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Indiana bat maternity roost habitat preference within Midwestern United States upland Oak-Hickory (*Quercus-Carya*) forests

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ABSTRACT

The Indiana bat (*Myotis sodalis*) is a federally listed endangered species negatively impacted by human disturbance, habitat change, and disease. Habitat protection and management of summer roosting habitat and cave hibernacula are recommended for the recovery of this species. We studied roost tree and landscape characteristics of 19 known summer maternity colony habitats in Illinois and Iowa upland oak-hickory (*Quercus-Carya*) forests. Landscape variables can be highly correlated in fragmented forest habitats and not all the roost tree and landscape variables are relevant to roost tree selection. We employed an algorithm to approximate the data set by using singular value decomposition (SVD) to identify the primary factors governing the selection of maternity roosts. The proposed method (formally referred to as a feature selection algorithm) approximates the data by discarding highly correlated features and features that can be removed without incurring much loss of information. Results indicated that summer maternity roosts were trees closer to forest edge, larger in diameter and typically trees with crowns in the upper canopy of the forest. In addition, partial bark cover and locations within 1 km of water bodies positively influenced the tree selection. Although live or dead shagbark hickory (*Carya ovata*) were preferred as maternity roosts, snags of other trees species common to Midwest upland oak-hickory forests were also used. We incorporated a joint probability density estimation and the Wilcoxon rank sum test to investigate the relationship between tree species and dead/live tree status for roost tree selection. There was sufficient evidence to infer that the chosen live trees were taller and in more favorable locations compared to the chosen snags. We further observe that the joint distribution for quantitative attributes among dead or declining shagbark hickory was not significantly different compared to the other chosen tree species, indicating that a lack of shagbark hickory may not limit the Indiana bat population. Knowledge of these complex relationships regarding maternity roost habitat preferences is useful for future management of the Indiana bat throughout Midwest oak-hickory forests.

1. Introduction

Despite being one of the most studied bats in North America (Bogan et al., 1996) uncertainty about the habitat requirements of the endangered Indiana bat (*Myotis sodalis*) continues to limit efforts to manage and recover populations of this endangered species. Initial conservation efforts focused on identifying and protecting hibernacula where thousands of bats may gather for winter, but by the early 2000s, the focus shifted to identifying and managing summer habitat (USFWS, 2007). These efforts were broadly successful, with population trends stabilizing or increasing in three of the four recovery units designated by the U.S. Fish and Wildlife Service (Thogmartin et al., 2012). Population estimates declined by > 15% during 2007–2015 (USFWS, 2015), but this decline was associated with the arrival of White-nose syndrome. White-nose syndrome, a disease caused by the fungus *Pseudogymnoascus destructans*, is associated with dramatic population declines of multiple species of bats, including Indiana bats (Powers et al., 2015; Silvis et al., 2016; Thogmartin et al., 2012), with most bats dying during winter when they are exposed to the pathogen and have limited capacity for immune responses.

Even if focus on managing winter habitat increases, conservation and management of summer habitat remains an important component in efforts to avoid extinction and eventually recover the species (USFWS, 2007). Maternity roosts are a key component of summer habitat because it is within these roosts that female bats give birth to and raise their young. Several studies have established that maternity roost

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tree selection is governed by various tree characteristics, including tree height, diameter, species, sloughing bark, canopy opening, and live/dead status (Bergeson et al., 2015; Brack, 2006; Britzke et al., 2003, 2006; Carter and Feldhamer, 2005; Johnson et al., 2010; Lacki et al., 2009; Timpone et al., 2010; Watrous et al., 2006), and certain landscape properties, including distance to forest edge, distance to water, and greater distance from human development (Bergeson et al., 2015; Clark et al., 1987; Jachowski et al., 2014; Jachowski et al., 2016; Kurta et al., 2002; Miller et al., 2002; Sparks et al., 2005; Watrous et al., 2006). Most commonly, researchers identify these attributes by comparing statistics for each attribute of known maternity roost trees to those of randomly selected surrounding trees or regions (Bergeson et al., 2015; Brack, 2006; Britzke et al., 2003; Britzke et al., 2006; Carter and Feldhamer, 2005; Clark et al., 1987; Johnson et al., 2010; Silvis et al., 2015; Timpone et al., 2010). Comparisons between summer roost trees and non-roost trees are valuable in identifying preferred characteristics associated with tree choices. They can provide information that can aid in bat habitat management. However, the non-roost data set used for comparison may contain some trees that have a high likelihood for selection, leading to errors in analysis. (See Silvis et al. (2015) for a long-term study and wide-ranging discussion regarding inferences of roost selection based only on comparisons of roosts to non-roosts.) Further, comparisons may yield spurious results, particularly when variables are correlated and sample sizes are small. Analysis of presence-only data has become more accepted in habitat analysis, indicated by recent bat research (Hammond et al., 2016; Pauli et al., 2015a; Weber and Sparks, 2013). In this paper, we utilize a sample of maternity roost trees (presence-only data) to identify the most relevant features and to model the distribution of attributes given the trees were selected. We introduce a systematic approach for building a model by selecting those features which are least correlated with one another, and by adding new features until essentially no new information about selection is gained.

Variables describing tree conditions and location with respect to habitat resources are incorporated in a single model for evaluating Indiana bat maternity roost selection. Tree conditions that have previously been found to be important include height and the size of the roost tree crown opening, which is related to solar exposure (Carter and Feldhamer, 2005; Foster and Kurta, 1999; Timpone et al., 2010), and the presence of bark crevices for pup protection and warmth (Carter and Feldhamer, 2005; Racey, 1982; Timpone et al., 2010). Tree species and dead or live status were also found to be important (Gardner and Cook, 2002; Yates and Muzika, 2006). From a landscape perspective, researchers have found that Indiana bats occupy maternity roosts of forested areas surrounded by open areas with near proximity to water and food sources (Callahan, 1993; Carter et al., 2002; Gardner et al., 1991; Jachowski et al., 2016; Kurta et al., 1989, 1990, 2002; Pauli et al., 2015a; USFWS, 2016; Watrous et al., 2006; Wolcott and Vulinec, 2012). Proximity to hibernacula may also be important; however, migratory distance has been found to vary greatly in different studies, with the average being 26.9 km (Britzke et al., 2006) and the maximum found being 575 km (357 mi) (Rockey et al., 2013; Perry et al., 2016). Fragmented landscapes can create correlations between the variables that have been identified as important, requiring a methodical approach to identify the most important variables.

