Systematic Review of the Roost-Site Characteristics of North American Forest Bats: Implications for Conservation

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Abstract: Continued declines in North American bat populations can be largely attributed to habitat loss, disease, and wind turbines. These declines can be partially mitigated through actions that boost reproductive success; therefore, management aimed at promoting availability of high-quality roosting habitat is an important conservation goal. Following the principles of the umbrella species concept, if co-occurring species share similar roost-tree preferences, then management practices targeting one species may confer conservation benefits to another. We conducted a systematic review of roost-site characteristics of thirteen species inhabiting eastern temperate forests to: (1) synthesize existing knowledge across species; (2) assess niche overlap among co-occurring species; and (3) evaluate the potential for currently protected species to serve as conservation umbrellas. We performed multivariate ordination techniques to group species based on the seven most-reported roost-site characteristics, including tree species, diameter at breast height, tree health, roost type, tree height, canopy closure, and roost height. Species sorted into three roosting guilds: (1) southern wetland inhabitants; (2) foliage specialists; and (3) dead tree generalists. *Myotis septentrionalis* and *Perimyotis subflavus* had significant roost-niche overlap with five and four other species respectively, and their existing protections make them suitable umbrellas for other bats in the North American eastern temperate forests.

Keywords: bats; forests; conservation; review; roost; habitat; umbrella species

1. Introduction

Bats are the most widely distributed land mammal globally, inhabiting every continent except Antarctica [1]. Bats are also one of the most speciose mammalian groups, second only to rodents [2], encompassing >1400 species and comprising ~20% of all mammals on Earth [3]. They range in size from the bumblebee bat, *Craseonycteris thonglongyai*, with a wingspan of ~170 mm and weighing ~2 g [4], to the golden crowned flying fox, *Acerodon jubatus*, with a wingspan of ~1.6 m and weighing over 1 kg [5]. This tremendous diversity allows bats to exploit several niches across a variety of ecosystems, providing many ecosystem services [6], including insect pest management [7–9], pollination (e.g., [10,11]), and seed dispersal [12,13]. Their economic value to the U.S. agricultural industry has been estimated at $22.9 billion US dollars annually [14], and they are critical to the socioeconomic stability of small-scale agricultural enterprises globally [11,15].

Despite their importance, bats are in decline across much of the world; ~15% of bat species are considered "threatened" by the International Union for Conservation of Nature [16]. An additional 18% are "data-deficient", and 57% have unknown population trends, which results in a staggering

80% of global bat species with risk of extinction [16]. The number of species in need of conservation attention renders species-specific actions impractical at a large scale, making the development of management practices benefitting multiple species an important goal [17]. The use of umbrella species (a species whose conservation benefits co-occurring species and/or an ecosystem) may be a practical way to increase the number of bats receiving conservation benefits [18–20]; yet, few studies evaluate the potential of bats as conservation umbrellas (but see [21,22]). Successful selection of conservation umbrellas requires a quantitative evaluation of species' habitat characteristics and geographic distribution [23,24], as well as a standardized review of explicit relevant criteria [25]. Some bat species are already under regulatory protection; thus, understanding their potential to serve as conservation umbrellas is an important first step in prioritizing limited conservation resources across this large and diverse taxonomic group.

In eastern North America, bat populations are still being impacted by the fungal pathogen, *Pseudogymnoascus destructans*, the cause of white-nose syndrome [26–28]. In addition to significant white-nose induced declines, insectivorous bats within this region are affected both directly and indirectly by pesticides and insect resistant crop strains [29,30]. In addition, wind turbines cause significant mortality [31], with estimates of up to 500,000 bats per year in North America alone [32–34]. As urbanization continues to reduce the natural areas that bats rely on for foraging and roosting [35], efficiently managing bat habitat is especially critical [36]. In particular, preserving or creating high-quality roosting sites is critical for maximizing bat diversity and abundance [37]. During the spring and summer, many bat species make extensive use of tree roosts for giving birth and raising pups [38]. These maternity roosts are vital resources for female bats as they exit hibernation and begin expending energy to rear their young [39]. Because of their importance, many studies of roost-site characteristics have been conducted. Existing studies of roost-site characteristics tend to focus on a single site or species (e.g., [40,41]). Accurately synthesizing these data and comparing the roosting niche of forest-dwelling bats may provide a reliable reference for multi-species habitat management, as well as identifying candidate umbrella species.

Here, we conduct a systematic review of the roost-site characteristics of bat species occurring within North American eastern temperate forests, an ecoregion that dominates the mid- and southeastern half of the continent [42]. Our primary objectives are to: (1) synthesize existing knowledge across species; (2) assess niche overlap among co-occurring species; and (3) evaluate the potential for currently protected species to serve as conservation umbrellas. We then discuss the implications of our analyses to bat conservation in North America.

2. Materials and Methods

2.1. Study Region and Species

Our study area consisted of approximately 2,723,400 km^2 of eastern temperate forest (Figure 1), as described by the U.S. Environmental Protection Agency's ecoregion level 1, type 8 [42]. Eastern temperate forests are characterized by diverse forest cover, seasonal temperature changes, and precipitation that is relatively evenly distributed throughout the year [43]. The ecoregion extends from eastern Texas and northern Florida, USA in the south to Ontario and Quebec, CA in the north. Eastern temperate forest primarily occurs within the United States, with coverage in 34 states, while only ~0.5% of the ecoregion occurs in the Canadian Provinces of Quebec, Ontario, Prince Edward Island, New Brunswick, and Nova Scotia (~11,700 km^2).

There are 17 bat species with geographic ranges that overlap our study region. Because our focus was on tree roost-site characteristics, we excluded bats that primarily roost in caves, mines, or rocks [44]. Therefore, we reviewed the roost-site characteristics of the 13 remaining eastern temperate forest bat species (Table 1).
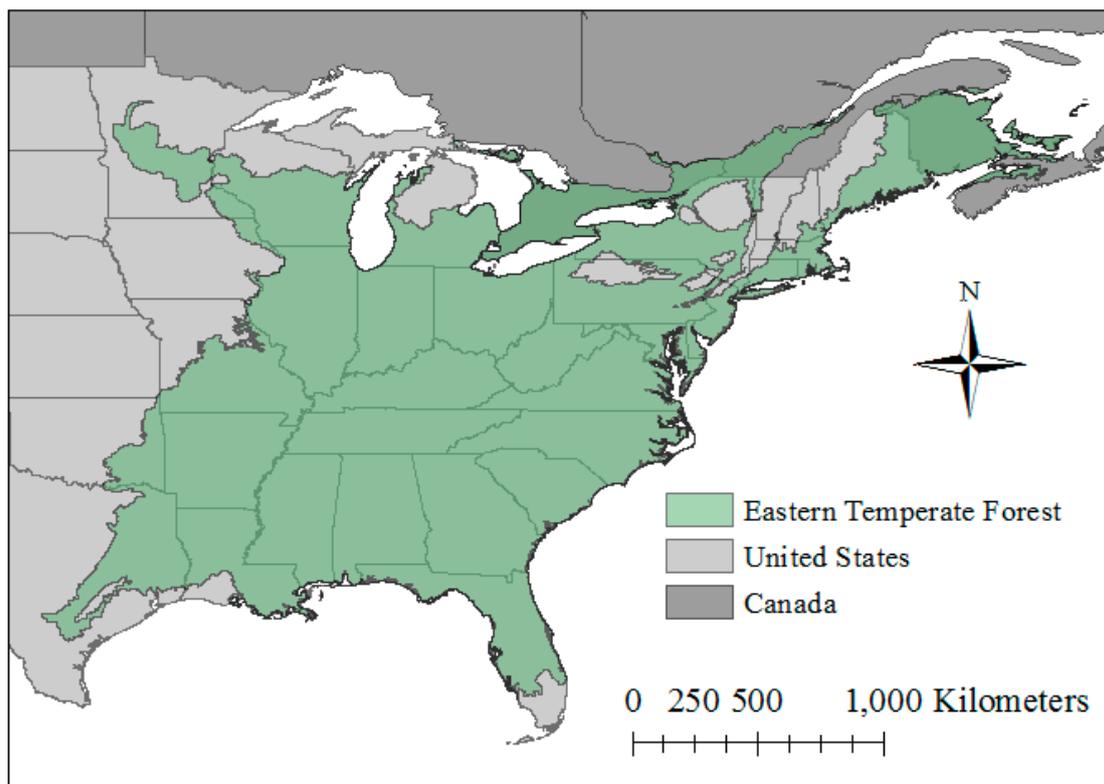
Figure 1. Eastern temperate forest ecoregion of North America. The green shaded area represents the geographic extent from which we included studies.

Table 1. Tree-roosting bat species occurring in eastern temperate forests of North America, and their global and federal conservation status as designated by the International Union for Conservation of Nature (IUCN) [45], United States Fish and Wildlife Service (USFWS), and Canadian Wildlife Service (CWS) [46].

