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Unique Land Cover Classification to Assess Day-Roost Habitat Selection of Northern Long-Eared Bats on the Coastal Plain of North Carolina, USA

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Abstract: Reproductively successful and over-wintering populations of the endangered northern long-eared bat (*Myotis septentrionalis*) have recently been discovered on the Coastal Plain of North Carolina. Empirical data on resource selection within the region is limited, likely hindering management of these coastal forests. Our objectives were to determine roosting home range size, selection of day-roost tree species, second- and third-order roosting habitat selection, and to quantify the overall availability of resources in the surrounding landscape. We found core and peripheral roosting home range estimates were large, yet similar to observations from other areas of contiguous forests. Prior to juvenile volancy, female northern long-eared bats appear to select red maple (*Acer rubrum*), water ash (*Fraxinus caroliniana*), and loblolly pine (*Pinus taeda*) as day-roosts, but then use sweetgum (*Liquidambar styraciflua*), swamp bay (*Persea palustris*), and water tupelo (*Nyssa aquatica*) after juvenile volancy. At the second-order spatial scale, roosting home ranges were associated with woody wetlands farther from anthropogenic development and open water. However, within the third-order scale, northern long-eared bats were associated with undeveloped woody wetlands and upland forests, areas containing shorter trees and occurring proximal to open water. Peripheral and core areas were predicted to comprise approximately 20% of the local landscape. Our results show that complex and large tracts of woody wetlands juxtaposed with upland forests in this part of the Coastal Plain may be important for northern long-eared bats locally, results largely consistent with species management efforts in eastern North America.

Keywords: roosting home range; kernel density; land cover classification; multinomial regression; *Myotis septentrionalis*; northern long-eared bat; random forest; roosting habitat; North Carolina

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1. Introduction

White-nose syndrome (WNS), a disease caused by the fungal pathogen *Pseudogymnoascus destructans* (Pd), has led to considerable population declines of the northern long-eared bat (*Myotis septentrionalis*) and other cave-hibernating myotis in North America. Declines in the inland northeastern United States through the central and southern Appalachians have exceeded 90%, with the formerly common species being largely absent in most of the landscape [1,2]. The presence of the fungus in caves in karst areas, especially in the Appalachian Mountains, where long hibernation periods occur, has resulted in rapid functional extirpation where some individuals are present but non-reproductive, and populations are non-viable [3–5]. Because of this multi-region decline, the northern long-eared bat was listed as federally endangered in Canada during 2013 [6] and was proposed for uplisting from federally threatened to endangered in the United States after reassessment in 2022 [7–9]. In addition to direct mortality caused by WNS, juvenile recruitment from surviving adult females appears to have declined [10–12]. Moreover, many extant maternity colonies in the region have experienced early-season colony collapse indicative of reproductive failure [12,13].

Once thought to only persist as far south and east as the Great Dismal Swamp in southeastern Virginia, recent survey efforts in eastern North Carolina and South Carolina (hereafter the "Carolinas") have revealed the presence of both successful maternity colonies and overwintering populations of northern long-eared bats [14–16]. Similarly, recent work has documented reproductive populations as far south as the upper Gulf Coastal Plain of Louisiana and, similar to northern long-eared bats of the coastal Carolinas, evidence suggests that these bats are year-round residents [17,18]. Despite these resilient coastal and Southern populations, documented colony collapses and failed recruitment suggests that in much of the eastern United States the species may be functionally extirpated [11,12,19]. Specifically, successful reproduction in the eastern United States appears restricted to the lower Piedmont/upper Coastal Plain of Virginia and lower Coastal Plains of the Carolinas [12,14,16,20–22], coastal Massachusetts [23] and New York [24,25], and the far western Appalachian Plateau of West Virginia [26].

Habitat use often differs seasonally within northern long-eared bat colonies. For example, recent research has documented variation in day-roost selection by colonies within the same maternity season [27], behavior likely driven by colony subgroup associations and reproductive status [28,29]. Specific to the geographic range, or first-order scale [30], ecological niche modeling of the Indiana bat (*Myotis sodalis*) has demonstrated that bat habitat use and suitability may vary regionally [31]. More specifically, researchers have found that climactic factors driving the range distribution may differ from those related to selection at the local-level [32]. This interregional and multiscale variation suggests that similar analyses regarding northern long-eared bat habitat associations could be contributory to their conservation and management.