The primary objective of this paper is to investigate maternity roost trees located in several Midwest U.S. oak-hickory (*Quercus-Carya*) forest sites to understand the contribution of various tree characteristics and landscape properties for maternity roost selection. We hypothesized that Indiana bats select trees based on tree structure characteristics, including: (1) tree species, (2) dead/live status of the tree, (3) diameter of the tree, (4) tree height, (5) available exfoliating bark structure (percent exfoliating bark), and (6) size of the tree gap opening (percent canopy opening). We further postulated that the distance of maternity roost trees to important food sources, cover, and potential replacement maternity roost tree habitat are also important factors in roost tree selection. Landscape-scale variables include: (1) distance to the forest edge, (2) distance to water, (3) distance to the nearest hibernaculum, (4) distance between maternity colony habitats, and (5) availability of nearby potential maternity colony habitat (available forest area within 1.5 km radius). We propose an algorithm that combines an unsupervised feature selection method with a non-parametric density estimation to investigate maternity roost tree selection variables. We first approximate the roost tree and landscape data, which can be represented by a matrix, using a lower ranked matrix with minimal information loss. The refined data set is then used to obtain the conditional probability distribution for the variables, given that the trees are maternity roosts. We summarize the specific aims of this study below.

1. Distinguish which features are most relevant among those collected by discarding highly correlated features and features that can be removed without incurring much loss of information about selection.
2. Model the joint probability density function of the chosen quantitative attributes among the selected roost trees and evaluate the nature of the contribution of each.
3. Compare the likelihoods that a roost tree has quantitative attributes that are similar to those of the dead trees, versus those of the live trees, to assess the preference for each category. Perform a similar evaluation for tree species.

In recent literature, presence-only data was utilized to evaluate preferred characteristics of Indiana bat maternity habitats based on landscape-scale environmental variables (Hammond et al., 2016; Pauli et al., 2015a). These studies were based on the likelihood approach presented by Royle et al. (2012) and maximum entropy modeling (Phillips et al., 2006), without any presence-absence comparisons. The analyses here are also based on presence-only data and we utilize estimations of the conditional joint probability distribution of both tree species characteristics and landscape-scale environmental variables, given that the trees are maternity roosts, to assess the nature of the contributions. The proposed analysis does not depend on a set of candidate models specified before the analyses are conducted. The proposed analysis, combined with data from random samples of trees in the forest, can be utilized to estimate the probability that a tree will be used as a summer maternity roost based on various habitat variables (see Appendix A). This paper will stand as a valuable addition, extending understanding of Indiana bat habitat characteristics, as well as providing an introduction to a robust, systematic approach for analysis.

2. Material and methods

2.1. Study area

We studied maternity roost tree habitats in four locations: in Lucas and Van Buren counties in Iowa, and in LaSalle and Ford counties in Illinois (see Fig. 1). The study area in Lucas County covers approximately 512 hectares within Stephens State Forest and sites in LaSalle, Van Buren, and Ford counties were on private property. Sites were not located near large rivers or lakes, were upland habitat, and were selected based on known Indiana bat roost locations.

2.2. Data collection

The Illinois Natural Heritage Database and the Iowa Department of Natural Resources provided known locations of 19 Indiana bat roost trees, which were identified during the summers of 2006–2010 by biologists (other than the authors) who used radio-telemetry to track pregnant, lactating, or post-lactating females bats to a tree. We returned to these sites between May and August 2011, and used a standard protocol to measure each tree. Measurements taken included: diameter at breast height in using a DBH tape (Forestry Suppliers, Jackson, MS),

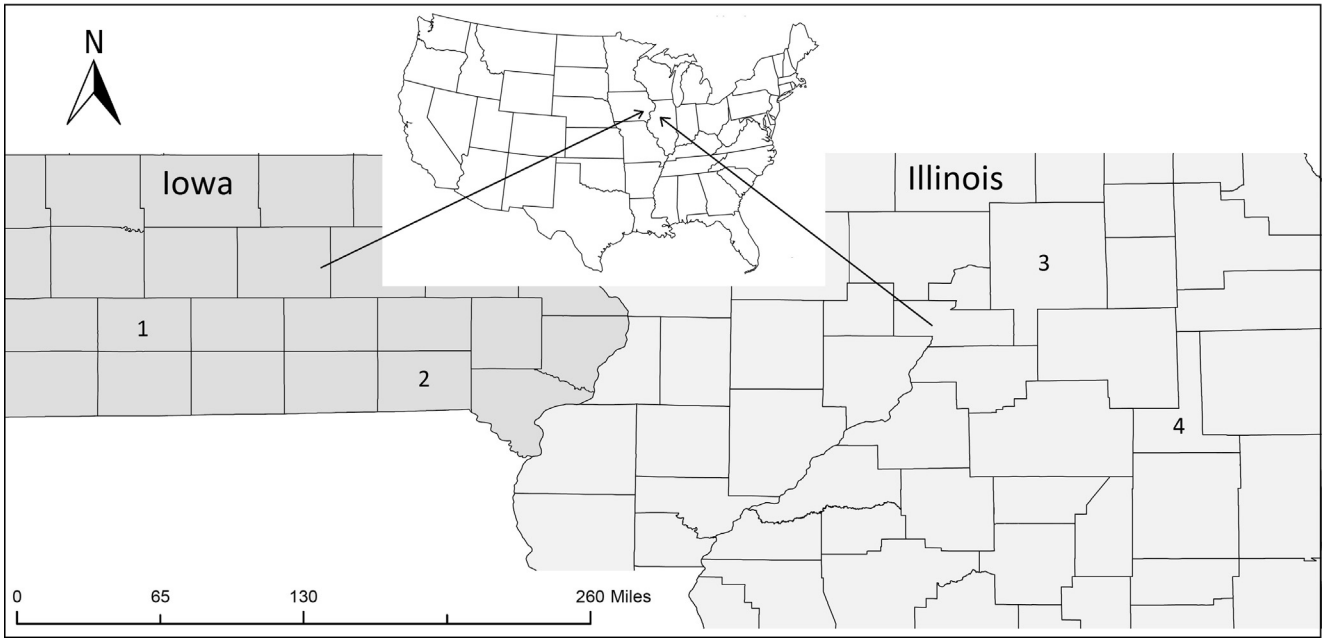

Fig. 1. Study site locations in Iowa and Illinois, USA: 1. Lucas County, 2. Van Buren County, 3. LaSalle County 4. Ford County.

height in meters using a clinometer (SUUNTO, Vaanta, Finland), tree species (Mohlenbrock, 2006), available bark as a percentage, canopy opening measured at the ground (1-% canopy cover; densitometer, Geographic Resource Solutions, Arcata, CA), tree status (dead/declining/alive), and location using a Global Positioning System (GPS, Garmin GPSmap 76 unit, ± 10 m, Olathe, Kansas). Trees were classified as declining (or partially dead) if the tree had at least one dead limb with the rest of the tree still living.