Latin Binomial	Common Name	IUCN [1]	USFWS [2]	CWS [2]
Corynorhinus rafinesquii	Rafinesque's big-eared bat	LC	NL	NL
Eptesicus fuscus	big brown bat	LC	NL	NL
Lasionycteris noctivagans	silver haired bat	LC	NL	NL
Lasiurus borealis	eastern red bat	LC	NL	NL
Lasiurus cinereus	hoary bat	LC	NL	NL
Lasiurus intermedius	northern yellow bat	LC	NL	NL
Lasiurus seminolus	Seminole bat	LC	NL	NL
Myotis austroriparius	southeastern myotis	LC	NL	NL
Myotis lucifugus	little brown bat	EN	UR	EN
Myotis septentrionalis	northern long-eared bat	NT	TH	EN
Myotis sodalis	Indiana bat	NT	EN	NL
Nycticeius humeralis	evening bat	LC	NL	NL
Perimyotis subflavus	tri-colored bat	VU	UR	EN

[1] LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered; [2] NL = Not Listed, UR = Under Review, TH = Threatened, EN = Endangered.

2.2. Data Sources and Search Strategy

We used ISI Web of Science, Science Direct, and Google Scholar to generate a database of potential studies for inclusion in our systematic review of tree roost-site characteristics of eastern temperate forest bats. For each species, we used the search terms: "<Latin name> AND roost*" within each search engine for a total of 39 searches. Because *Perimyotis subflavus* received a new taxonomic classification in 1984 [47], we included its former name, *Pipistrellus subflavus*, to ensure that we incorporated all existing

relevant datasets. Google Scholar returned several thousand results for each species-specific search, but the relevance of each hit noticeably declined by approximately the 100th article. Accordingly, for each species, we considered only the first 200 Google Scholar hits in addition to all returns for ISI Web of Science and Science Direct.

The search returned 2564 unique references, which we then screened for relevance using the following a priori criteria: the study (1) occurred within the eastern temperate forest ecoregion; (2) was published between 1990–2018; and (3) contained information on the tree roost-site characteristics of one or more of the thirteen target species. We first filtered search returns by title, eliminating studies obviously irrelevant to our study topic. We filtered remaining studies by reading the abstracts and assessing whether they met the criteria listed above. We then read the remaining studies to extract data. Where studies measured roost-site characteristics of multiple species, we treated the species-specific datasets separately.

2.3. Systematic Review

We counted number of datasets published for each species, as well as the number of studies conducted in each state/province. For studies with data pertaining to two or more focal species, we considered them to be separate datasets in our count of species' totals. When recording the number of studies published in each state/province, every study was only counted once, regardless of how many datasets a study contained.

For each study, we recorded all reported variables of roost tree/site and subsequently narrowed down our study to the seven most-reported variables: tree genus, diameter at breast height (dbh), tree health, roost type, tree height, canopy closure, and roost height.

For continuous variables, we calculated the pooled mean for each of the 13 species weighted by the dataset sample sizes by multiplying the mean value reported in each dataset by the sample size, adding the products, and then dividing by the number of roost trees reported for each species per dataset (Equation (1)).

$$Mean_i = \frac{\sum_i (N_{dataset} * Mean_{dataset})}{\sum_i (N_{dataset})} \tag{1}$$

where i = species.

We then calculated a pooled variance for each of the weighted means based on the standard deviations (or converted standard error) reported in the datasets extracted from the studies.

Because reporting of qualitative roost-site characteristics differed slightly in many studies, we created three standardized categorical variables under which to incorporate non-quantitative roost-site descriptions into our analysis: tree health, roost type, and tree genus. The majority of studies classified roost trees as either dead or alive; and, in few cases, the roost site was located within a dead portion of a living tree. We elected to reclassify roost trees as dead (no foliage or living tissue), partially dead (one or more dead branches and/or trunks), and live. As a representative way to assess species-specific tree health preferences, we calculated the percent of dead roost trees by dividing the number of dead roost trees by the total number of roost trees for each species.

We defined roost type as the specific tree feature used by roosting bats, which included exfoliating bark (bark peeling away from the main bole or branch of the tree), cavities (visible holes in the wood), crevices (splits in the wood) and foliage (clumps of leaves on the tree, either dead or alive). For each dataset, we recorded how many roosts were in each of these four categories. Because the majority of species either roosted exclusively in foliage, or never roosted in foliage, we quantified roost type as the percentage of roosts per dataset that were in foliage. Foliage roosts tend to be away from the large branches and bole of the tree, distinguishing them from the other three roost types.

We also recorded the genus of each roost tree used by bats. Because of the broad taxonomic range of trees used as roosts, and the variation in regional species composition, we simplified these categories more broadly into either deciduous or coniferous trees and calculated the percentage of roosts in deciduous trees for subsequent analyses.

2.4. Assessment of Potential Umbrella Species

While there is no unified consensus in evaluating the efficacy of conservation umbrellas across taxa, ecosystems, or spatiotemporal scales [25], good candidates should exhibit a high degree of spatial overlap with their target group, thus affording habitat protections across a wide geographic range [18,48]. Species should also select habitat (in this case, roost trees) with similar characteristics as their focal group [19,49]. From a practical standpoint, species that already carry conservation protections may be effective umbrella species if they satisfy the above-mentioned spatial and niche overlap criteria [50]. We, therefore, evaluated the conservation umbrella potential of the thirteen species in this study based on three criteria: (1) existing regulatory protection; (2) degree of niche overlap; and (3) degree of spatial overlap.

To assess niche overlap among species, we first performed an ANOVA of the means of the seven most-reported variables identified in the systematic review to test for significant differences among roost-site characteristics. For statistically significant results, we performed pairwise Tukey's honest significant difference (Tukey HSD) tests to identify differences between species. We interpreted statistically insignificant ANOVAs and Tukey HSDs as an overlap in roosting niche, operating under the null hypothesis that there is no difference among/between the species for the target roost-site characteristic.

We then performed a series of multivariate statistical ordination techniques to identify potential roosting groups based upon shared roost-tree preferences. Not all studies reported data for all variables. Canopy closure and roost height were reported in 40%, while tree height and dbh were reported in 65% and 90% of the studies, respectively. To address missing values in our dataset, we pulled random numbers from a normal distribution based on the pooled mean and the pooled standard deviation estimated from the standard deviations and means of the full data set. We then imputed missing values for the four continuous variables using the pooled mean for each variable and each species. The pooled variance associated with that mean created a normal distribution from which to sample. In one case, no data on canopy closure or tree height were found within the dataset included for *Lasionycteris noctivagans*. In this case, the mean canopy closure was taken from a publication outside of eastern temperate forests [51].

Using the imputed dataset, we performed a cluster analysis using Ward's method [52]. The analysis generated a dendrogram using hierarchical clustering with *p*-values via multiscale bootstrap resampling in R [53] using the "pvclust" package [54]. We used the unit interval to standardize our units between 0 and 1 because the roost-site characteristics differed by orders of magnitude. We also performed a principal component analysis with the correlation matrix of the seven roost-site characteristics in R. Similar to the unit interval, using the correlation matrix scales the data when they vary by orders of magnitude. Finally, we used a discriminant function analysis of the raw, non-standardized data to visualize the species' roost tree preferences in 2-dimensional space. The three multivariate analyses allowed us to visualize the mathematical distance between the species in terms of their roosting niche; those with poor separation can be considered to have a high degree of niche overlap with each member of their group [55].

To evaluate spatial overlap among species, we downloaded species' range maps from the IUCN website [45]. We clipped each range map to the size of the eastern temperate forest ecoregion and then converted them into geographic information system (GIS) raster layers with a 1 km^2 cell size. Within each group of bats identified by our multivariate analyses, we used the raster layers to quantify range overlap between species in a pairwise manner. We added the raster layers together using Map Algebra in ArcGIS (version 10.2.2) to obtain the number of cells that overlap for each species pairing. We quantified spatial overlap by dividing the number of cells occupied by both Species A and Species B by the number of cells occupied by either species A or Species B, resulting in a percentage of range overlap. We used the measurements of overlapping area to calculate how much of any given species' range is contained within the range of another.

3. Results

3.1. Search Results

In total, 95 studies [41,56–149] met our criteria for data extraction (Figure 2). Some of the retained studies included data for two or more focal species; therefore, our systematic review consisted of 116 datasets describing 4908 roost trees.
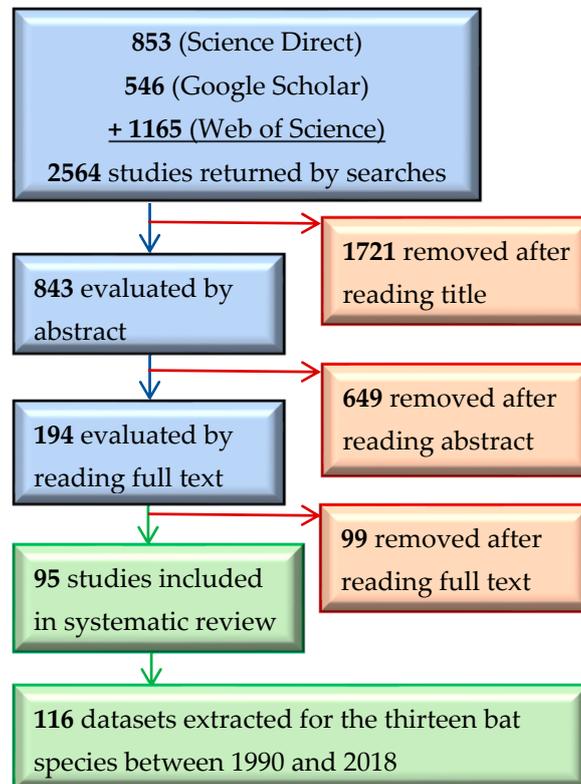
Figure 2. Flowchart of the search strategy and process for identifying studies for inclusion in the systematic review.