Roosting home ranges of northern long-eared bat colonies are typically small (i.e., <20 ha; [33–37]), therefore, it is helpful to evaluate resource use via unique and fine-resolution land cover classification data. Existing and widely available land cover datasets, such as the National Land Cover Dataset (NLCD) [38], are spatially coarse and often miss fine-scale information important in quantifying animal resource associations [39]. High-resolution ($\leq$1 m) aerial imagery, such as the National Agricultural Imagery Program (NAIP) [40], has become more widely available and these data have been successfully used in the creation of highly accurate local land cover classification [39,41,42]. Additionally, machine learning techniques offer an effective and efficient means to classify these high-resolution, remotely-sensed imagery [43].

Because social and seasonal habitat selection varies for northern long-eared bats, effective conservation requires knowledge of resource selection during multiple time periods and at several spatial scales. Moreover, little is known regarding specific habitat selection or distribution of the species at local spatial scales. Therefore, the development of models investigating foraging and day-roosting habitat suitability can be important management tools [4]. The combination of these unknowns at a local scale and the advancement of aerial imagery provides a novel opportunity to fill empirical data gaps in terms of northern long-eared bat habitat and resource selection for a region potentially important to species long-term survival.

Herein, we examine habitat selection of northern long-eared bats at multiple spatial scales using custom land cover data to mitigate potential spatial resolution and classification induced modeling error. Our objectives were: (1) To assess day-roost tree species selection pre- and post-juvenile volancy; (2) to determine roosting home range size of the maternity colony; (3) to assess second- (i.e., home range within a region) and third-order (i.e., core home range within a periphery) roosting habitat selection [30]; (4) and to quantify the overall availability of these areas in the surrounding landscape. We hypothesized that core and peripheral day-roosting home ranges of the northern long-eared bat maternity colony would be similar relative to the core of the species' range, but that selection and availability of resources, including roost trees pre- and post-volancy, would differ locally.

2. Materials and Methods

2.1. Study Area

The Coastal Plain of North Carolina is characterized as a predominately flat alluvial plain ranging < 180 m in elevation at the boundary with the Piedmont (i.e., Fall Line) to sea level at the coast [44]. We conducted our study at the North Carolina Wildlife Commission's North River Game Land (NRGL; 7700 ha) in Camden and Currituck counties, North Carolina (Figure 1). Approximately 97% of NRGL is forested, with 96% of forests being woody wetland [38]. Native upland forests are a southern warm-temperate mixed forest of oak (*Quercus* spp.), hickory (*Carya* spp.), and pine (*Pinus* spp.), historically containing a large proportion of longleaf pine (*Pinus palustris*; [44]). Locally, much of the natural pocosin wetlands and forested swamps were converted to short-rotation pine plantations, largely loblolly pine (*Pinus taeda*) and agricultural fields [44,45]. At NRGL, the alluvial woody wetlands are primarily composed of water tupelo (*Nyssa aquatica*), swamp tupelo (*Nyssa biflora*), and bald cypress (*Taxodium distichum*), whereas non-alluvial wetlands often contain pond pine (*Pinus serotina*) and bays (*Persea* spp.). Mean temperature is 26 °C during the maternity season (June–August) and is 8 °C during the overwintering season (November–February). The region receives 100–150 cm of precipitation annually [44,46].