During the field visit, we photographed each tree from multiple angles at a standard distance. Upon return to the lab, we traced the images from the photographs onto 1/8 in. graph paper by overlaying them. Peeling bark was marked on the graph paper by shading. We calculated the percentage of peeling bark for each picture by dividing the number of shaded squares by the total number of squares encompassed by the tree. The percentage of available bark for the entire tree was the average percentage of all the images for the tree.

We used a Geographic Information System (ArcGIS 9.3.1. ESRI Redlands, CA) to examine the landscape context of each roost. Using the ArcGIS measurement tool and 2016 National Agriculture Imagery Program Aerial Photography, we obtained the distance (in km) from the maternity roost to the nearest water body and to the nearest forest edge. We also measured the distance from the maternity roost to the nearest hibernaculum, the distance between maternity roosts, and the amount of forested habitat (in km^2) within 1.5 km of each roost tree.

2.3. Data analysis

All but two of the variables collected for this study were continuous. Tree species and tree status, conversely, are categorical, and thus we assigned ranks to these data prior to conducting additional analyses. We assigned tree statuses as live = 1, declining = 2, and dead = 3, where the category of dead included snag stages 3 and above, as defined in Thomas et al. (1979). Six tree species were represented in the data and we assigned values 1 through 6 by minimizing the variance inflation factor (VIF): black locust (*Robinia pseudoacacia*) = 1, red oak (*Quercus rubra*) = 2, shagbark hickory (*Carya ovata*) = 3, elm (*Ulmus* spp.) = 4, black oak (*Quercus velutina*) = 5, and walnut (*Juglans nigra*) = 6 (VIF = 2.156, max r = 0.45). These assignments provide a numerical labeling for the tree species for further analysis and the minimum VIF minimizes the possibility of creating false relationships between the assigned labels and the other variables. These assignments allow us to include the tree statuses, tree species, and all the quantitative variables in a single numerical matrix representation of data set that is useful in identifying a refinement.

Our examination of all variables relied on a pair of multivariate tools available in the MATLAB software package. We applied QR decomposition with a column-pivoting algorithm and singular value decomposition (SVD) to identify those variables that contribute most significantly toward the total sum of the squared singular values (referred to as the Frobenius norm). First, we used the QR decomposition, which uses both an orthogonal matrix (Q) and an upper triangular matrix (R) (Francis, 1961, 1962) to rank the variables. Here, QR is not an abbreviation, but rather the name somewhat arbitrarily given by Francis in his original paper (1961) to represent the matrices. We then used SVD to identify the most informative features (Businger and Golub, 1965; Gu and Eisenstat, 1996; Hong and Pan, 1992; Stewart, 1984). We selected the minimum number of variables that, when combined, contributed 95% or more of the Frobenius norm of the original data set, and eliminated all other variables, so that the chosen variables characterized the data set well. We evaluated all the eliminated variables for their correlations with the chosen variables to identify highly correlated discarded variables that may still be important characteristics for Indiana bat maternity roost selection.

For the quantitative variables among the selected salient features (say X_j for $j = 1, \ldots, k$), we used relative frequency histograms to assess the nature of the contribution of each variable towards maternity roost tree selection. Each histogram is a non–parametric estimator for the marginal density of the corresponding variable and, hence, is suitable for evaluating the contribution of uncorrelated variables. We defined a model – a *potential function* – for the data set by $f(X_1,\ldots,X_k) = C\prod_{j=1}^{k} f_j(X_j)$, where $f_j(X_j)$ is a kernel estimate of the univariate probability density function of the variable X_j and C is a constant. We chose the value of C to scale the function so that $f(\hat{X}_1,\ldots,\hat{X}_k) = 1$, where $(\hat{X}_1,\ldots,\hat{X}_k)$ corresponds to the roost tree from the data set with the largest joint probability density. The potential function is a scaled version of the joint probability density, and the two functions would be identical if the normalization constant C was chosen as unity. We used this function to compare the likelihoods that a roost tree has quantitative attributes that are similar to those of the dead trees, versus those of the live trees, selected as maternity roosts in this

study. We performed a similar evaluation for tree species. See Appendix B for a proof that the ratios between mean potentials within each status/species can be used to estimate the ratios between the aforementioned probabilities. Most of the features of interest for roost selections have bounded domains. We employed the positive part of third order polynomials to approximate the densities of these variables with bounded domains. We seek to determine whether the potential values are similar between tree statuses and between tree species or whether one status/species has higher or lower potential values than others. We tested the null hypothesis that the distribution of potentials does not differ with respect to tree status. We also tested the null hypothesis that the distribution of potentials for shagbark hickory (the species that was most frequently chosen among dead or declining trees) does not differ from the distribution of the other chosen tree species. The potential function attains values between 0 and 1 with an unknown distribution. Subsequently, we used Wilcoxon rank sums to test the aforementioned null hypotheses (see Appendix D for assumptions).

3. Results

Indiana bats selected ten shagbark hickory trees, three red oaks, two elms, two walnuts, one black oak and one black locust. Four of the shagbarks were live trees, with all remaining roosts being snag or declining trees. In Table 1, we summarize the statistics and the labels we utilized throughout this section.

SVD analysis showed that the first six singular values explained 96% of the Frobenius norm. The corresponding six principal factors governing tree selection were: tree species, roost tree height (X_1), distance from maternity roost to forest edge (X_2), distance from maternity roost to water (X_3), roost tree diameter (X_4), and percentage of bark cover (X_5). No multicolinearity was present between the selected quantitative variables, as the VIF was less than 2 for all the variables (Table 2 rows 1–5). Each of the discarded landscape-scale environmental variables showed a noteworthy correlation to the other four landscape-scale variables (VIF $>$ 4, Table 2 rows 6–8). Canopy opening did not show any considerable correlation to the other variables except for tree status. Tree status showed a noticeable relationship to height, distance to forest edge, percentage bark cover, and canopy opening (Multiple $R^2 = 0.8$, VIF = 5). We summarize the mean attributes of the related variables for tree status in Table 3.

Fig. 2 shows the relative frequency histograms for the features selected through SVD, as well as for canopy opening. The histograms indicate that, within the given data range, there was a higher preference for roosting in tall trees near forest edges. All the trees were within 200 m of forest edges (Fig. 2b). Around two-thirds of the chosen trees were taller than 14 m (Fig. 2a). More than half the trees had diameters between 37 and 46 cm (Fig. 2d) and, except for one tree, the percentage bark cover was 60% or lower (Fig. 2e). All the trees were within 1 km of water bodies and the distribution was roughly uniform (Fig. 2c). The histogram for canopy opening did not suggest a significant preference for a particular range (Fig. 2f).