The number of datasets pertaining to each focal species ranged between 1–27. The two most well-studied species were *Myotis sodalis* (27 datasets describing 1375 roost trees) and *M. septentrionalis* (19 datasets describing 1094 roost trees). Six bat species encompassed >10 datasets each, while the remaining seven species had six or fewer. Roost-site characteristics of both *M. lucifugus* and *Lasiurus intermedius* were described in only two datasets each (containing 68 and 21 roost trees, respectively), and *Lasionycteris noctivagans* returned a single dataset of 28 roost trees. *Lasiurus cinereus* had the fewest total roost trees (*n* = 17) drawn from three datasets.

Nearly 39% of the studies (37 of 95) were conducted in the four U.S. states of Arkansas (11 studies), Indiana (10 studies), South Carolina (eight studies), and Kentucky (eight studies; Figure 3). Nine U.S. states returned a single study; nine additional states returned zero studies. Only two Canadian studies were included in this review; one from New Brunswick [65] and one from Prince Edward Island [88], both focusing on *Myotis septentrionalis*.

3.2. Summary of Roost-Site Characteristics

The seven most-reported variables were tree genus (92 out of 95 studies; Figure 4), dbh (86 studies), tree health (76 studies), roost type (74 studies), tree height (66 studies), canopy closure (43 studies), and roost height (38 studies). The next most-reported variable was the distance of the roost tree to the nearest source of water (30 studies). However, those 30 studies only contained information on seven of

the thirteen focal species of this systematic review; thus, we used only the first seven most frequently reported variables for further analyses of niche overlap, for which there were data for almost all species.
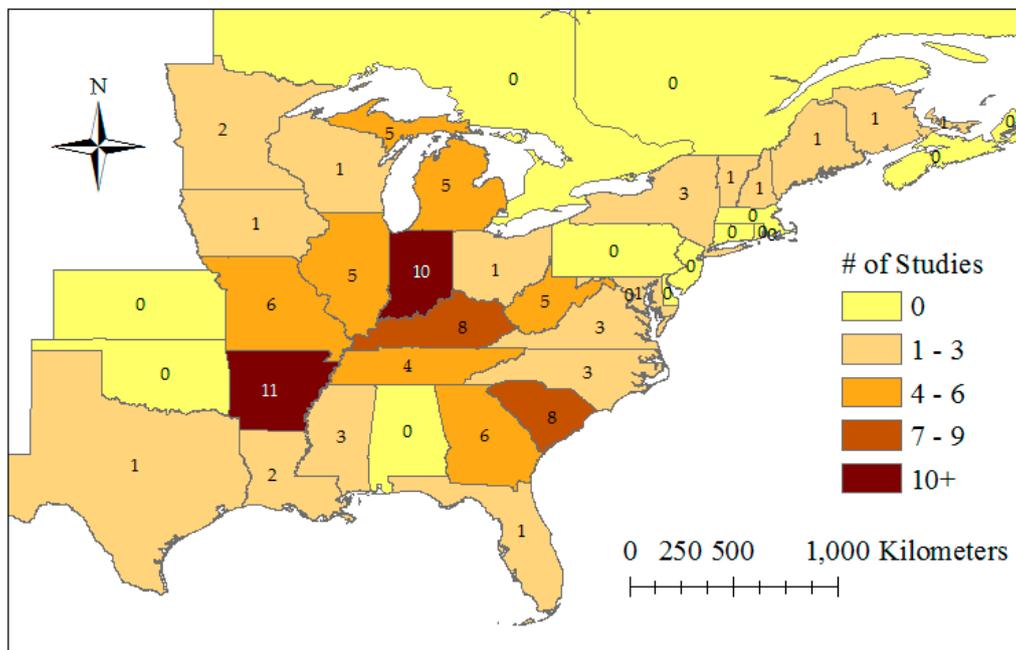
Figure 3. The number of studies (N_{total} = 95) included in our review that were published in each U.S. state or Canadian province within the eastern temperate forest ecoregion.
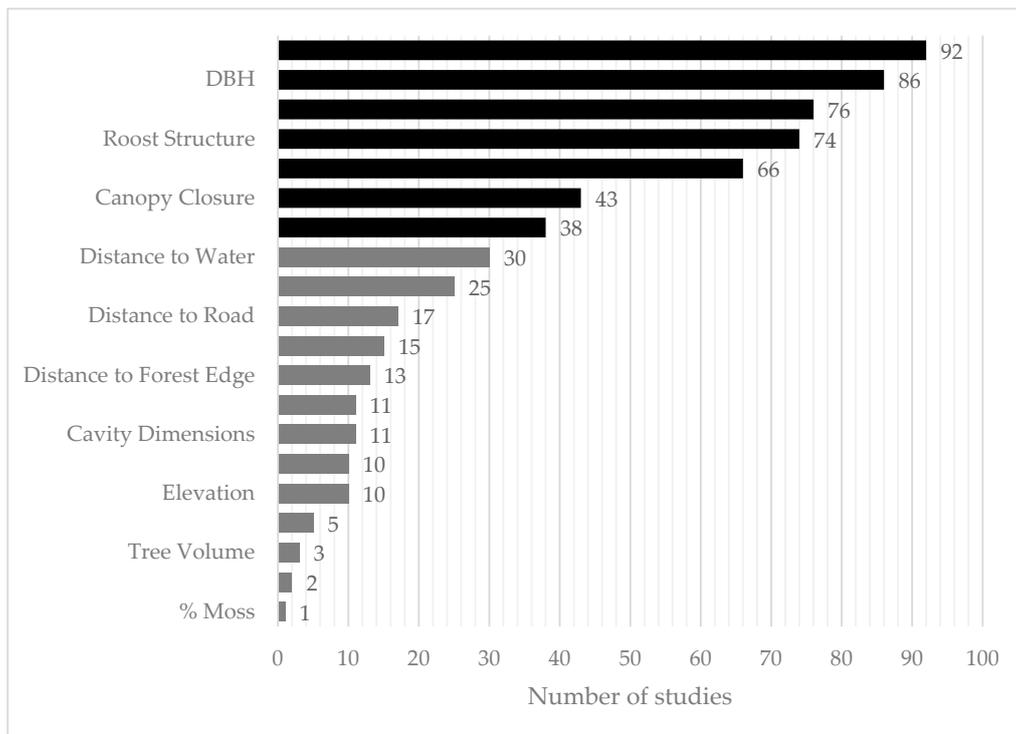
Figure 4. Frequency distribution of the number of studies reporting data on each predictor of tree roost sites. Black bars indicate the roost tree characteristics used in our analysis of niche overlap.

Mean dbh, tree height, roost height, and canopy closure for all bats were 44.29 cm (N = 4451), 19.25 m (N = 3046), 8.79 m (N = 1621), and 67.04% (N = 2325), respectively. Nearly 36% (N = 1758) of all bats roosted in live trees, 34.5% (N = 1692) in dead trees, and 4.1% (N = 202) in partially dead

trees. There were 36 genera of trees used as roosts in total (Figure A1). *Myotis austroriparius* and *Corynorhinus rafinesquii* had the greatest mean dbh (μ = 80.3, σ = 9 cm and μ = 117.8 cm, σ = 10.9 cm, respectively). The other eleven bats had substantially lower mean dbh, ranging from 26.4–45.5 cm (Table 2). Roost height varied significantly among the thirteen species, with *Lasiurus cinereus* roosting the highest above the ground (μ = 21.1 m, σ = 4.6 m). In contrast, the lowest roosting bats were *Myotis austroriparius* (μ = 1.6 m, σ = 1.3 m), *L. intermedius* (μ = 2.3 m, σ = 1.5 m). Canopy closure was greatest for *M. austroriparius* (μ = 87.5%, σ = 11.5%), and the lowest average canopy closure was recorded for *Lasionycteris noctivagans* at (μ = 41.5%, σ = 11.9%). *Perimyotis subflavus* and the four bats belonging to the genus *Lasiurus* roosted almost exclusively in foliage on live trees. *Myotis austroriparius* and *Corynorhinus rafinesquii* roosted primarily in cavities, and the remaining six roosted mostly in either exfoliating bark or crevices. *L. seminolus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, and *Myotis lucifugus* roosted mostly in coniferous trees.

Table 2. A summary of roost tree characteristics for the thirteen species of bats found in eastern temperate forests. Means (and standard deviations) for the four continuous characteristics used in our analyses of the 116 datasets.