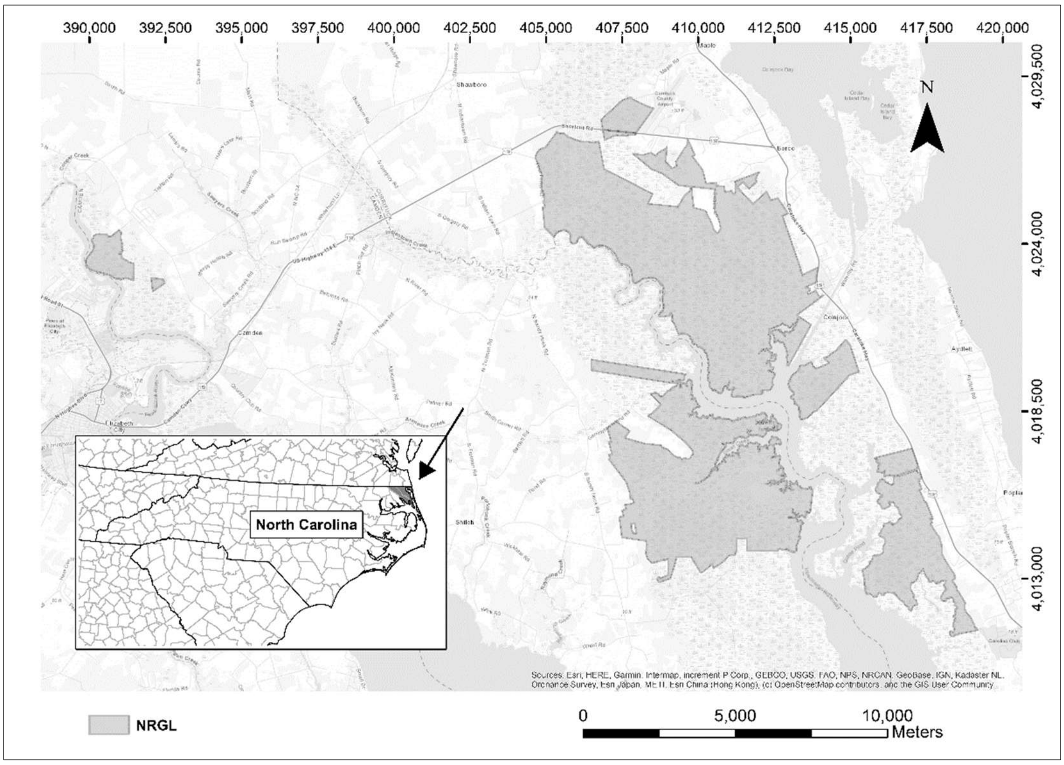

Figure 1. Location of North River Game Land (NRGL) in Camden and Currituck counties, North Carolina, 2019.

2.2. Bat Sampling and Tracking

We captured northern long-eared bats along streams, trails, and single-track forest road corridors using mist nets (2.6–7.8 m high × 6–12 m wide with a 38-mm mesh; Avinet, Inc., Portland, ME) at NRGL during 5 May–18 May and 17 June–28 June, 2019. We conducted mist-net captures nightly from sunset for a minimum of 2–5 h post-sunset [47]. We identified captured bats based on morphological characteristics (e.g., ear and tragus length, presence/absence of calcar) and overall appearance of the animal [48], and determined age (i.e., juvenile, adult) by degree of epiphyseal-diaphyseal fusion (i.e., calcification) of long bones in the wing [49].

We outfitted reproductively active adult (i.e., pregnant, lactating, or post-lactating) female northern long-eared bats with radio transmitters (0.27 g, LB-X; Holohil Systems Ltd., Woodlawn, ON, Canada). The radio transmitter, surgical adhesive, and any other markings (e.g., wing bands) weighed less than 5% of pre-attachment body weight [50] to comply with state and federal permits. Due to weight ratio limitations, we did not attach transmitters to juvenile bats. We tracked radio-tagged bats daily to day-roosts using TRX-1000 WR tracking receivers (Wildlife Materials, Murphysboro, IL, USA) and continued this process until transmitters were shed, malfunctioned, or depleted in battery life. We tracked bats simultaneously until located or for a minimum of 4 h of ground effort for each tagged bat. Upon location, we recorded day-roost GPS locations via waypoint averaging using a Garmin GPSMAP 64 s (Garmin Ltd., Olathe, KS, USA). All bat handling procedures were approved and permitted by the Virginia Tech Institutional Care and Use Committee Permit # 16–240, NC Wildlife Resources Commission Scientific Collecting Permit # 19-ES00348, and U.S. Fish and Wildlife Service Research Recovery Permit # TE88353B-0.

2.3. Roost Tree Selection and Roosting Home Range Estimates

We assessed the equitability among day-roost tree species used by a maternity colony of northern long-eared bats using a chi-square goodness-of-fit test with respect to pre- and post-volancy of juvenile bats [37,51]. We defined these pre-and post-volancy periods as occurring before and after the first capture of a juvenile bat (16 June 2019) [21]. We used geospatial roosting data of the maternity colony to construct day-roost home ranges using the Gaussian, fixed kernel method, with plug-in estimator for the smoothing parameter (h), in the program Geospatial Modeling Environment (GME, version 0.7.4.0) using the function 'kde'; we constructed 50% and 95% utilization distributions (UD) using the function 'isopleth' [52,53].