Fig. 3 displays density approximations using third-order polynomials and Gaussian kernels. The Gaussian kernel density approximations result in nontrivial probabilities for negative distances and for percentages outside 0–100%. The third-order polynomial kernels produce bounded approximations with means very close to the sample means.

Table 4 summarizes the mean potential for each tree status as well as between dead and declining shagbark hickory and other species. (See Eq. (B.1) for the relationship between the mean potential and the probability of a roost tree having quantitative attributes similar to that of a given category.) Potentials for the live trees were more than twice those of dead trees. The Wilcoxon rank sum test indicated rejection of null hypothesis that the distribution of the potentials for live and declining trees does not differ from the distribution of the potentials for dead trees (p-value = 0.0358, rank sum test statistic = 95). Live and declining trees were treated as one category to increase the sample size. Another Wilcoxon rank sum test indicated that there is not enough evidence to reject the null hypothesis that the distribution of the potentials for shagbark hickory trees does not differ from the distribution of the potentials for other species (p-value = 0.6889, rank sum test statistic = 44). We did not include live trees for the second test, as they were all Shagbark Hickory.

Table 1
Descriptive statistics for maternity roost habitat variables related to the19 studied summer maternity colony habitats of Indiana bats (*Myotis sodalis*) in Illinois and Iowa upland oak-hickory (*Quercus-Carya*) forests.

Feature	Label	Mean	Median	SD	Range
Tree height (m)	X_1	13.49	14.02	3.09	8.23–17.68
Distance to forest edge (m)	X_2	69.34	62.07	50.69	0–196.44
Distance to water (m)	X_3	464.74	400	279.81	0–880
Diameter (cm)	X_4	45.99	41.40	19.69	15.24–104.14
Bark cover (%)	X_5	36.63	34.17	20.16	1.71–71.44
Canopy opening (%)	X_6	46.25	33.75	29.99	7.5–100
Distance between maternity colonies (km)	X_7	100.92	90.07	22.10	49.7–131.89
Distance to nearest hibernaculum (km)	X_8	137.95	122.45	66.35	1.85–227.16
Potential maternity colony habitat (km^2)	X_9	3.13	2.49	1.20	1.87–5.46

Table 2
Variance impact factors (VIFs) between Indiana bat maternity roost tree attributes selected by a feature selection algorithm (rows 1–5) and correlation between landscape-scale variables (rows 6–8).

Feature	Selected Y/N	Regressed covariates	Multiple R^2	VIF
Tree height (X_1)	Y	X_2, X_3, X_4, X_5	0.189	1.233
Distance to forest edge (X_2)	Y	X_1, X_3, X_4, X_5	0.253	1.339
Distance to water (X_3)	Y	X_1, X_2, X_4, X_5	0.391	1.642
Diameter (X_4)	Y	X_1, X_2, X_3, X_5	0.328	1.488
Exfoliating bark (X_5)	Y	X_1, X_2, X_3, X_4	0.442	1.792
Distance between maternity colonies (X_7)	N	X_2, X_3, X_8, X_9	0.772	4.378
Distance to nearest hibernaculum (X_8)	N	X_2, X_3, X_7, X_9	0.872	7.794
Potential maternity colony habitat size (X_9)	N	X_2, X_3, X_7, X_8	0.927	13.755

Table 3
Sample means by tree status for the quantitative attributes of maternity roost trees correlated with tree status.

Tree status	Mean height (m)	Mean distance to forest edge (m)	Mean peeling bark (%)	Mean canopy opening (%)
Live (1)	15.24	43.2	53.1	17.2
Declining (2)	14.12	51.3	40.1	24.6
Dead (3)	12.75	82.6	30.3	61.4

4. Discussion

In this paper, we utilized an SVD feature selection algorithm to evaluate the hypothesis that Indiana bats select maternity roost trees based on six tree structure characteristics and five distance relationships. SVD allows for an exact representation of any matrix using singular values, making it easy to eliminate variables that are strongly correlated or of lesser importance to produce an approximation with any desired lesser number of dimensions. SVD is the preferred choice for many feature selection algorithms to determine what features are

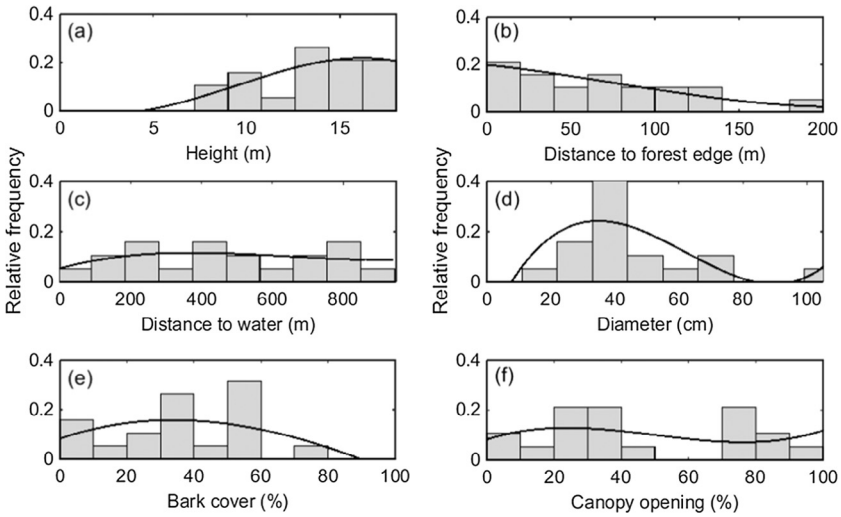

Fig. 2. Relative frequency histograms for six quantitative attributes of Indiana bat summer maternity roost trees in Illinois and Iowa upland oak-hickory forests. The subplots represent histograms for (a) height, (b) distance to forest edge, (c) distance to water, (d) diameter, (e) percentage exfoliating bark, (f) percentage canopy opening. The dark curves represent third-order polynomial approximations for the histograms. The corresponding equations are given by Eq. (C.1)-(C.6) in Appendix C.

