations in the Black Hills of western Washington. *Northwest Sci.* **2003**, *77*, 126–130.
35. Holzhaider, J.; Kriner, E.; Rudolph, B.U.; Zahn, A. Radio-tracking a Lesser horseshoe bat (*Rhinolophus hipposideros*) in Bavaria: An experiment to locate roosts and foraging sites. *Myotis* **2002**, *40*, 47–54.
36. Kaňuch, P.; Krištín, A. Altitudinal distribution of bats in the Pol'ana Mts area (Central Slovakia). *Biologia* **2006**, *61*, 605–610. [[CrossRef](#)]
37. Nardone, V.; Cistrone, L.; Di Salvo, I.; Ariano, A.; Migliozi, A.; Allegrini, C.; Ancillotto, L.; Fulco, A.; Russo, D. How to be a male at different elevations: Ecology of intra-sexual segregation in the trawling bat *Myotis daubentonii*. *PLoS ONE* **2015**, *10*, e0134573. [[CrossRef](#)]
38. Mirek, Z. The Tatra Mountains and the Tatra National park—General information. In *Nature of the Tatra National Park*; Mirek, Z., Głowaciński, Z., Klimek, K., Piękoś-Mirkowa, H., Eds.; TPN: Kraków, Poland, 1996; pp. 17–26. ISBN 83-85832-08-4.
39. Mirek, Z.; Piękoś-Mirkowa, H. Flora and vegetation of the Polish Tatra Mountains. *Mt. Res. Dev.* **1992**, *12*, 147–173. [[CrossRef](#)]
40. Fabijanowski, J.; Dziewolski, J. Forest management. In *Nature of the Tatra National Park*; Mirek, Z., Głowaciński, Z., Klimek, K., Piękoś-Mirkowa, H., Eds.; TPN: Kraków, Poland, 1996; pp. 675–696; ISBN 83-85832-08-4.
41. Sproull, G.J.; Bukowski, M.; McNutt, N.; Zwijacz-Kozica, T.; Szwagrzyk, J. Landscape-level spruce mortality patterns and topographic forecasters of bark beetle outbreaks in managed and unmanaged forests of the Tatra Mountains. *Polish J. Ecol.* **2017**, *65*, 24–37. [[CrossRef](#)]
42. Bodziarczyk, J.; Szwagrzyk, J.; Zwijacz-Kozica, T.; Zięba, A.; Szewczyk, J.; Gazda, A. The structure of forest stands in the Tatra National Park: The results of 2016–2017 inventory. *For. Res. Pap.* **2019**, *80*, 13–21. [[CrossRef](#)]
43. Ochtyra, A. Forest disturbances in Polish Tatra Mountains for 1985–2016 in relation to topography, stand features, and protection zone. *Forests* **2020**, *11*, 579. [[CrossRef](#)]
44. Mehr, M.; Brandl, R.; Hothorn, T.; Dziock, F.; Förster, B.; Müller, J. Land use is more important than climate for species richness and composition of bat assemblages on a regional scale. *Mamm. Biol.* **2011**, *76*, 451–460. [[CrossRef](#)]
45. Ciechanowski, M. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern Poland. *Eur. J. Wildl. Res.* **2015**, *61*, 415–428. [[CrossRef](#)]
46. Hill, M.O. Diversity and evenness: A unifying notation and its consequences. *Ecology* **1973**, *54*, 427–432. [[CrossRef](#)]
47. Jost, L. Entropy and diversity. *Oikos* **2006**, *113*, 363–375. [[CrossRef](#)]
48. Jost, L. Partitioning diversity into independent alpha beta concepts. *Ecology* **2007**, *88*, 2427–2439. [[CrossRef](#)] [[PubMed](#)]
49. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 2–9.