Bat Species	DBH (cm)		Tree Height (m)		Roost Height (m)		Canopy Closure (%)		Deciduous Roosts %	% Dead Roosts	% Foliage Roosts
Corynorhinus rafinesquii	117.8	(10.9)	22.4	(4.7)	6.3	(2.5)	75.2	(24.8)	83.4	8.4	0.0
Eptesicus fuscus	26.4	(5.1)	13.9	(3.7)	7.7	(2.8)	61	(4.9)	22.7	86.4	0.0
Lasiurus borealis	29.6	(5.4)	19	(4.4)	14.4	(3.8)	81	(17.5)	81.0	0.2	80.3
Lasiurus cinereus	35.2	(5.9)	22.4	(4.7)	21.1	(4.6)	80	(16.3)	41.2	0.0	100.0
Lasiurus intermedius	45.5	(6.7)	15.4	(3.9)	2.3	(1.5)	71.2	(17.8)	100.0	0.0	100.0
Lasiurus seminolus	40.2	(6.3)	26	(5.1)	16.3	(4)	71.8	(17.2)	5.4	0.0	62.5
Lasionycteris noctivagans	33.1	(5.8)	26.7	(7.8)	5.1	(2.3)	41.5	(11.9)	17.9	0.0	0.0
Myotis austroriparius	80.3	(9)	23.1	(4.8)	1.6	(1.3)	87.5	(11.5)	79.0	11.1	0.0
Myotis lucifugus	40	(6.3)	10.7	(3.3)	8.4	(2.9)	62.4	(19.4)	22.1	23.5	0.0
Myotis septentrionalis	35.4	(5.9)	16.8	(4.1)	7.9	(2.8)	67.7	(25.3)	76.8	41.9	0.0
Myotis sodalis	37.7	(6.1)	18.3	(4.3)	10.1	(3.2)	52.5	(34.9)	64.9	60.9	0.0
Nycticeius humeralis	39.4	(6.3)	18	(4.2)	11.8	(3.4)	67	(26)	49.6	39.3	0.2
Perimyotis subflavus	27.5	(5.2)	20	(4.5)	13.7	(3.7)	49.1	(29.7)	89.5	33.1	100.0

3.3. Niche Overlap of Eastern Temperate Forest Bats

The three multivariate ordination analyses consistently classified bats into three groups. *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Nycticeius humeralis*, *Myotis sodalis*, *M. septentrionalis*, and *M. lucifugus* comprise the largest group. The second group contains *Perimyotis subflavus*, *Lasiurus seminolus*, *L. cinereus*, *L. borealis*, and *L. intermedius*. Finally, *Corynorhinus rafinesquii* and *Myotis austroriparius* are paired together. Discriminant functions 1 and 2 of the DFA explained 90.4% of the variation seen in the data (Table 3, Figure 5). Bootstrapped cluster analysis using Ward's method produced a dendrogram that supported the DFA, and the approximately unbiased p-values associated with the nodes ranged from 69–100% (Figure A2). The PCA plot also agreed with the group generated by the dendrogram and the DFA (Figure A3).

Six of the seven variables used in our analyses were statistically different across species ($p < 0.01$), with the sole exception being canopy closure ($p = 0.206$, df = 12, F = 1.41). The Tukey HSD tests identified differences between species (Table A1). All significant differences in dbh can be attributed to either *Corynorhinus rafinesquii* or *Myotis austroriparius* roosting in trees with significantly greater mean dbh compared to other species. There were no significant differences between *C. rafinesquii* and *M. austroriparius* themselves ($p = 0.149$). *C. rafinesquii* and *M. austroriparius* also tended to roost lower on the tree than most other species. For example, *Lasiurus cinereus* had the highest mean roost height, and it differed significantly from both *C. rafinesquii* ($p = 0.002$) and *M. austroriparius* ($p = 0.0003$). The latter also roosted significantly lower than bats such as *L. seminolus* ($p = 0.0146$) and *Perimyotis subflavus* ($p = 0.006$). The most divisive characteristic was the percentage of roosts in foliage, with most species either roosting exclusively in foliage, or never in foliage. All differences in percentage of foliage roosts are attributed to the four *Lasiurus* species and *P. subflavus*.

Table 3. The coefficients for the seven variables for the two discriminant functions that explained 90.4% of the variation in the data for the roost tree characteristics of the thirteen species of tree-roosting bats in eastern temperate forests.

Discriminant Function	Canopy Closure	Tree Height	Roost Height	DBH	%Deciduous Roosts	%Dead Roosts	%Foliage Roosts
DF 1 (69.02%)	−0.00002	−0.00086	0.00336	−0.0025	0.0336	−0.0382	0.6683
DF 2 (21.38%)	0.00177	0.00179	−0.00713	0.00557	−0.1103	−0.1491	0.17786
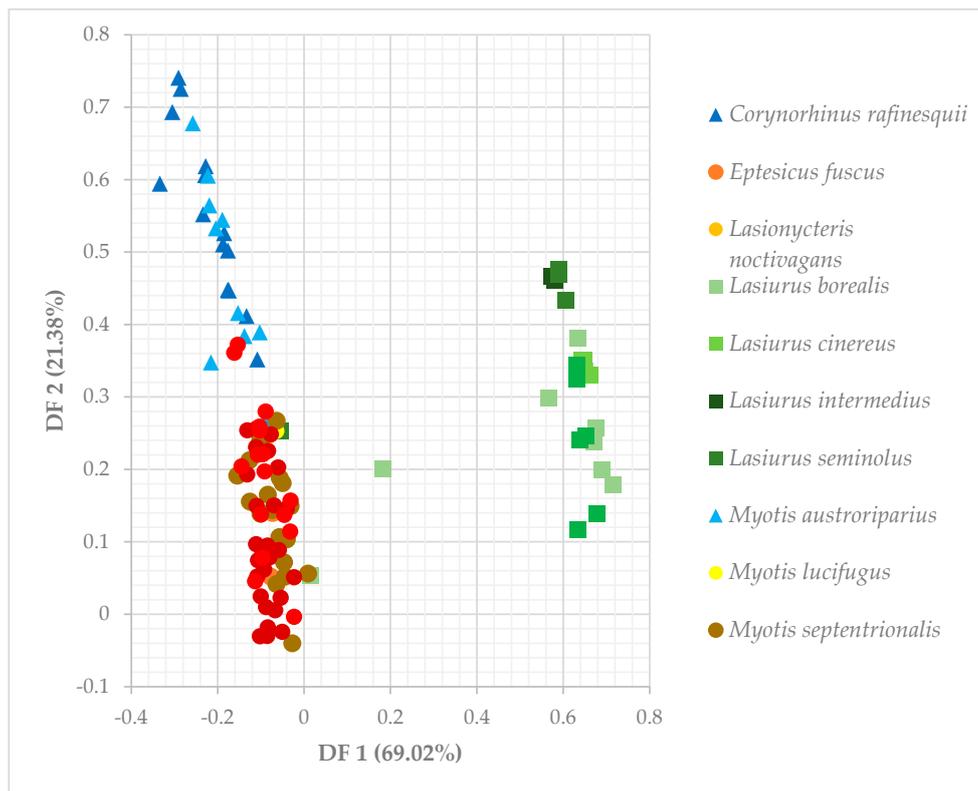
Figure 5. Discriminant function analysis of roost-site characteristics of North American eastern temperate forest bats indicates that the thirteen bat species separate into three distinct groups.

3.4. Spatial Overlap Among Eastern Temperate Forest Bats

The percentage of eastern temperate forest contained within the geographic range of each species varied between 20.3–93.7%. *Lasiurus cinereus*, *L. borealis*, and *Lasionycteris noctivagans* were the most widespread species, each occupying >93% of the eastern temperate forest. *Perimyotis subflavus* (~89%), *Eptesicus fuscus* (~87%), *Myotis lucifugus* (~82%), *Nycticeius humeralis* (~72%), and *M. septentrionalis* (~67%) were also well distributed across the ecoregion. *M. sodalis* and *Corynorhinus rafinesquii* had smaller ranges that each covered ~44% of the ecoregion. *Lasiurus seminolus*, *Myotis austroriparius*, and *L. intermedius* were the most geographically restricted species, with ranges that overlapped with eastern temperate forest by 35%, 28%, and 20%, respectively.

At least one species within each roosting group encompassed >90% of the total range of its group members. *C. rafinesquii* has a range that contains ~92% of *M. austroriparius's* range (Table 4, Group 3), while the range of *Eptesicus fuscus* includes between 90.6–100% of the range of *L. noctivagans*, *M. lucifugus*, *M. septentrionalis*, and *M. sodalis* (Table 4, Group 1). Of the species in the remaining group, *L. borealis*, *L. cinereus*, and *P. subflavus* all encompass >92% of the ranges of group members (Table 4, Group 2). In contrast, the federally threatened *M. septentrionalis* contains an average of 74.3% of its group members' ranges (Table 4, Group 2). The federally endangered *M. sodalis* provides just 53.2% coverage, on average, of its group members' ranges.

Table 4. Total range for each tree-roosting bat species in eastern temperate forests. Percentage values denote the fraction of a species' range that is encompassed in the habitat area of another species (e.g., 58.5% of the *Corynorhinus rafinesquii*'s range falls within the range of *Myotis austroriparius*). "EPFU" = *Eptesicus fuscus*, "LANO" = *Lasionycteris noctivagans*, "MYLU" = *Myotis lucifugus*, "MYSE" = *Myotis septentrionalis*, "MYSO" = *Myotis sodalis*, "NYHU" = *Nycticeius humeralis*, "LABO" = *Lasiurus borealis*, "LACI" = *Lasiurus cinereus*, "LAIN" = *Lasiurus intermedius*, "LASE" = *Lasiurus seminolus*, "PESU" = *Perimyotis subflavus*, "CORA" = *Corynorhinus rafinesquii*, "MYAU" = *Myotis austroriparius*.