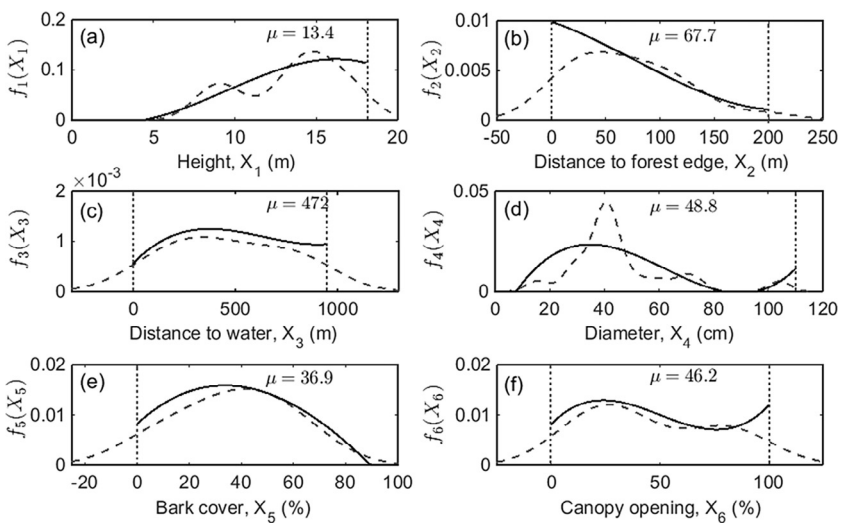

Fig. 3. Probability density function (pdf) approximations for quantitative attributes of Indiana bat summer maternity roost trees using third-order polynomials (continuous curves) and Gaussian kernels (dashed curves). The curves represent the (a) pdf of height, $f_1(X_1)$, (b) pdf of distance to forest edge, $f_2(X_2)$, (c) pdf of distance to water, $f_3(X_3)$, (d) pdf of diameter, $f_4(X_4)$, (e) pdf of exfoliating bark, $f_5(X_5)$, and (f) pdf of percentage canopy cover, $f_6(X_6)$. Means for the polynomial density approximations are given by μ and the vertical lines represent the domain boundaries.

Table 4
Mean potential for Indiana bat maternity roost trees categorized according to the tree status (live/declining/dead) and for shagbark hickory trees compared to all other species.

Tree status	Tree species	Mean potential
Live (n = 4)	Shagbark Hickory (*Carya ovata*)	0.711
Declining (n = 3)	Shagbark Hickory and Elm (*Ulmus* spp.)	0.456
Dead (n = 12)	Five tree species	0.291
Tree species	Tree status	Mean potential
Shagbark Hickory	Declining (n = 2) and dead (n = 4)	0.334
Elm, Walnut (*Juglans nigra*), Red Oak (*Quercus rubra*), Black Locust (*Robinia pseudoacacia*), Black Oak (*Quercus velutina*)	Declining (n = 1) and dead (n = 8)	0.319

most relevant (Businger and Golub, 1965; Duda et al., 2001; Gu and Eisenstat, 1996; Hong and Pan, 1992; Stewart, 1984). We identified four tree attributes (tree species, available bark structure, tree diameter and height) and two landscape attributes (distance to the forest edge and to water bodies) as primary contributors. Distance between maternity colony habitats, the amount of forested area surrounding the maternity roost site for replacement roost trees, and the distance to the nearest hibernaculum were highly correlated (Table 2) and their contributions towards the selection were not distinctive. The observed correlation may be attributed to the highly fragmented habitat structure (See Fig. 3 for landscape surrounding the roost trees in a Midwest upland oak-hickory forest in Iowa.) and possible spurious relationships. Canopy opening measured at the ground appeared to be an irrelevant feature. Apart from the obvious relation to status as dead (large canopy opening) or live (small canopy opening), the feature selection algorithm did not indicate any further relevance. We could not abstract tree mortality status as a clear contributor from the SVD analysis, possibly due to the significant correlation to other contributing factors (Table 3). The variables we obtained through SVD analysis displayed very little correlation to each other (Table 2) and offered the optimal set of quantitative features for independent evaluation.

Shagbark hickory was the most common tree species observed in this study as Indiana bat maternity roosts in upland Midwest oak-hickory forests in Iowa and Illinois. Both live and dead shagbark hickory provide exfoliating bark and crevices necessary for Indiana bat pups. This result corresponds to previous research indicating the use of shagbark hickory by this endangered species (Carter and Feldhamer, 2005; Kurta, 2004; Pauli et al., 2015a). Our data also indicate Indiana bat use of loose, sloughing bark of dead elm (*Ulmus* spp.), oak (*Quercus* spp.), and walnut (*Juglans nigra*), species typical of the region. Similar

to previous studies, most roosts were in dead trees (Callahan et al., 1997; Carter and Feldhamer, 2005). However, there were four roosts in live shagbark hickory trees and three roosts in declining trees. Roosts in live shagbark hickories have been previously observed, particularly as alternate roosts (Britzke et al., 2003; Callahan et al., 1997; Foster and Kurta, 1999; Humphrey et al., 1977). We observed several distinct characteristics for chosen live trees compared to others. Live trees had the greatest mean height and the smallest mean distance to the forest edge, followed by declining trees (Table 3). Tree crowns of taller trees located near the forest edge are exposed to greater solar radiation compared to crowns covered with adjacent vegetation. While our observations possibly relate to the preference for high solar exposure at roost locations, the percentage of canopy opening at the roost level is necessary to conclude such preference. The live trees also had the lowest canopy opening at the base and the most bark cover, both intrinsic to the live status (Table 3).

To identify possible reasons for choices of various tree species with different mortality stages as maternity roosts, we introduced a potential function. This function is a rudimentary estimation for the likelihood of a small region encompassing the chosen data point in the domain. A value of the potential function that is close to unity indicates quantitative tree characteristics that are highly favorable for selection. The potential function was so named because it can be used to compare suitable trees in various landscapes for the likelihood of Indiana bats selecting them as maternity roosts. However, the potential function must also be combined with data from a random sample of trees in the forest to estimate the probability that a tree will be used as a summer maternity roost based on various habitat variables (see Eq. (A.1)). We constructed the potential using the product of univariate kernel density estimates for each quantitative variable. Univariate kernel functions usually utilized for density estimates are symmetric with one peak, located at the origin, such as Gaussian, logistic, and cosine functions. However, the aforementioned kernel functions produce estimates with nontrivial probabilities outside of the range of the attributes, making them less appropriate for the features of interest (see Fig. 3 for the Gaussian kernel). We used third-order polynomial approximations as a simple alternative for density estimation in bounded domains.

Table 4 shows that the live trees clearly had the highest contribution to the potential from the chosen quantitative characteristics. In fact, the Wilcoxon rank sum test indicated that the distribution of the potentials for live and declining trees differ from the distribution of the potentials for dead trees. This is a strong indication of high preference for the dead tree status, as live trees were chosen only when they had favorable characteristics and were located near the forest edge. This observation is a good example of the complexity of the tree choices and the importance of mature hickory trees located in preferred places. While declining and dead shagbark hickory were the most common choices, the mean potential did not differ much compared to other declining and dead species. The Wilcoxon rank sum test indicated that there is not enough evidence to distinguish shagbark hickory from the other species. The prevalence of the choice of shagbark hickory may be a result of tree composition in these forests. A comparison study on tree composition between the selected trees and surrounding trees is necessary to assess the reasons behind the choices and is beyond the scope of this paper. Lack of shagbark hickory will not likely limit the Indiana bat population, due to the many alternate maternity roost tree species available in this forest type such as red oak, black oak, elm, and maple (*Acer* spp.). See Table 1 in Kurta (2004) for literature survey of species of trees used by Indiana bats.

