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Bat community structure within riparian areas of northwestern Georgia, USA

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Abstract. Although it is well known that bats commonly forage in riparian areas, which provide water resources and insect concentrations, the role that the physical structure of riparian areas plays in influencing local bat communities is less certain. In 2000–2002, we used acoustic monitoring to determine bat species presence at 338 riparian sites in northwestern Georgia, USA. We used a 2-dimensional nonmetric multidimensional scaling (NMDS) ordination to assess how separations among species were partially associated with riparian conditions. Our NMDS analysis found some degree of habitat partitioning among bat species occurring in northwestern Georgia and was dictated in part by riparian condition. *Myotis grisescens* and *M. septentrionalis* were associated with low-elevation lotic waterways, whereas *M. lucifugus*, *Lasiurus borealis*, and *Eptesicus fuscus* were associated with high-elevation lentic waterways with sparse canopy cover. However, riparian conditions had weak relations with NMDS axes, possibly resulting in coincidental associations in some cases. Regression tree analysis indicated that higher bat species richness was associated with apparently uncommon small, high-elevation waterways with sparse canopy cover as well as larger streams and rivers that had wetlands adjacent to them. Including high-elevation waterways with existing management recommendations for endangered *M. grisescens* foraging areas (large, low-elevation streams and rivers) will be the most effective conservation strategy to benefit the most bat species in northwestern Georgia and probably elsewhere in the southern Appalachians.

Key words: Anabat, *Eptesicus*, *Lasiurus*, *Myotis*, nonmetric multidimensional scaling, *Perimyotis*, regression tree, species richness

Introduction

It is widely accepted that bat foraging activity is commonly greatest in areas associated with water sources, both lentic and lotic systems, as well as wetlands (Racey 1998, Grindal et al. 1999). These areas provide drinking water and abundant insects for foraging bats (Racey et al. 1998). Moreover, roost trees often occur in adjacent riparian zones, reducing commuting distances to foraging areas (Daniel et al. 2008). Linear riparian features such as wooded buffers along streams and rivers that serve as foraging habitats can also serve as efficient commuting corridors (LaVal et al. 1977, Menzel et al. 2005). Despite the importance of riparian areas as bat habitat, very few studies have examined the association between bat activity patterns and the physical structure and condition of riparian areas (Ciechanowski 2002, Lloyd et al. 2006, Williams et al. 2006, Ober & Hayes 2008). It has been suggested that retaining a diversity of seral stages, i.e., shrub-stage and mature forest, in riparian areas could provide foraging habitat for most bat species in a given area (Lloyd et al. 2006, Williams et al. 2006, Ober & Hayes 2008). A diversity of riparian habitat condition is necessary because of the differences in foraging habitat selection among bat species, which spatially partition themselves among various cover types to reduce competition for food resources (Kunz 1973, LaVal et al. 1977).

Foraging habitat selection by bats is dictated by physical, i.e., wing loading and jaw morphology, as

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well as echolocation characteristics (Kusch & Schotte 2007, Lacki et al. 2007). Bats with high wing-loading and low-frequency echolocation calls typically select open areas such as fields or large waterways over which to forage (Fenton & Bell 1981, Ford et al. 2005). Bats with low wing-loading and broadband, high-frequency echolocation calls are capable of efficiently foraging in cluttered conditions such as forest canopies and headwater streams (Ratcliffe & Dawson 2003, Lacki et al. 2007). Bats with intermediate wing-loading commonly are more plastic in the types of foraging areas that they use; they are capable of efficiently foraging in relatively cluttered as well as open areas (Lacki et al. 2007). A bat community, therefore, is an assemblage of species able to efficiently forage in various cover types or environments of variable amounts of physical complexity or structure. Some bat species, for example those with high wing-loading, are more likely to occur together when foraging than with species with low wing-loading. Species with intermediate wing-loading may occur in many different cover types, thereby increasing the likelihood that they will occur with species with both high or low wing-loading. Considered together, the various foraging strategies exhibited by different bat species suggest that a diversity of riparian conditions is beneficial for more species (Lloyd et al. 2006, Williams et al. 2006, Ober & Hayes 2008).