Species	EPFU	LANO	MYLU	MYSE	MYSO	NYHU	LABO	LACI	LAIN	LASE	PESU	CORA	MYAU
Range (km^2)	2,360,598	2,544,272	2,237,050	1,811,663	1,210,854	1,958,280	2,551,433	2,552,372	553,416	946,051	2,432,854	1,181,713	751,674
Dead Tree Generalists													
E. fuscus	100	90.6	97.6	97	99.9	100	-	-	-	-	-	-	-
L. noctivagans	97.7	100	94.8	99.6	99.3	87.9	-	-	-	-	-	-	-
M. lucifugus	92.5	83.4	100	98.1	99.4	81.7	-	-	-	-	-	-	-
M. septentrionalis	74.5	70.9	79.4	100	86.8	60	-	-	-	-	-	-	-
M. sodalis	51.2	47.3	53.8	58	100	55.9	-	-	-	-	-	-	-
N. humeralis	83	67.7	71.5	64.8	90.5	100	-	-	-	-	-	-	-
Foliage Specialists													
L. borealis	-	-	-	-	-	-	100	98.1	100	99.9	99.1	-	-
L. cinereus	-	-	-	-	-	-	98.1	100	92.1	95.4	98.1	-	-
L. intermedius	-	-	-	-	-	-	21.7	20	100	55.9	22.1	-	-
L. seminolus	-	-	-	-	-	-	37	35.4	95.5	100	38.2	-	-
P. subflavus	-	-	-	-	-	-	94.5	93.5	97.1	98.2	100	-	-
Southern Wetland Species													
C. rafinesquii	-	-	-	-	-	-	-	-	-	-	-	100	91.9
M. austroriparius	-	-	-	-	-	-	-	-	-	-	-	58.5	100

4. Discussion

This work presents the most comprehensive and current synthesis of existing knowledge about roost-site characteristics of tree-roosting bats in North American eastern temperate forests. Previous work has elucidated the roosting niche of a subset of bat species in the form of a meta-analysis or power analysis [150–152], as well as bat roosting behavior at a global scale [153]. We have built upon this foundation by examining multiple bat species across a large ecoregion of North America. Our study reveals an inequality in bat research attention. In eastern temperate forests, *Myotis sodalis* received disproportionate attention, perhaps because of its federal protections in the United States. *M. sodalis* has been a high-priority research species for over 40 years [154], including studies highlighting habitat [155], foraging [156], and mating [157]. *M. septentrionalis* is also well-represented in the literature, perhaps because of its high abundance prior to the emergence of white-nose syndrome [131,158].

In contrast to these well-studied species, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*, *L. intermedius*, *L. seminolus*, and *M. lucifugus* have fewer than five datasets each. The paucity of datasets may be a product of our study design, as we restricted our focus to studies reporting roost-site characteristics within eastern temperate forests between 1990–2018. Species such as *Lasionycteris noctivagans* and *Lasiurus cinereus* have large geographic ranges and do not rely exclusively on eastern temperate forests for summer roosting habitat [159,160]. Similarly, *Lasiurus intermedius* occupies eastern temperate forests only in the northern extent of its range. A large portion of its range is in central America, where they make use of palms and other substrates uncommon in temperate areas [161,162]. Finally, tree-roost publications for *E. fuscus* and *M. lucifugus* may be explained by their propensity for roosting in man-made structures [163,164]. However, none of the bats included in our review are obligate manmade-structure inhabitants. We chose to include them in our study of tree-roosting bats because they are generalists that will make use of a wide variety of roosting media (including trees) [165,166]. Nonetheless, additional studies can increase our understanding of roosting behavior in data-deficient species, as well as refine the precision of measured roost-site characteristics in relatively well-studied species.

The seven most-reported roost-site characteristics used in our analyses are widely applicable and ecologically relevant for determining habitat selection in bats [167]. These variables in general are easily recorded, with many (e.g., tree genus and health, roost type) classified by a visual survey. Other quantitative metrics (e.g., dbh, roost height, canopy closure) can be measured quickly with readily available forestry equipment. In contrast, relatively few studies reported on more specialized roost-site metrics, such as cavity dimensions, microclimate, and tree volume, likely due to the time and effort required for accurate measurement. However, these characteristics can provide valuable insight on the roosting behavior of bats. Specifically, roost microclimate is an important determinant of reproductive success, with female bats tending to prefer warmer sites as maternity habitat [168,169]. How tree or roost structure affects microclimate can provide critical guidance for maintaining appropriate roosting sites. Even foliage roosting bat species (e.g., *Lasiurus cinereus*) will seek clumps of leaves that provide sufficient shelter from the elements [159]. Across studies, simpler measurements were often used as a proxy for more detailed microclimate metrics [170–172]. However, substitute measurements may fail to capture the primary determinants of roost selection. For example, canopy closure is often used as a substitute for solar exposure, an important criterion for maternity colonies [169]. However, an observer on the forest floor may be well-shaded, while the roost is exposed to direct sunlight. Canopy closure can be estimated from the ground [173] or from aerial imagery [174], but perhaps neither accurately represent the canopy closure experienced by the bat while roosting. Instead, properly attached temperature-sensitive radio transmitters could be used to infer roost microclimate characteristics directly [175], rather than estimate based on the relationship between canopy closure, solar exposure, and microclimate.

Relative to the tree scale, landscape-scale characteristics were less reported. Distance from the roost tree to the nearest source of water, forest edge, or corridor were not reported as often as other measurements. If the latitude and longitude of the roost trees were recorded, then these measurements

can be made remotely, in most cases, with the use of aerial imagery. Easy access to these metrics make them readily available data sources. Preferable roost trees tend to be near water [106,176] and/or corridors [86,177], thus reducing the energetic demands of foraging. While males and nonreproductive females may be less restricted by their biological needs, pregnant and lactating females tend to select roosts with closer proximity to foraging resources [140]. Landscape attributes have significant predictive power when evaluating roost-site suitability [177], and including more data regarding the landscape in which roosts are situated may have provided additional context for the results of our study. However, we did not have enough datasets containing these measurements to explore the topic further.

Our three multivariate analyses classified our focal species into three groups, hereafter *roosting guilds*, which share ecologically significant roost-site preferences. Approximately 95% of significant pairwise Tukey HSD tests between roost tree characteristics occurred between bats that were in different guilds (Table A1). There were only four cases of a statistically significant difference within guilds, and they all occurred in the guild containing the foliage specialists. All four within-guild differences pertained to either *Lasiurus seminolus* or *L. intermedius*. Three of these differences can be attributed to *L. seminolus* datasets reporting many roosts in coniferous trees [111,113,121], and the other one is because of the *L. intermedius* dataset reporting very low roost heights when using Spanish moss [90]. It is unclear whether these differences are reliable, or if they are a product of the small sample size of reported roosts for those species. With few exceptions, the Tukey HSD tests provide additional support to our guild assignments by quantitatively demonstrating the overlap in roosting niches within guilds and the divergence of roosting niches between guilds.

Corynorhinus rafinesquii and *Myotis austroriparius* comprise the southern wetlands guild, as they share the tendency to roost in cavities of live trees with greater dbh, and they are geographically restricted to the southern portion of eastern temperate forests [83,178]. It is worth noting that range data were not included in the multivariate analyses, so the relationship between these two species was evident by roost-site characteristics alone. They both have strong preferences for cavities in large *Nyssa aquatica* and *Taxodium distichum* in bottomland-riparian forests [76,137], and they had complete overlap in roost site characteristics as determined by Tukey HSD tests. They each also had at least one significantly different roost characteristic with the other eleven bats in our study (the exception being *M. austroriparius*, which had no significant differences with *M. lucifugus* or *Lasionycteris noctivagans*, two bats outside of its guild).

The dead tree generalist roosting guild consists of *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Nycticeius humeralis*, *Myotis sodalis*, *M. septentrionalis*, and *M. lucifugus*. These bat species all tend to prefer exfoliating bark, cavities, or crevices [65,123,126,179]. As the name of the guild suggests, the species here have an affinity for dead or dying trees when selecting a roost [57,87,122]. This guild also contains species known to take advantage of manmade structures, *E. fuscus* and *M. lucifugus* [180,181]. The bats differ in geographic range from *M. sodalis* occupying just the central area of the ecoregion, to *E. fuscus*, *L. noctivagans*, and *M. lucifugus* occupying nearly all of it. *M. septentrionalis* and *N. humeralis* cover approximately two thirds of the ecoregion, but the former covers the northern area, and the latter covers the southern. The dead tree generalists had high within-guild overlap based on Tukey HSD tests. For example, *M. septentrionalis* did not significantly differ from its five groupmates, but it had at least one significantly different roost tree characteristic from each bat outside of its group. Aside from *L. noctivagans*, *M. austroriparius*, and *M. lucifugus*, no species had completely overlapping roost tree characteristics with any species outside of its guild.