Tree height results indicate that roost trees were primarily in the upper canopy, where prior to senescence, they competed with adjacent trees to develop adequate canopy openings. Average roost tree height was greater in previous research studies: 23.3 m in Michigan in a forest type composed primarily of white ash (*Fraxinus Americana*) and silver maple (*Acer saccharinum*) (Kurta et al., 1993), and 17.5 m in southern Illinois (Carter and Feldhamer, 2005), compared to 13.5 m in our study in upland oak-hickory forests. However, the relative frequency distributions indicated that increased height increases the relative frequency (Fig. 2a). The frequency distribution for the tree diameter indicated that the majority of the maternity roost trees had a diameter of 37–46 cm (Fig. 2d). This is similar to previous research that indicated a preference for mean diameter ranging from 39 to 41.4 cm throughout the Indiana bat range (Carter and Feldhamer, 2005; Lacki et al., 2009). Carter and Feldhamer (2005) also indicated that this diameter was similar to that of surrounding trees not selected as roost trees.

The mean percentage of bark cover was 36.7% with standard deviation 20.2% and, except for one tree, the percentage of bark cover was 60% or lower (Fig. 2e). These observations differ from the research by Callahan et al. (1997) in northern Missouri, where the larger primary roost trees maintained an average of 81.9% bark attachment. However, the finding was similar to the study in Southern Illinois by Carter and Feldhamer (2005), in which percentage of bark cover among roost trees was 47% with standard deviation 26.7%. We collected data several years after the identification of the roost trees. Bark coverage of snags is expected to decrease from year to year and we did not account for the decay rates. This may have impacted the lower mean percentage we observed in our study.

Canopy openings ranged from small, 7.5%, to completely open, 100% (mean = 46%, standard deviation = 30%). Previous research also identified variable canopy openings from 12 to 80% (Gardner et al., 1991; Humphrey et al., 1977; Kurta et al., 2002; Sparks, 2003; Whitaker and Brack, 2002). SVD analysis indicated that the percentage of the canopy opening at ground level had little contribution toward selection. The density function approximation indicated very little change in values between various canopy openings (Fig. 3f). The understory may have caused the canopy cover measurement to become an irreverent feature. The average solar exposure may be best measured by the canopy closure at the roost height, obtaining the proportion of the sky's hemisphere obscured by vegetation. Also, information about the surrounding tree heights and canopy openings is necessary to interpret the findings.

SVD analysis confirmed the importance of forest edge habitat for maternity roost selection. Indiana bats selected roosts within 200 m of the forest edge and the histogram indicates a higher preference for roost trees near the forest edge (Fig. 2b). Roost locations clearly showed that, even in the very fragmented landscape, roosts were selected very close to the edge (see Fig. 4). Numerous studies have detected bats foraging along forest edges (Brack, 1983; Humphrey et al., 1977; LaVal et al., 1977; Menzel et al., 2001), and they may use forest edges to commute to other foraging areas (Murray and Kurta, 2004). Recent research by Yates and Muzika (2006) indicates the importance of a complex of forested and non-forested cover types in the habitat landscape for Indiana bats roosting and foraging habitat.

In our study, Indiana bats selected maternity roost trees within 1 km of water bodies and SVD analysis indicated that distance to water is important. Previous studies have identified the importance of water bodies as a hydration source and foraging area for maternity colonies (Kurta et al., 1989, 1990, 2002; Jachowski et al., 2014; Watrous et al., 2006; Humphrey et al., 1977). Small ponds and riparian areas are important for insect foraging (Brack, 1983; Gardner et al., 1991; Garner and Gardner, 1992; Menzel et al., 2001; Jachowski et al., 2014; Silvis et al., 2016). However, the histogram (Fig. 2c) reveals that the distribution of distances is approximately uniform within the 1 km range. This finding is similar to the probability of occupancy results given by Pauli et al. (2015a). Almost every tree within a 12 km^2 region covering each maternity site is within 1 km of a water body (Fig. 5), preventing a definitive conclusion about the range using our data set.

5. Conclusion

Indiana bats' choice of maternity roost habitat depends on a complex combination of tree and landscape characteristics. While

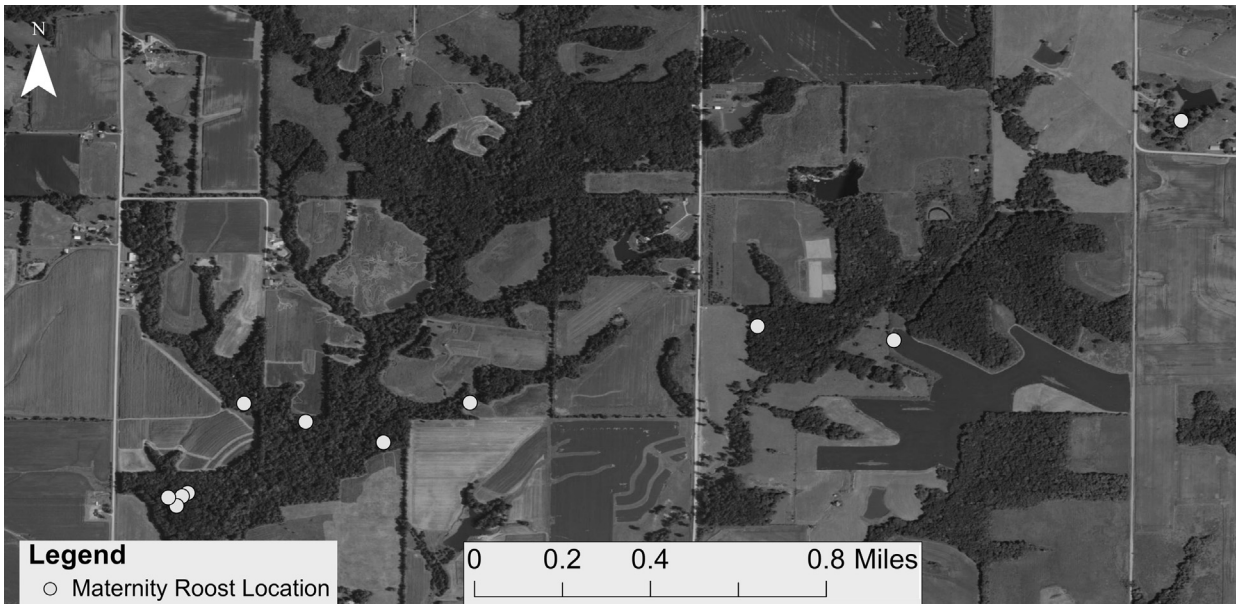

Fig. 4. Roost locations in a Midwest upland oak-hickory forest in Iowa, illustrating the location of maternity roosts near the forest edge.