Riparian areas serve numerous ecological functions, not only as habitat for bats and other wildlife, but also for erosion and flood control, and biogeochemical cycling (Naiman & Décamps 1997). In the southeastern United States, there is growing concern regarding urbanization and other development near riparian zones and potential impacts on riparian function and wildlife (Zhang et al. 2008). Similar to other southeastern states, Georgia, particularly the northern, mountainous portion, is experiencing increasing development and urbanization (Turner & Ruscher 1988). The Cumberland Plateau and Ridge and Valley physiographic provinces of northwestern Georgia together exist as a region that is high in bat species richness compared to other areas of the state (Menzel et al. 2000), as well as other plant and animal groups (Wharton 1978). Regionally, 12 bat species potentially occur, including *Corynorhinus rafinesquii*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus borealis*, *L. cinereus*, *Myotis grisescens*, *M. leibii*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, *Nycticeius humeralis*, and *Perimyotis subflavus* (Menzel et al. 2000). *Myotis grisescens* and *M. sodalis* are federally-listed endangered species, and *Corynorhinus rafinesquii* and *M. leibii* are rare species in the southeastern United States. Because the importance of conserving riparian areas in northwestern Georgia cannot be overemphasized from a biodiversity standpoint, it is imperative that riparian areas are identified and characterized, and that their relevance to bat communities is understood in terms of how physical structure of riparian areas and adjacent land uses affect bats. Accordingly, our objectives were to determine the degree to which different bat species occurred together and if their occurrence was related to riparian condition in northwestern Georgia. Also, we determined if bat species richness was influenced by riparian condition. We predicted that within riparian zones, bat species would be partitioned according to the physical structure of the vegetation adjacent to water sources and the size of the water source itself; *E. fuscus*, *N. humeralis*, *L. cinereus*, and *M. grisescens* would be associated with larger water sources with less canopy cover (LaVal et al. 1977, Ford et al. 2005). *Myotis septentrionalis*, *Corynorhinus rafinesquii*, *M. sodalis*, and *M. leibii* would occur at small, headwater streams and small pools with dense canopy cover (Ford et al. 2005, Menzel et al. 2005). *Lasiurus borealis*, *P. subflavus*, *L. noctivagans*, and *M. lucifugus* would occur in a variety of riparian conditions, with no preference for either large or small water sources (Ratcliffe & Dawson 2003, Ford et al. 2005). All species would occur throughout the area, regardless of elevation, with exception of *M. grisescens*, which commonly is associated with larger waterways in valleys (LaVal et al. 1977). Species such as *E. fuscus* and *M. lucifugus* would occur at riparian areas with surrounding development, as these species are known to roost in anthropogenic structures (Barbour & Davis 1969).

Methods

Study area

We conducted our study in the Cumberland Plateau and Ridge and Valley physiographic provinces (34º10′ – 35º00′ N; 84º49′ – 85º37′ W) in northwestern Georgia (Fig. 1). Long, linear ridges characterized the Ridge and Valley province, with sharp escarpments rising 100–300 m above valley floors. River valleys were wide and flat in the Ridge and Valley province, with waterways forming more deeply incised, narrow gorges to the northwest in the Cumberland Plateau province, which was predominated by the Lookout Mountain massif. Our study area encompassed approximately 8820 km of streams and rivers, and approximately 5700 ponds and lakes (Simley & Carswell 2009). *Quercus* spp. – *Pinus* spp. forests were predominate in uplands, and riparian areas included forest communities of *Liquidambar* *styraciflua*, *Platanus occidentalis*, *Liriodendron tulipifera* or shrub wetlands consisting of *Cephalanthus occidentalis* and *Salix nigra*. Most alluvial valleys in the Ridge and Valley province have been cleared for pasture and row crops. Limestone geology underlies most of the area, and caves occur throughout (Wharton 1978).