50. Wood, S.N. *Generalized Additive Models: An Introduction with R*; Chapman and Hall: Dordrecht, The Netherlands, 2006. [[CrossRef](#)]
51. Sachanowicz, K.; Wower, A. Assemblage structure and use of anthropogenic roosts by bats in the Eastern Carpathians: Case study in the Bieszczady National Park (SE Poland). *Ital. J. Zool.* **2013**, *80*, 139–148. [[CrossRef](#)]
52. Vlaschenko, A.; Kravchenko, K.; Prylutska, A.; Ivancheva, E.; Sitnikova, E.; Mishin, A. Structure of summer bat assemblages in forests in European Russia. *Turkish J. Zool.* **2016**, *40*, 876–893. [[CrossRef](#)]
53. Wermundsen, T.; Siivonen, Y. Foraging habitats of bats in southern Finland. *Acta Theriol.* **2008**, *53*, 229–240. [[CrossRef](#)]
54. Piksa, K.; Bogdanowicz, W.; Tereba, A. Swarming of bats at different elevations in the Carpathian Mountains. *Acta Chiropterol.* **2011**, *13*, 113–122. [[CrossRef](#)]
55. Piksa, K.; Nowak, J. The bat fauna hibernating in the caves of the Polish Tatra Mountains, and its long-term changes. *Cent. Eur. J. Biol.* **2013**, *8*, 448–460. [[CrossRef](#)]
56. Buckley, D.J.; Lundy, M.G.; Boston, E.S.M.; Scott, D.D.; Gager, Y.; Prodöhl, P.; Marnell, F.; Montgomery, W.I.; Teeling, E.C. The spatial ecology of the whiskered bat (*Myotis mystacinus*) at the western extreme of its range provides evidence of regional adaptation. *Mamm. Biol.* **2013**, *78*, 198–204. [[CrossRef](#)]

57. Taake, K. Strukturelle Unterschiede zwischen den Sommerhabitaten von kleiner und grosser Bartfledermaus *Myotis mystacinus* und *Myotis brandtii* in Westfalen. *Nyctalus* **1984**, *2*, 16–32.
58. Piksa, K.; Brzuszkowski, T.; Cichocki, J.; Gubała, W.J. Species diversity of bats Chiroptera in the Tatra National Park during the summer activity period. *Chrońmy Przyr. Ojcz.* **2017**, *73*, 121–134.
59. Kurek, K.; Gewartowska, O.; Tołkacz, K.; Jędrzejewska, B.; Mysłajek, R.W. Home range size, habitat selection and roost use by the whiskered bat (*Myotis mystacinus*) in human-dominated montane landscapes. *PLoS ONE* **2020**, *15*, e0237243. [[CrossRef](#)] [[PubMed](#)]
60. Piksa, K.; Nowak, J.; Zmihorski, M.; Bogdanowicz, W. Nonlinear distribution pattern of hibernating bats in caves along an elevational gradient in mountain (Carpathians, Southern Poland). *PLoS ONE* **2013**, *8*, e68066. [[CrossRef](#)]
61. Piksa, K.; Wołoszyn, B.W. The postglacial bat remains from the Polish Tatra caves. *Lynx* **2001**, *32*, 301–311.
62. De Jong, J. Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. *Mammalia* **1994**, *58*, 535–548. [[CrossRef](#)]
63. Pandurska, R. Altitudinal distribution of bats in Bulgaria. *Myotis* **1996**, *34*, 45–50.
64. Rebelo, H.; Tarroso, P.; Jones, G. Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Glob. Chang. Biol.* **2010**, *16*, 561–576. [[CrossRef](#)]
65. Rydell, J.; Elfström, M.; Eklöf, J.; Sánchez-Navarro, S. Dramatic decline of northern bat *Eptesicus nilssonii* in Sweden over 30 years. *R. Soc. Open Sci.* **2020**, *7*, 191754. [[CrossRef](#)] [[PubMed](#)]
66. Masson, D.; Sagot, F. Les Chiroptères de la haute vallée d'Ossau (Pyrénées occidentales): Résultats des recherches estivales 1985–1986–1987. *Doc. D'écologie Pyrénéenne* **1988**, *5*, 173–196.
67. Rehak, Z. Areal and altitudinal distribution of bats in the Czech part of the Carpathians (Chiroptera). *Lynx* **2006**, *37*, 179–205.
68. Froidevaux, J.S.; Barbaro, L.; Vinet, O.; Larrieu, L.; Bas, Y.; Molina, J.; Calatayud, F.; Brin, A. Bat responses to changes in forest composition and prey abundance depend on landscape matrix and stand structure. *Sci. Rep.* **2021**, *11*, 10586. [[CrossRef](#)] [[PubMed](#)]
69. Russo, D.; Jones, G. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: Conservation implications. *Ecography* **2003**, *26*, 197–209. [[CrossRef](#)]
70. Bütler, R.; Angelstam, P.; Ekelund, P.; Schlaepfer, R. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biol. Conserv.* **2004**, *119*, 305–318. [[CrossRef](#)]
71. Basile, M.; Asbeck, T.; Jonker, M.; Knuff, A.K.; Bauhus, J.; Braunisch, V.; Mikusiński, G.; Storch, I. What do tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds, and insects? *J. Environ. Manag.* **2020**, *264*, 110401. [[CrossRef](#)]
72. Martin, K.; Aitken, K.E.H.; Wiebe, K.L. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *Condor* **2004**, *106*, 5–19. [[CrossRef](#)]
73. Kusch, J.; Weber, C.; Idelberger, S.; Koob, T. Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zool.* **2004**, *53*, 113–128.