comparison studies are the norm for distinguishing preferred characteristics, we utilized a feature selection algorithm and analysis of distributions to determine the primary characteristics of importance and the nature of the preference. The data set was analyzed based on the research objective, as well as within the limitations embedded in the data set itself. The findings regarding analyzed tree and landscape characteristics were consistent with existing literature. Our analysis presented specific details related to the choice of live and dead trees. Dead versus live tree comparisons showed the importance of landscape-scale environmental variables. A comparison between species among the dead and declining roost trees indicated that the various tree species shared similar selection likelihoods. Further, SVD analysis indicated that observing the canopy cover at ground level was irrelevant for maternity roost selection. Understanding these complex relationships regarding maternity roost habitat preferences may be useful for future management of Indiana bats throughout Midwest oak-hickory forests, particularly regarding timber harvesting and forest stand improvement (Pauli et al., 2015b). Silvicultural prescriptions that improve the suitability of habitats for maternity roosts may include removal of a portion of the trees with smaller diameter in an effort to reduce tree competition for trees suitable as maternity roosts and management of shagbark hickory within forest stands to provide roosting habitat long-term. Our research indicates that these efforts within 200 m of the forest edge would provide the most benefit for Indiana bats.

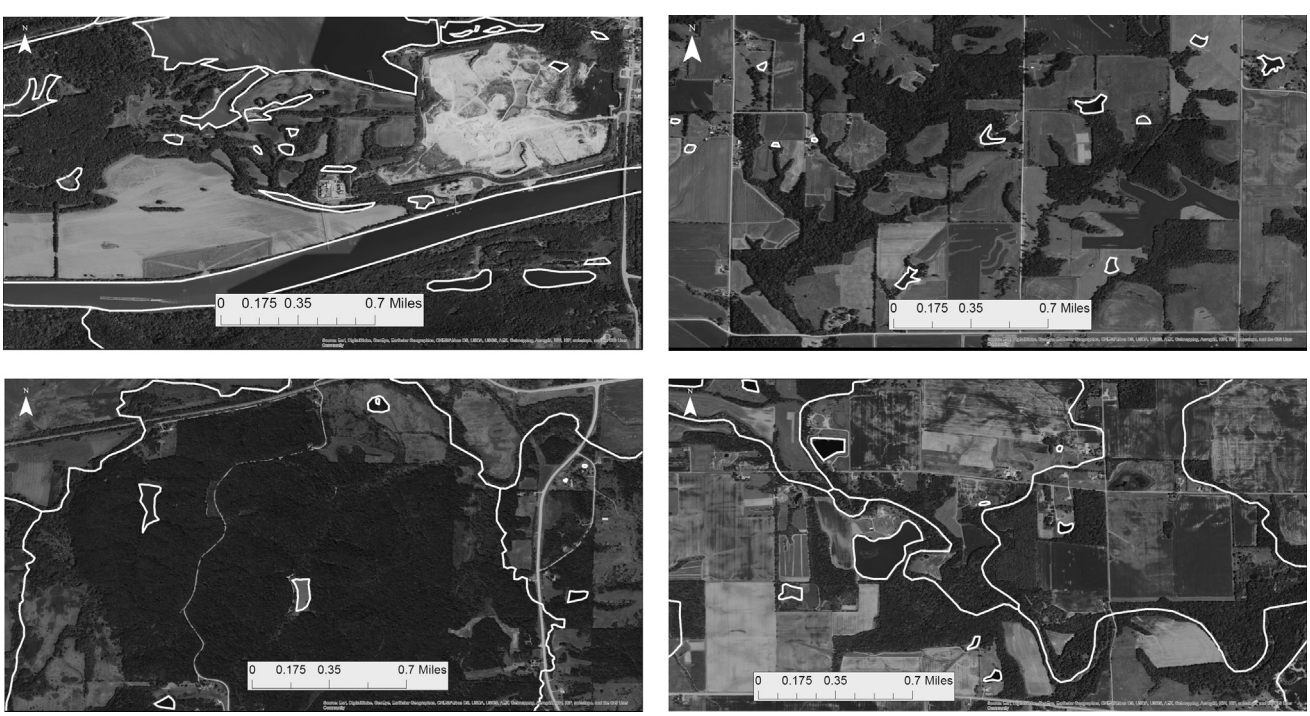

Fig. 5. Water bodies (marked with white curves) located in four Midwest upland oak-hickory forests, studied for maternity colony habitats in Illinois and Iowa. Almost every forest area is located within 1 km of water bodies.

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Appendix A

For a given region, suppose $S \in \{0,1\}$ represents a tree's occupancy (no = 0, yes = 1) by bats as a maternity roost. Let $X_1,\ldots,X_n$ be mutually independent continuous random variables, such that $X_1,\ldots,X_k$, $k < n$, are landscape scale variables and $X_{k+1},\ldots,X_n$, are variables representing tree characteristics. Define the random vector $\boldsymbol{X} = [X_1,\ldots,X_n]^T$. We may describe the joint distribution of $\boldsymbol{X}$ and S by $\mathbb{P}(S = s, \boldsymbol{X} \leqslant \boldsymbol{x}) = \int_{-\infty}^{x_n}\int_{-\infty}^{x_{n-1}}\ldots\int_{-\infty}^{x_1} f_{S,\boldsymbol{X}}(s,t_1,\ldots,t_n)dt_1\ldots dt_n$, where $\boldsymbol{x} = [x_1,\ldots,x_n]^T$ and $f_{S,\boldsymbol{X}}$ is the density of the mixed distribution. Then, $p_S(1) = \mathbb{P}(S = 1) = \int_{-\infty}^{\infty}\ldots\int_{-\infty}^{\infty} f_{S,\boldsymbol{X}}(1,t_1,\ldots,t_n)dt_1\ldots dt_n$, and the probability density of $\boldsymbol{X}$ is $f_{\boldsymbol{X}}(\boldsymbol{x}) = f_{S,\boldsymbol{X}}(0,\boldsymbol{x}) + f_{S,\boldsymbol{X}}(1,\boldsymbol{x})$. If $p_s(1) > 0$, we have $f_{\boldsymbol{X}|S}(\boldsymbol{x}|1) = f_{S,\boldsymbol{X}}(1,\boldsymbol{x})/p_S(1)$, and if $f_{\boldsymbol{X}}(\boldsymbol{x}) > 0$, then $p_{S|\boldsymbol{X}}(1|\boldsymbol{x}) = f_{S,\boldsymbol{X}}(1,\boldsymbol{x})/f_{\boldsymbol{X}}(\boldsymbol{x})$. Assuming uniform distributions for landscape scale variables and a Bernoulli distribution for S, we obtain the relationship