2.4. Landscape-Scale Habitat Variables

We examined habitat availability across the local landscape by measuring distance to land cover classes and forest fragments and by extracting vegetation heights at n = 100 stratified random point samples as training data. Data were extracted from core and peripheral roosting home range estimates and from within a 2.5 km buffer, respectively. This 2.5 km buffer approximates the maximum reported distance from capture site to roost location and likely encapsulates all resources available to northern long-eared bats at NRGL [33]. Distance was the Euclidean distance from point samples to the nearest instance of each land cover and fragmentation class [54], as measured by the Joins and Relates tools of ArcGIS (version 10.3; Environmental Systems Research Institute, Inc. Redlands, CA, USA). We based our forest fragmentation assessment on a forest/non-forest reclassification of NLCD 2018 data and examined proximity to large (>200 ha) core forests [26,38,55]. We recorded vegetation height at each point sample from NAIP photogrammetric point cloud data [56].

We extracted land cover classes from 2018 NAIP aerial imagery (0.6-m resolution) [40] using a supervised and object-based random forest [53] image classification technique using R (version 3.4.1; [57]), with models built using the 'randomForests' package [58]. Random forest machine-learning is a highly accurate classification technique insensitive to overfitting, even with small training sample size, and is capable of handling large datasets of high dimensionality and multicollinearity [43,59,60]. We created spectral objects using a segment mean shift in ArcGIS to identify feature objects in the NAIP imagery [61]. Segmentation groups pixels into spectrally similar neighborhoods [62], which enhances the ability to delineate between spectrally similar land cover classes [63], particularly from high-resolution imagery. We extracted five land cover classes: woody wetland, upland forest, herbaceous, developed, and open water. We validated classification accuracy by out-of-bag (OOB) error rate on training data, kappa statistic (K), and user and producer accuracy of the resulting classification [58,64].

2.5. Habitat Selection and Availability Analyses

We assessed landscape variables affecting roosting habitat of northern long-eared bats at the second- and third-order spatial scales [30]. To compare landscape characteristics between core and peripheral roosting home ranges of northern long-eared bats to the surrounding landscape, we fit a global multinomial model using neural networks in the R package 'nnet' [65]. We selected the most parsimonious model by AIC [66] using a backward/forward stepwise procedure [67,68]. We assessed model goodness-of-fit using a log-likelihood-ratio tests against a null model, Nagelkerke's R^2, and McFadden's P^2, and evaluated predictive performance using 5-fold cross-validation [68,69]. Lastly, we used ArcGIS to examine modeled predictions across the local landscape. We exported these predictions to raster-data format to create the classes: third-order, second-order, and landscape. We used these classes to determine the probable availability of northern long-eared bat habitat within 2.5 km of our study area [70].

3. Results

3.1. Roost Selection and Roosting Home Range Size

We tracked 11 northern long-eared bats to 35 day-roosts comprising 10 tree species at NRGL. These included: Carolina ash (*Fraxinus caroliniana*; n = 9, 26%), red maple (*Acer rubrum*; n = 8, 23%), water tupelo (n = 6, 17%), loblolly pine (n = 3, 9%), sweetgum (*Liquidambar styraciflua*; n = 2, 6%), swamp bay (*Persea palustris*; n = 2, 6%), red elm (*Ulmus rubra*; n = 2, 6%), American holly (*Ilex opaca*; n = 1, 3%), sweetbay magnolia (*Magnolia virginiana*; n = 1, 3%), and bald cypress (n = 1, 3%). Most northern long-eared bats roosted in cavities (n = 25; 71%), with only 10 (29%) found roosting under exfoliating bark. The colony used different tree species and/or their proportions prior to and after juvenile volancy (χ^2 = 17.3, df = 9, p = 0.04). Specifically, colony members used red maple, water ash, and loblolly pine prior to juvenile volancy, but used sweetgum, swamp bay, and water tupelo after volancy and colony diffusion. Based on n = 35 roost trees, 50% UD and 95% UD colony roosting home ranges were 11.3 ha and 43.6 ha, respectively.