The foliage specialist roosting guild is comprised of *Perimyotis subflavus*, *Lasiurus seminolus*, *L. cinereus*, *L. borealis*, and *L. intermedius*. These species are known to roost in clumps of foliage on living trees [111,124,145], and they tended to roost in locations on the tree that were much higher than the other species because most foliage tends to grow towards the top of forest trees. However, *Lasiurus intermedius* had a much lower roost height than its guildmates. It is uncertain whether this difference is an artefact of small sample size, as only one of the two *L. intermedius* datasets included in this review

reported roost height. All bats in that dataset roosted in clumps of low-hanging Spanish moss [90]; therefore, more studies of the roost-site characteristics of *L. intermedius* will improve our understanding of their niche. *L. borealis*, *L. cinereus*, and *P. subflavus* have broad geographic ranges that nearly include the entirety of the ecoregion. *L. intermedius* and *L. seminolus* are more limited to the southern portion of eastern temperate forests. Their preference for southern forests may be related to an energetic demand relating to their thermal physiology or a preference for a certain type of foliage.

The literature suggests that a suitable umbrella species should have a large geographic range with spatial overlap with its guildmates, sufficiently overlapping niche with those guildmates, and ideally with existing protections [50]. Many species fit only one or two of these criteria. For example, the most widespread species within each guild are *Lasiurus cinereus*, *Corynorhinus rafinesquii*, and *Lasionycteris noctivagans*. However, *Lasiurus cinereus* and *Lasionycteris noctivagans* are among the least studied species in their respective guilds. Their large ranges are offset by their poorly quantified roosting preferences within eastern temperate forests. Additionally, these three species have no existing protections from the U.S., Canada, or the IUCN making them poor potential conservation umbrellas.

Based upon the synthesized data presented here, *M. septentrionalis* is the best candidate umbrella for the dead tree generalist roosting guild. While both *M. sodalis* and *M. septentrionalis* both have existing regulatory protections [182,183], our study supports the conclusions drawn by previous studies that *M. septentrionalis* has more generalist roosting preferences [68,79,141]. In addition, *M. septentrionalis* occurs over a wider geographic range than *M. sodalis* [42,45]. This species has an acceptable tradeoff between broad spatial range, well-studied generalist roosting niche, and existing protections. Forest management techniques that promote roosting habitat for *M. septentrionalis* will also likely benefit its guildmates at a broad scale. While *M. lucifugus* has a greater geographic range than either *M. septentrionalis* or *M. sodalis*, we found very few studies focusing on its tree-roosting behaviors, and it frequently takes advantage of buildings as roosts instead [180,181]. It is important to note that the tree-roosting protections provided by an umbrella species for this guild would only benefit the *Eptesicus fuscus* and *M. lucifugus* individuals that make regular use of trees, and the individuals that roost in rocks or manmade structures may require separate considerations [184].

Taking into consideration its geographic range, existing protections, and its need for conservation attention, we propose *Perimyotis subflavus* as a conservation umbrella for the foliage-specialist guild. All five species in this guild have no current federal protections in the United States, but *P. subflavus* is listed as an endangered species in Canada [46], and as "vulnerable" on the IUCN Red List of Threatened Species [45]. *P. subflavus* is widespread across eastern temperate forests covering approximately 90% of the ecoregion [42,45], and its range and niche overlap significantly with its guildmates within the ecoregion [45]. There is a recent increase in interest in protecting the species because *P. subflavus* populations have been negatively impacted by white-nose syndrome [185], leading to it currently being under review for protected status in the United States. If it were to receive those protections, then the four bat species sharing its guild would also experience benefits. *Lasiurus borealis* also has high spatial overlap and niche overlap with its guildmates, and it is the most well-studied species in its guild.

The southern wetland guild is small, geographically restricted, and behaviorally distinct. Neither of the species in this guild have existing protections. *Myotis austroriparius* and *Corynorhinus rafinesquii* did not meet our three criteria for umbrella species status in the context of this study: Spatial overlap with many species, niche overlap with many species, and existing protections. Therefore, we refrain from assessing their potential as umbrella species at this time.

Our guild assignments are based on studies published within eastern temperate forests, most of which are in the United States. Bat species such as *Lasiurus cinereus*, *Myotis lucifugus*, and *Lasionycteris noctivagans* have ranges that extend well beyond eastern temperate forests, while *M. sodalis* and *Lasiurus seminolus* have ranges that are mostly contained by the ecoregion. Associations and patterns including those highlighted by our work may be specific to our study region. It is worth noting that the choices of umbrella species described by our study may not necessarily apply to other ecoregions.

Our study has identified potential applications of the umbrella species strategy in North American bat conservation. The potential umbrella species identified by synthesizing these studies are valuable targets for forest managers and conservation specialists that may be interested in maintaining or creating bat habitat. This study has taken thirteen species, and it has reduced them into three guilds. Bats that share significant aspects of their niche could effectively be treated as a single ecological unit. Actions that benefit one member of the guild should have similar benefits on the other members. For example, if we were to manage a forest in such a way as to increase roosting opportunities for *Myotis septentrionalis*, then we would also be increasing roosting habitat for species such as *M. lucifugus*. *M. septentrionalis* is known to benefit from protecting standing dead trees in forest interiors [186]. Removing dead trees is a common practice in forest management because they could damage healthy trees or property when they fall. Retaining standing dead trees in a natural forest would provide crevices, cavities, and exfoliating bark that would benefit *M. septentrionalis* and the guild underneath its umbrella. *M. septentrionalis* has also been known to preferentially forage and roost in burned areas after a prescribed burn [187]. However, not all bat species benefit from conventional management techniques. *Perimyotis subflavus* avoided roosting in areas of active timber harvest [187].

Our results indicate that habitat conservation efforts focused on *Myotis septentrionalis* and *Perimyotis subflavus* are of high priority. Within the eastern temperate forests of North America, forest management objectives aimed at maintaining bat roosting habitat can be largely streamlined by focusing on the roost-site requirements of these proposed umbrella species. It is important to note, however, that targeted conservation measures may be needed for ensuring persistence of individual species. As an example, the protection and regeneration of bottomland habitats in the midwestern United States may contribute disproportionately to Indiana bat recovery due to their reliance on hydric habitats [188]. Such finer-scaled directives may be apparent under the conservation umbrella approach.

5. Conclusions

Our systematic review of the tree-roosting eastern temperate forest bats of North America revealed three distinct groups exhibiting significant roosting niche overlap. Within these roosting guilds, *M. septentrionalis* and *P. subflavus* emerge as species with high potential to serve as conservation umbrellas for their groups. The existing federal protections of *M. septentrionalis* (in the U.S. and Canada) and *P. subflavus* (in Canada), and the probable future protections of *P. subflavus* in the U.S., further facilitating their potential to confer conservation benefits. However, approximately half of the species reviewed here were not well-represented in the literature. In particular, additional research on tree roost-site selection of *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Lasiurus seminolus* may refine the inferences drawn from the current body of knowledge. As many bat species are in decline and/or data-deficient, it is crucial that we highlight the need for further study of the ecologically and economically important Chiropterans.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A
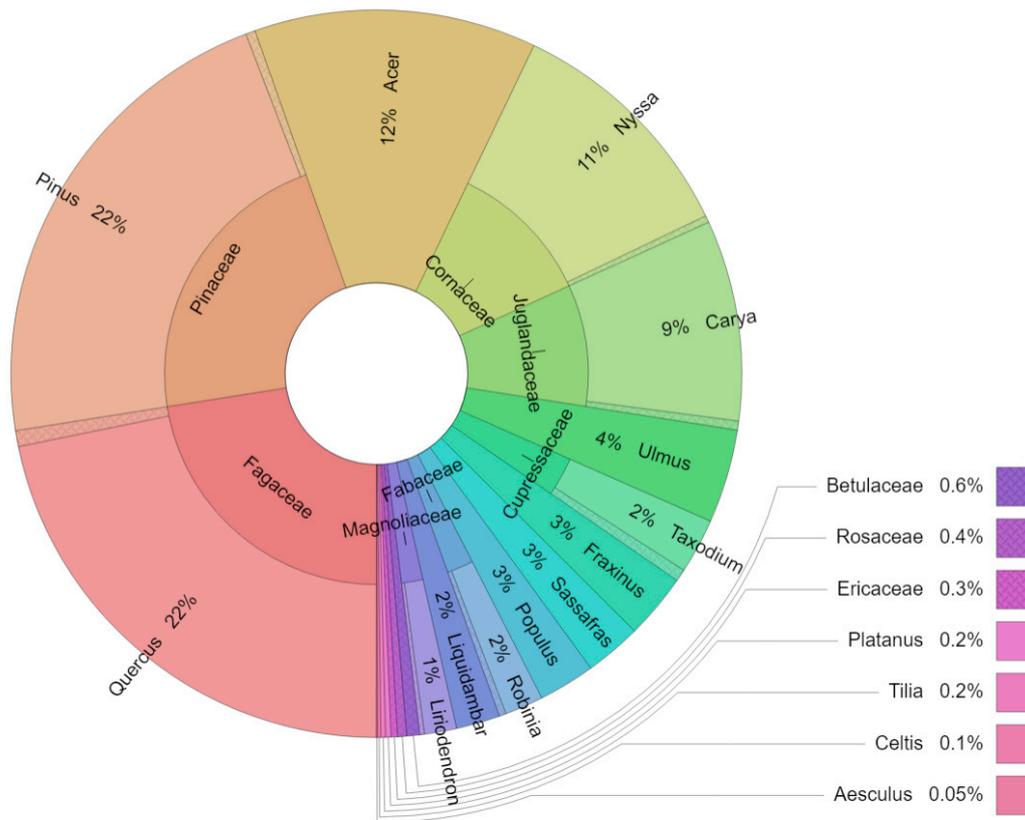
Figure A1. Distribution of tree genera used as roosts by bats of eastern temperate forests (N = 4228).