$$p_{S|\boldsymbol{X}}(1|\boldsymbol{x}) = \frac{f_{\boldsymbol{X}|S}(\boldsymbol{x}|1)p_S(1)}{f_{\boldsymbol{X}}(\boldsymbol{x})} = \frac{kf_{\boldsymbol{X}|S}(\boldsymbol{x}|1)}{\prod_{i=k+1}^{n} f_{X_i}(x_i)}, \tag{A1}$$

for some constant k, where $f_{X_i}(x_i)$ represents the density function for distributions of tree characteristics X_i for the given region. With the aforementioned assumptions, the probability of occupancy given the quantitative attributes, $p_{S|\boldsymbol{X}}(1|\boldsymbol{x})$, can be completely characterized by the ratio between $f_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$ and $\prod_{i=k+1}^{n} f_{X_i}(x_i)$, where $f_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$ is the conditional joint probability distribution of both tree characteristics and landscape-scale environmental variables, given that the trees are maternity roosts (presence only), and $\prod_{i=k+1}^{n} f_{X_i}(x_i)$ is the product of the distributions of tree characteristics for the given region. In this paper, the potential function is defined to be $f(\boldsymbol{x}) = C\hat{f}_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$, where $\hat{f}_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$ is a density estimation for $f_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$ and C is a constant.

Appendix B

Suppose $\boldsymbol{X}$ and S are defined as in Appendix A and $\hat{f}_{\boldsymbol{X}|S}(\boldsymbol{x}|1)$ is the conditional joint density estimation of $\boldsymbol{X}$ given a chosen tree. For a point $\boldsymbol{x}_i = [x_{i1},\ldots,x_{in}]^T$ in the domain of $f_{\boldsymbol{X}|S}$, let $\boldsymbol{\delta}_i$ be a delta-hypercube with the centroid at $\boldsymbol{x}_i$ and with side length δ. By choosing δ sufficiently small, we can approximate the probability that $\boldsymbol{X} \in \boldsymbol{\delta}_i$ by $\mathbb{P}(\boldsymbol{X} \in \boldsymbol{\delta}_i|S = 1) \approx \delta^n\hat{f}_{\boldsymbol{X}|S}(\boldsymbol{x}_i|1) = \delta^n f(\boldsymbol{x}_i)/C$, where f is the potential function. Let A be a categorical variable that takes values $a_1,\ldots,a_k$ (in our case, either the tree statuses or tree species). The data set of the maternity roost trees provides 19 disjoint points $(\boldsymbol{x}_i)$ such that each point belongs to only one category of A (see the data file). Consider the partition of $i = 1,\ldots,19$ such that $i \in I_j$ corresponds to $A = a_j$ for each $j = 1,\ldots,k$. Then

$$\mathbb{P}(\boldsymbol{X} \in \textstyle\bigcup_i \boldsymbol{\delta}_i|i \in I_j, S = 1) = \frac{\mathbb{P}(\boldsymbol{X} \in \bigcup_{i\in I_j}\boldsymbol{\delta}_i|S = 1)}{\mathbb{P}(i \in I_j|S = 1)} = \frac{\sum_{i\in I_j}\mathbb{P}(\boldsymbol{X} \in \boldsymbol{\delta}_i|S = 1)}{\mathbb{P}(i \in I_j|S = 1)} \approx \frac{19\delta^n\sum_{i\in I_j} f(\boldsymbol{x}_i)}{CN(I_j)},$$

where $N(I_j)$ is the number of trees belonging to category a_j in our dataset. Hence,

$$\mathbb{P}(\boldsymbol{X} \in \textstyle\bigcup_i \boldsymbol{\delta}_i|i \in I_1, S = 1):\cdots:\mathbb{P}(\boldsymbol{X} \in \bigcup_i \boldsymbol{\delta}_i|i \in I_k, S = 1) \approx \frac{\sum_{i\in I_1} f(\boldsymbol{x}_i)}{N(a_1)}:\cdots:\frac{\sum_{i\in I_k} f(\boldsymbol{x}_i)}{N(a_k)}, \tag{B1}$$

where the right-hand side of the equation corresponds to the proportion of mean potentials for each category. These analyses demonstrate that the ratios between mean potentials within each category can be used to estimate the ratios between the probabilities of a roost tree having quantitative attributes that are similar to those of the trees within each category.

Appendix C

Let variables x_1, x_2, x_3, x_4, x_5 and x_6 be height, distance to forest edge, distance to water, diameter, bark cover, and canopy opening, respectively. Then the third-order polynomial approximations in Figs. 2 and 3 are given by

Height: $p_1(x_1) = -1.86 \times 10^{-4}x_1^3 + 0.0053x_1^2 - 0.0243x_1 + 0.0211$ (C1)

Distance to forest edge: $p_2(x_2) = 2.17 \times 10^{-8}x_2^3 - 5.02 \times 10^{-6}x_2^2 - 7.47 \times 10^{-4}x_2 + 0.1983$ (C2)

Distance to water: $p_3(x_3) = 3.92 \times 10^{-10}x_3^3 - 7.51 \times 10^{-7}x_3^2 + 3.98 \times 10^{-4}x_3 + 0.0531$ (C3)

Diameter: $p_4(x_4) = 3.0 \times 10^{-6}x_4^3 - 5.6 \times 10^{-4}x_4^2 + 0.0281x_4 - 0.1841$ (C4)

Bark cover: $p_5(x_5) = 1.84 \times 10^{-7}x_5^3 - 7.94 \times 10^{-5}x_5^2 + 0.0047x_5 + 0.0818$ (C5)

Canopy opening: $p_6(x_6) = 8.2 \times 10^{-7}x_6^3 - 0.0001x_6^2 + 0.0045x_6 - 0.0816$ (C6)

The potential function is given by $f(x_1,x_2,x_3,x_4,x_5) = C\prod_{i=1}^{5} p_i(x_i)$, where $C = 7022.5$.

Appendix D

The Wilcoxon rank sum test is a non-parametric test that can be used to test for significant differences in a continuous dependent variable according to a single dichotomous independent variable. We assumed following to perform the test.

1. The potential function is the dependent variable that is assigned to each tree and is continuous on the interval [0, 1].
2. The sample of trees can be partitioned using an independent dichotomous variable. Partitioning can be either snags versus not snags or shagbark hickory versus all other species.
3. There is no relationship between the observations within each partition of the independent variable nor between the partitions.
4. The shapes of the distributions of potentials for category of the independent variable are unknown and thus the shapes of the distributions are assumed to be different.

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