3.2. Image Classification, Habitat Selection, and Habitat Availability

Our land cover classification of 2018 NAIP aerial imagery was highly accurate, with the random forest model producing an OOB error rate of 4.1%, producer and user accuracies of 57.9–99.4%, and K = 0.93. The final model differentiating landscape characteristics at second- and third-order spatial scales contained canopy height, proximity to woody wetlands, upland forests, developed land, open water, large core forest, and non-forest areas (Table 1); only herbaceous cover types were removed during the AIC stepwise model selection process. This model provided a better fit than the null model (log-likelihood = −182.86, $p < 0.01$) and displayed satisfactory goodness-of-fit (ρ^2 = 0.45; R^2 = 0.70). Additionally, based on 5-fold cross-validation, our final model displayed a mean accuracy rate of 72% in differentiating habitat selection at multiple spatial scales.

At the second-order spatial scale, roosting home ranges were associated with unbroken woody wetlands of an advanced successional stage (Figure 2A,B,F). Additionally, these areas were generally farther from anthropogenic development and open water (Figure 2D,E). Within the third-order scale, northern long-eared bat day-roosting habitat was associated with shorter trees nearer to contiguous tracts of both woody wetlands and upland forests (Figure 2A–C). Similar to peripheral habitats, these core areas were farther from anthropogenic development than random (Figure 2D) but were nearer to open water (Figure 2E). Peripheral (12%) and core (8%) areas were predicted to comprise approximately 20% of the local landscape (Figure 3).

Table 1. Parameters included in a top multinomial logistic regression model as selected by AIC to assess second- and third-order habitat selection by northern long-eared bats (*Myotis septentrionalis*) at the North Carolina Wildlife Resource Commission's North River Game Land (NRGL) in Camden and Currituck counties, North Carolina, 2019.

Variable			**DF**	**Wald X^2**	**$p > X^2$**
Canopy height			2	24.38	<0.01
Woody wetland			2	15.20	<0.01
Upland forests			2	22.74	<0.01
Development			2	11.52	<0.01
Open Water			2	99.47	<0.01
Large core forests			2	64.30	<0.01
Non-forest areas			2	5.92	0.05
Final model	Log-likelihood	$p > X^2$	ρ^2	R^2	Accuracy
Canopy height + woody wetland + upland forest + development + open water + large core forests + non-forest areas	−182.86	<0.01	0.45	0.70	0.72

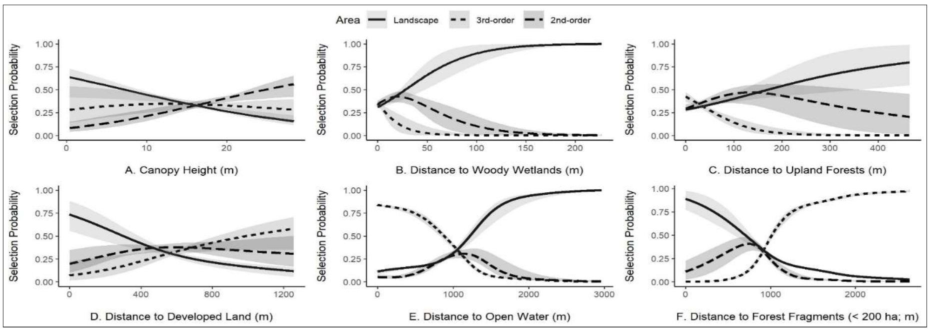

Figure 2. Partial effect plots describing the relation of (**A**) canopy height and distance to (**B**) woody wetlands, (**C**) upland forests, (**D**) developed land, (**E**) open water, and (**F**) forest fragments with northern long-eared bat (*Myotis septentrionalis*) habitat at multiple spatial scales at the North Carolina Wildlife Resource Commission's North River Game Land (NRGL) in Camden and Currituck counties, North Carolina, 2019.