Table A1. Pairwise Tukey's Honest Significant Difference test p-values for the seven most reported roost-site characteristics eastern temperate forest bats. Colored cells indicate a significant difference (*p* < 0.05). Blue cells indicate a difference between roosting guilds, and green cells indicate differences within guilds. DBH = diameter at breast height, T.Hgt = tree height, R.Hgt = roost entrance height, CC = canopy closure, Decid = percentage of deciduous trees used as roosts, Snag = percentage of dead trees used as roosts, Fol = percentage of roosts that were in clumps of foliage.

Species Pair	DBH	T.Ht	R.Ht	CC	Decid	Snag	Fol
Eptesicus fuscus - Corynorhinus rafinesquii	<0.0001	0.9639	0.9999	1.0000	0.4085	0.6792	1.0000
Lasionycteris noctivagans - Corynorhinus rafinesquii	0.0045	0.9934	1.0000	0.9644	0.1918	0.9999	1.0000
Lasiurus borealis - Corynorhinus rafinesquii	<0.0001	0.9592	0.4567	1.0000	0.9999	0.9714	<0.0001
Lasiurus cinereus - Corynorhinus rafinesquii	<0.0001	0.9586	0.0020	1.0000	0.1050	0.9934	<0.0001
Lasiurus intermedius - Corynorhinus rafinesquii	0.0498	0.9900	0.9992	0.9479	1.0000	0.9983	<0.0001
Lasiurus seminolus - Corynorhinus rafinesquii	<0.0001	0.8938	0.0838	1.0000	<0.0001	0.9983	<0.0001
Myotis austroriparius - Corynorhinus rafinesquii	0.1487	1.0000	0.9256	0.9966	1.0000	1.0000	1.0000
Myotis lucifugus - Corynorhinus rafinesquii	0.0007	0.5812	0.9989	1.0000	1.0000	0.7967	1.0000
Myotis septentrionalis - Corynorhinus rafinesquii	<0.0001	0.9305	0.5664	1.0000	0.9903	0.1896	1.0000
Myotis sodalis - Corynorhinus rafinesquii	<0.0001	1.0000	0.0723	0.7962	0.7977	0.0080	1.0000
Nycticeius humeralis - Corynorhinus rafinesquii	<0.0001	0.8844	0.0749	1.0000	0.1694	0.6818	1.0000
Perimyotis subflavus - Corynorhinus rafinesquii	<0.0001	1.0000	0.0572	0.9970	1.0000	1.0000	<0.0001
Lasionycteris noctivagans - Eptesicus fuscus	1.0000	0.7767	1.0000	0.9999	0.9995	0.7167	1.0000
Lasiurus borealis - Eptesicus fuscus	1.0000	1.0000	0.9990	0.9994	0.7165	0.1480	<0.0001
Lasiurus cinereus - Eptesicus fuscus	1.0000	0.5247	0.1584	0.9999	1.0000	0.2682	<0.0001
Lasiurus intermedius - Eptesicus fuscus	1.0000	1.0000	0.9879	1.0000	0.8063	0.4065	<0.0001
Lasiurus seminolus - Eptesicus fuscus	1.0000	0.4137	0.7530	1.0000	0.8792	0.4065	<0.0001
Myotis austroriparius - Eptesicus fuscus	0.0107	0.9227	0.9401	0.9892	0.4740	0.7647	1.0000
Myotis lucifugus - Eptesicus fuscus	0.9999	0.9985	1.0000	1.0000	0.9456	1.0000	1.0000
Myotis septentrionalis - Eptesicus fuscus	1.0000	1.0000	1.0000	1.0000	0.7836	1.0000	1.0000