74. Randall, L.A.; Barclay, R.M.; Reid, M.L.; Jung, T.S. Recent infestation of forest stands by spruce beetles does not predict habitat use by little brown bats (*Myotis lucifugus*) in southwestern Yukon, Canada. *For. Ecol. Manag.* **2011**, *261*, 1950–1956. [[CrossRef](#)]
75. Lawson, K.J.; Lausen, C.L.; Mancuso, K.A.; Volkmann, L.A.; Gooliaff, T.J.; Hutchen, J.; Teichman, K.J.; Kelly, A.J.; Hodges, K.E. Bat activity and richness in beetle-killed forests in southern British Columbia. *J. Mammal.* **2019**, *100*, 510–517. [[CrossRef](#)]
76. Baagøe, H.J. The Scandinavian bat fauna: Adaptive wing morphology, and free flight in the field. In *Recent Advances in the Study of Bats*; Fenton, M.B., Racey, P.A., Rayner, J.M., Eds.; Cambridge University Press: Cambridge, UK, 1987; pp. 57–74. ISBN 0521321603.
77. Entwistle, A.G. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philos. Trans. R. Soc. B Biol. Sci.* **1996**, *351*, 921–931. [[CrossRef](#)]
78. Russ, J. *The Bats of Britain and Ireland, Echolocation Calls, Sound Analysis and Species Identification*; Alana Ecology Ltd.: London, UK, 1999.
79. Fenton, M.B.; Bogdanowicz, W. Relationships between external morphology and foraging behaviour: Bats in the genus *Myotis*. *Can. J. Zool.* **2002**, *80*, 1004–1013. [[CrossRef](#)]
80. Erasmy, M.; Leuschner, C.; Balkenhol, N.; Dietz, M. Shed light in the dark—How do natural canopy gaps influence temperate bat diversity and activity? *For. Ecol. Manag.* **2021**, *497*, 119509. [[CrossRef](#)]
81. Müller, J.; Mehr, M.; Bäessler, C.; Fenton, M.B.; Hothorn, T.; Pretzsch, H.; Klemmt, H.J.; Brandl, R. Aggregative response in bats: Prey abundance versus habitat. *Oecologia* **2012**, *69*, 673–684. [[CrossRef](#)]
82. Chen, J.; Franklin, J.F.; Spies, T.A. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* **1993**, *63*, 219–237. [[CrossRef](#)]
83. Lewis, T.; Dibley, G.C. Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. *Ann. Appl. Biol.* **1970**, *66*, 477–484. [[CrossRef](#)]
84. Zimmerman, G.S.; Glanz, W.E. Habitat use by bats in Eastern Maine. *J. Wildl. Manag.* **2000**, *64*, 1032–1040. [[CrossRef](#)]
85. Flaquer, C.; Torre, I.; Arrizabalaga, A. Comparison of sampling methods for inventory of bat communities. *J. Mammal.* **2007**, *88*, 526–533. [[CrossRef](#)]
86. Russo, D. Elevation affects the distribution of the two sexes in daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae) from Italy. *Mammalia* **2002**, *66*, 543–551. [[CrossRef](#)]
87. Mcguire, L.P.; Boyle, W.A. Altitudinal migration in bats: Evidence, patterns, and drivers. *Biol. Rev.* **2013**, *88*, 767–786. [[CrossRef](#)]

88. Senior, P.; Butlin, R.K.; Altringham, J.D. Sex and segregation in temperate bats. *Proc. R. Soc. B Biol. Sci.* **2005**, *272*, 2467–2473. [[CrossRef](#)] [[PubMed](#)]
89. Audet, D. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *J. Mammal.* **1990**, *71*, 420–427. [[CrossRef](#)]
90. Drescher, C. Radiotracking of *Myotis myotis* (Chiroptera, Vespertilionidae) in South Tyrol and implications for its conservation. *Mammalia* **2004**, *68*, 387–395. [[CrossRef](#)]
91. Mackie, I.J.; Racey, P.A. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): Implications for conservation. *Biol. Conserv.* **2007**, *140*, 70–77. [[CrossRef](#)]
92. Cichocki, J.; Lupicki, D. Distribution of noctule bat *Nyctalus noctula* (Schreber, 1774) in the Polish Tatra Mts. *Chrońmy Przyr. Ojcz.* **2007**, *63*, 3–12.
93. Loeb, S.C.; O’Keefe, J.M. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *J. Wildl. Manag.* **2003**, *70*, 1210–1278. [[CrossRef](#)]