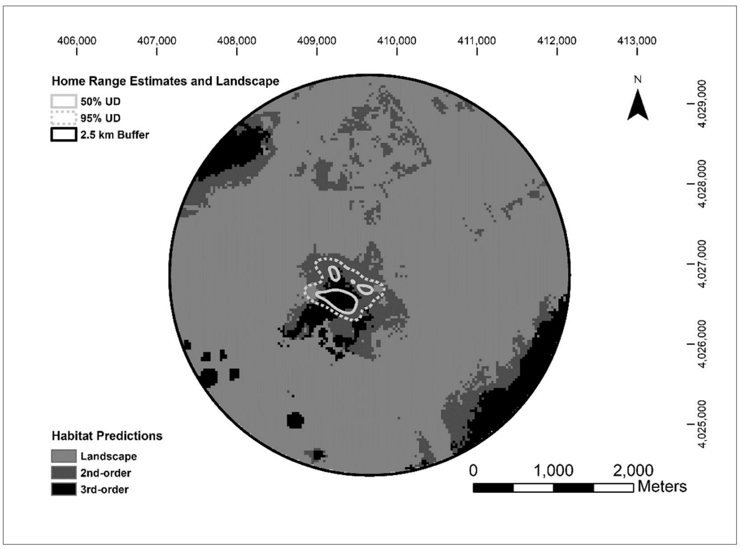

Figure 3. Northern long-eared bat (*Myotis septentrionalis*) roosting home range estimates and predicted second- and third-order cover within a 2.5 km buffer of the North Carolina Wildlife Resource Commission's North River Game Land (NRGL) in Camden and Currituck counties, North Carolina, 2019.

4. Discussion

To date, habitat selection of northern long-eared bats on the Coastal Plain of North Carolina is limited to observations from initial, simple descriptive efforts [14,15,21,71]. Nonetheless, these observations of northern long-eared bats on the coast of North Carolina support the hypothesis of ongoing range fragmentation and population localization of the species [13,21,72]. Selection of wetland obligates as roost trees on the Coastal Plain of North Carolina, an area heavily fragmented by agriculture, represent a significant departure from upland deciduous forests associations typically ascribed to the species throughout most of its range. Even so, northern long-eared bats at NRGL roosted in dense canopy forests and in small, suppressed trees that receive little direct sunlight, similar to selection in upland forest types by the species throughout the mid-Ohio Valley of Kentucky and Ohio, the central Appalachians of West Virginia, the Coastal Plain of New York, and the Piedmont and Coastal Plain of Virginia [12,24,25,28,36,72–74]. Despite tracking only 11 individuals, our results may be representative of reproductive habitat of the northern long-eared bat in the coastal Carolinas. Congruent with previous findings from Kentucky [28,75], northern long-eared bats at NRGL, exhibiting behavior likely linked to the hot and humid nature of the Coastal Plain, often used shorter and highly decayed (i.e., dead with loose bark) trees under the overstory canopy as day-roosts. As observed in Arkansas [76], it may also be that selection of lower canopy forests post-volancy represents the reduced thermoregulatory requirements related to fetal development [77]. Additionally, the early juvenile volancy (16 June 2019; [21]) documented at NRGL is likely related to the earlier onset of the growing season relative to the core of the species' range [78]. This early juvenile volancy contributed to the collection of roosting data during both colony cohesion and dissolution phases [27], and suggests our results represent tree species and roosting habitat requirements of northern long-eared bat colonies during these life-stages in the region.