Table A1. *Cont.*

Species Pair	DBH	T.Ht	R.Ht	CC	Decid	Snag	Fol
Myotis sodalis - Eptesicus fuscus	0.9994	0.9933	0.9998	1.0000	0.8953	1.0000	1.0000
Nycticeius humeralis - Eptesicus fuscus	0.9901	1.0000	0.9968	1.0000	0.9982	0.9990	1.0000
Perimyotis subflavus - Eptesicus fuscus	1.0000	0.9799	0.9081	1.0000	0.6081	0.4708	<0.0001
Lasiurus borealis - Lasionycteris noctivagans	1.0000	0.8224	0.9126	0.8210	0.3614	1.0000	<0.0001
Lasiurus cinereus - Lasionycteris noctivagans	1.0000	1.0000	0.0420	0.9642	0.9997	1.0000	<0.0001
Lasiurus intermedius - Lasionycteris noctivagans	1.0000	0.8509	1.0000	1.0000	0.4353	1.0000	<0.0001
Lasiurus seminolus - Lasionycteris noctivagans	1.0000	1.0000	0.3775	0.9861	1.0000	1.0000	<0.0001
Myotis austroriparius - Lasionycteris noctivagans	0.1904	0.9993	0.9999	0.6966	0.2190	0.9999	1.0000
Myotis lucifugus - Lasionycteris noctivagans	1.0000	0.3774	0.9999	0.9999	0.6629	0.7299	1.0000
Myotis septentrionalis - Lasionycteris noctivagans	1.0000	0.8201	0.9953	0.9933	0.4148	0.6841	1.0000
Myotis sodalis - Lasionycteris noctivagans	1.0000	0.9661	0.9172	1.0000	0.5285	0.3975	1.0000
Nycticeius humeralis - Lasionycteris noctivagans	0.9996	0.7824	0.8250	0.9927	0.8419	0.8877	1.0000
Perimyotis subflavus - Lasionycteris noctivagans	1.0000	0.9950	0.5225	1.0000	0.2883	1.0000	<0.0001
Lasiurus cinereus - Lasiurus borealis	1.0000	0.4030	0.3624	1.0000	0.3441	1.0000	0.8146
Lasiurus intermedius - Lasiurus borealis	0.9985	1.0000	0.4986	0.6826	1.0000	1.0000	0.9299
Lasiurus seminolus - Lasiurus borealis	0.9913	0.2325	0.9780	1.0000	0.0005	1.0000	0.8146
Myotis austroriparius - Lasiurus borealis	<0.0001	0.9141	0.0794	1.0000	1.0000	0.9783	<0.0001
Myotis lucifugus - Lasiurus borealis	0.9843	0.9510	0.9999	0.9997	1.0000	0.3353	<0.0001
Myotis septentrionalis - Lasiurus borealis	0.9560	1.0000	0.9970	0.9217	1.0000	0.0030	<0.0001
Myotis sodalis - Lasiurus borealis	0.4913	0.9968	1.0000	0.2186	0.9995	<0.0001	<0.0001
Nycticeius humeralis - Lasiurus borealis	0.2946	1.0000	1.0000	0.9863	0.7580	0.0325	<0.0001
Perimyotis subflavus - Lasiurus borealis	1.0000	0.9886	0.9996	0.8858	1.0000	0.9996	0.4902
Lasiurus intermedius - Lasiurus cinereus	1.0000	0.7512	0.0082	0.9672	0.6015	1.0000	1.0000
Lasiurus seminolus - Lasiurus cinereus	1.0000	1.0000	0.9960	1.0000	0.8563	1.0000	1.0000
Myotis austroriparius - Lasiurus cinereus	0.0014	0.9977	0.0003	1.0000	0.1574	0.9939	<0.0001
Myotis lucifugus - Lasiurus cinereus	0.9998	0.1966	0.2150	1.0000	0.8771	0.4231	<0.0001
Myotis septentrionalis - Lasiurus cinereus	1.0000	0.3362	0.0298	0.9998	0.3951	0.0580	<0.0001
Myotis sodalis - Lasiurus cinereus	0.9984	0.7724	0.0921	0.9511	0.5683	0.0055	<0.0001
Nycticeius humeralis - Lasiurus cinereus	0.9767	0.2887	0.2215	1.0000	0.9702	0.2341	<0.0001
Perimyotis subflavus - Lasiurus cinereus	1.0000	0.9779	0.7974	0.9968	0.2726	0.9999	1.0000
Lasiurus seminolus - Lasiurus intermedius	1.0000	0.6900	0.1160	0.9867	0.0159	1.0000	1.0000
Myotis austroriparius - Lasiurus intermedius	0.6534	0.9741	1.0000	0.5852	1.0000	0.9982	<0.0001
Myotis lucifugus - Lasiurus intermedius	1.0000	0.9999	0.9691	1.0000	1.0000	0.5183	<0.0001
Myotis septentrionalis - Lasiurus intermedius	1.0000	1.0000	0.7525	0.9910	1.0000	0.2092	<0.0001
Myotis sodalis - Lasiurus intermedius	1.0000	0.9982	0.4294	1.0000	0.9996	0.0462	<0.0001
Nycticeius humeralis - Lasiurus intermedius	1.0000	1.0000	0.3237	0.9915	0.9593	0.5000	<0.0001
Perimyotis subflavus - Lasiurus intermedius	0.9977	0.9932	0.1537	1.0000	1.0000	1.0000	1.0000
Myotis austroriparius - Lasiurus seminolus	0.0033	0.9924	0.0146	0.9986	0.0001	0.9982	<0.0001
Myotis lucifugus - Lasiurus seminolus	1.0000	0.1497	0.8376	1.0000	0.1451	0.5183	<0.0001
Myotis septentrionalis - Lasiurus seminolus	1.0000	0.1607	0.5201	1.0000	0.0004	0.2092	<0.0001
Myotis sodalis - Lasiurus seminolus	1.0000	0.5736	0.8194	0.9683	0.0008	0.0462	<0.0001
Nycticeius humeralis - Lasiurus seminolus	0.9999	0.1338	0.9540	1.0000	0.0201	0.5000	<0.0001
Perimyotis subflavus - Lasiurus seminolus	0.9908	0.9457	1.0000	0.9997	0.0005	1.0000	1.0000
Myotis lucifugus - Myotis austroriparius	0.1775	0.5022	0.8698	0.9929	1.0000	0.8401	1.0000
Myotis septentrionalis - Myotis austroriparius	<0.0001	0.8827	0.0486	0.8699	0.9976	0.4003	1.0000
Myotis sodalis - Myotis austroriparius	<0.0001	0.9995	0.0034	0.3331	0.9307	0.0476	1.0000
Nycticeius humeralis - Myotis austroriparius	0.0004	0.8302	0.0047	0.9386	0.3696	0.8620	1.0000
Perimyotis subflavus - Myotis austroriparius	<0.0001	1.0000	0.0060	0.7912	1.0000	1.0000	<0.0001
Myotis septentrionalis - Myotis lucifugus	1.0000	0.9248	1.0000	1.0000	1.0000	1.0000	1.0000
Myotis sodalis - Myotis lucifugus	1.0000	0.7098	1.0000	1.0000	1.0000	1.0000	1.0000
Nycticeius humeralis - Myotis lucifugus	1.0000	0.9496	0.9996	1.0000	0.9972	0.9978	1.0000
Perimyotis subflavus - Myotis lucifugus	0.9820	0.6444	0.9581	1.0000	1.0000	0.6469	<0.0001
Myotis sodalis - Myotis septentrionalis	0.9992	0.9936	0.9940	0.8859	1.0000	0.9929	1.0000
Nycticeius humeralis - Myotis septentrionalis	0.9566	0.9496	0.9463	1.0000	0.8000	0.9979	1.0000
Perimyotis subflavus - Myotis septentrionalis	0.9747	0.9852	0.6357	1.0000	0.9999	0.0697	<0.0001
Nycticeius humeralis - Myotis sodalis	0.9999	0.9814	1.0000	0.9417	0.9622	0.4726	1.0000
Perimyotis subflavus - Myotis sodalis	0.7046	1.0000	0.9486	1.0000	0.9918	0.0023	<0.0001
Perimyotis subflavus - Nycticeius humeralis	0.4754	0.9694	0.9980	1.0000	0.6663	0.3675	<0.0001
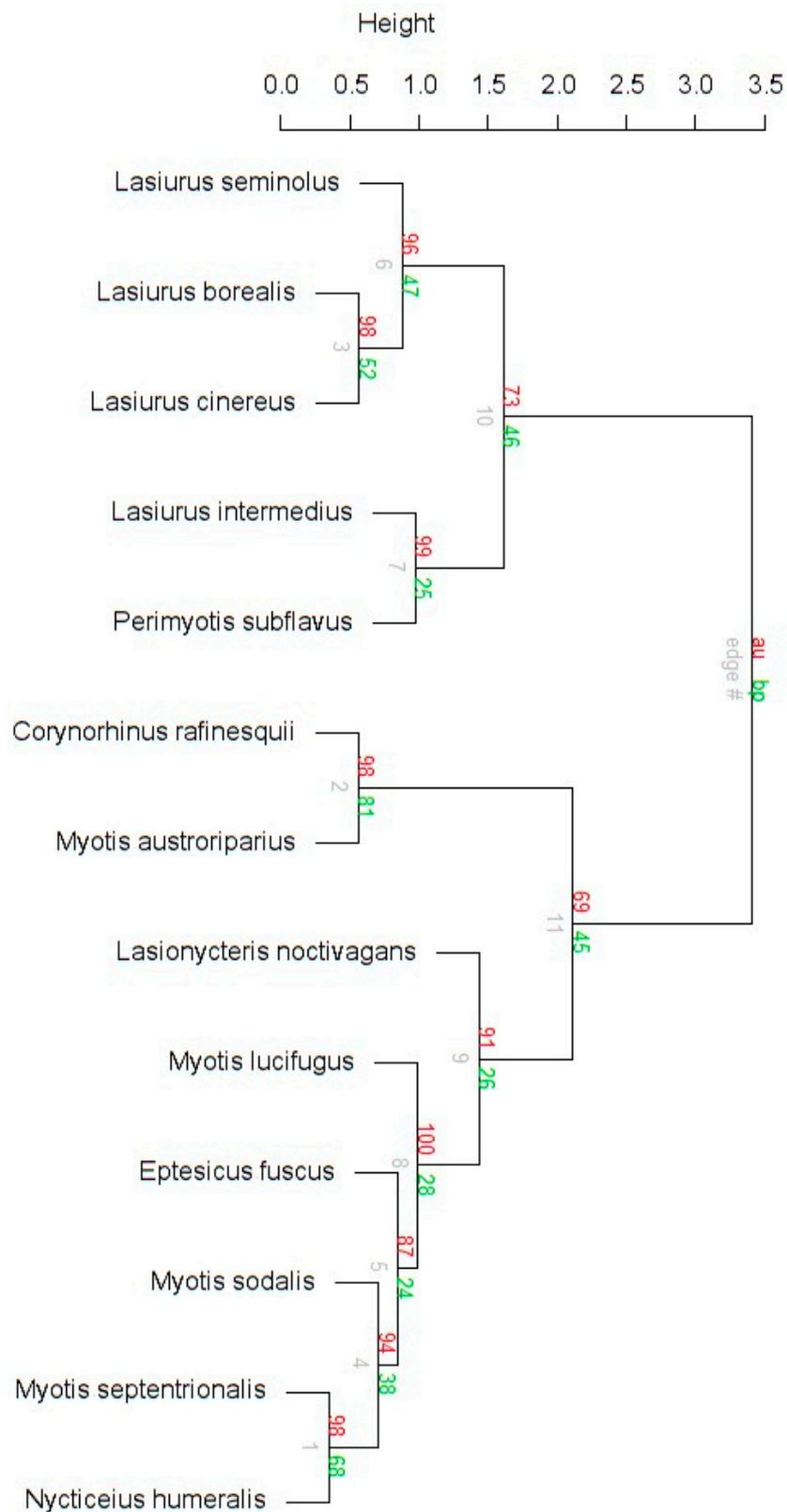
Figure A2. Cluster dendrogram with approximately unbiased (au) p-values in red, bootstrap probabilities (bp) in green, and the edge number labeling the nodes in gray. This figure separates North American eastern temperate forest tree-roosting bats using Ward's method and Euclidean distance.
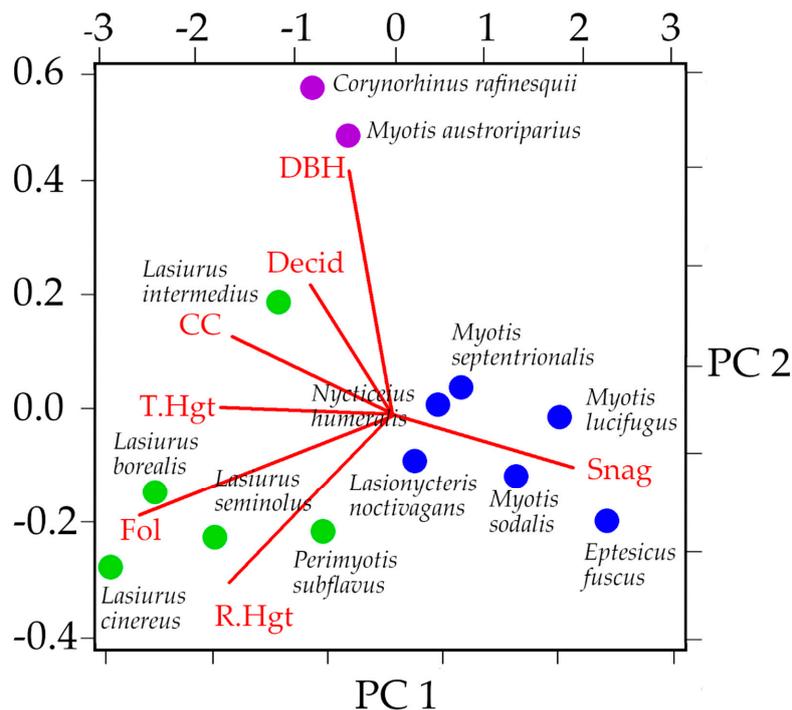
Figure A3. PCA on the correlation matrix of the seven most-reported roost tree characteristics. CC = canopy closure, DBH = diameter at breast height, T.Hgt = tree height, R.Hgt = roost entrance height, Snag = percentage of dead trees used as roosts, Decid = percentage of deciduous trees used as roosts, Fol = percentage of roosts that were in clumps of foliage.

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