Our results support the hypothesis that northern long-eared bats often select for contiguous forest regardless of available resources and physiographic province for both roosting [26,34,73,76,79–81] and foraging [82–88]. The 50% and 95% UD roosting home range estimates from NRGL are similar to those observed in other areas of large, contiguous forest [27]. Conservation practices on the Coastal Plain may need to consider that home range size tends to increase with poor resource quality and/or availability and can vary between core and peripheral populations with respect to first-order selection [89,90]. Measures of canopy closure often indicate that northern long-eared bats use suppressed and shaded trees that receive little direct sunlight, particularly in warmer climates and when bats use day-roosts of advanced decay [28,36,73–75]. Conversely, some findings suggest that northern long-eared bats may vary roost use between years with respect to temperature and select larger diameter trees in warmer conditions, provided these day-roosts afford sufficient thermal buffering [91]. Nevertheless, research indicates that the upper thermoneutral zone for bats of the family Vespertilionidae is 30 °C [75,92,93], and the use of small and highly shaded day-roosts at NRGL may be in response to hot summer temperatures characteristic of the region. Research also suggests that northern long-eared bats select forests frequently altered by small-scale disturbances, alterations that, while not stand-replacing, create more roosts and enhance the quality (i.e., increased solar exposure, exfoliating bark) of existing roosts available for use [4,19,94]. Our results demonstrate the use of suppressed and shaded roost trees, but also the selection of small-scale disturbances. Northern long-eared bats at NRGL selected for roosting areas in woody wetlands, but these areas were nearer to dry upland areas than expected if selection was random. Although trees readily establish or regenerate in this wetland/upland interface, the fluctuating water regime and overall high canopy cover stresses, promotes rot, and causes mortality of trees. Similar to previously described processes [28], it may be that the dynamic forces operating within this cover type interface promotes the continual formation of natural day-roosts and the variety of conditions necessary for use by northern long-eared bats seasonally. Northern long-eared bat habitat in the Coastal Plain might therefore be associated with the juxtaposition of woody wetland roosting areas with upland forest foraging areas, and the heterogeneous resources created at the overlapping edge of these cover types locally.

Proximal to NRGL, second- and third-order areas constitute 12% and 8% of the local landscape, respectively. The Coastal Plain of North Carolina, and adjacent southeastern Virginia, is comprised of approximately 33% woody wetlands and a combined 20% deciduous, evergreen, and mixed forests [38]. The composition of the region infers widespread potential for northern long-eared bat habitat and therefore reproductive colonies. Due to the potential occurrence of reproductive northern long-eared bat colonies and their habitat on the Coastal Plain, some conservation of the species can be addressed via broadscale management measures. Historically, loss of forested wetlands to anthropomorphic land change has been significant, particularly in North Carolina [45]. The continued conservation of state and federal sites where northern long-eared bats are present, use of conservation easements to protect woody wetland and upland forest mosaics on private land, and the implementation of habitat mitigation or enhancement measures on both could significantly promote habitat connectivity and the continued presence of northern long-eared bat habitat on the Coastal Plain [95]. Additionally, enrollment of private lands in forest certification programs, designed to ensure ecological sustainability of forestry practices, may contribute to the conservation of northern long-eared bat habitats in the region [96]. Recently, reproductively successful colonies have been documented on the Western Allegheny Plateau of West Virginia [26], the North Atlantic Coast of New York [24,25], and the Chesapeake Bay Lowlands of the Washington, District of Columbia area [20,22]. These populations may demonstrate persistence due to little or no exposure to WNS via use of unique hibernacula, and therefore lack of exposure to WNS-vectoring species such as little brown bats (*Myotis lucifugus*) [97], latitudinal migration (i.e., non-hibernation), or a combination of both alternative hibernacula and over-wintering in coastal forests. As more northern long-eared bat colonies collapse and recruitment fails [10–12], particularly in populations associated with traditional karst hibernacula inland, an understanding of why the species persists and successfully reproduces in isolated pockets of its range could be critical for the conservation of the species. Current research suggests that the mild climate along the Fall Line of Virginia [12], and of the Coastal Plain of Virginia and northeastern North Carolina [21], allows the species to persist on the landscape year-round, albeit perhaps at lower densities relative to pre-WNS in more inland sites, thus behaviorally avoiding WNS-impacted hibernacula completely [14,22]. Additionally, recent findings indicate that the use of unique, non-traditional hibernacula (e.g., basements, coal adits) in other portions of the distribution may allow the species to avoid long-term exposure to WNS in colder regions where northern long-eared bats still persist [23,98].

5. Conclusions

The use of novel cover types on the Coastal Plain presents conservation opportunities that may be tailored to manage maternity colonies of northern long-eared bats that successfully reproduce in the region. Our findings address conservation concerns specific to day-roost use, roosting home range size, and multi-scale habitat selection of northern long-eared bats on the Coastal Plain of North Carolina where the species appears to still be reproductively successful. Additionally, our results provide a basis for the assessment and formation of species management strategies and can be used to identify candidate areas for conservation planning in the region. We suggest that conservation efforts focus on contiguous tracts of woody wetlands adjacent to upland forests that contain small, cavity bearing live-trees and/or snags. Future research examining interannual selection variation and resource selection in relation to foraging behavior could be contributory next steps.

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