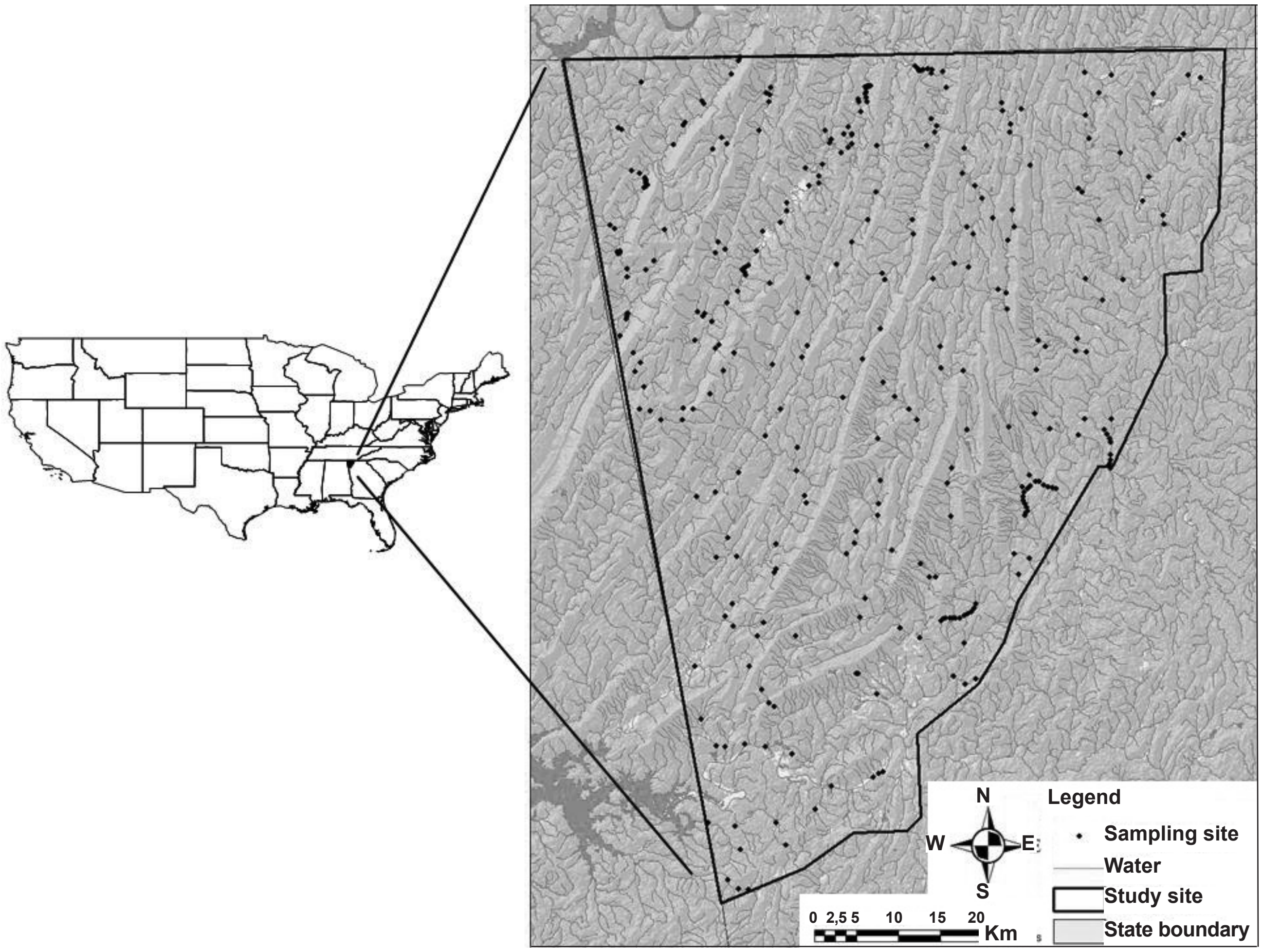

Fig. 1. *Acoustic sampling sites in northwestern Georgia, 2000–2002.*

Acoustic monitoring

In summers 2000–2002 (June–August), we conducted active acoustic monitoring at water sources with an Anabat II (Titley Electronics, Ballina, Australia) bat detector linked to a Compaq Presario 1200 laptop computer (Compaq Computer Corporation, Houston, Texas, USA) via an Anabat V Zero-Crossing Analysis Interface Module (ZCAIM) and Anabat 6.2d software (Corben 1999a, Broders et al. 2003). In 2000, we established an 8.3 × 9.4 km sampling grid over a 5100 km^2 study area in the northwestern corner of Georgia. We randomly sampled 3–4 water sources within 4 km of each grid intersection ($n = 69$) (Johnson et al. 2002). We sampled a variety of water sources, from small streams to large rivers, and ponds and lakes of various sizes. Moreover, we sampled at locations with different riparian vegetation, e.g., clearings and forests. In 2001, we focused our sampling along streams and rivers with varying vegetative complexity. In 2002, we sampled at streams in the Chickamauga and Chattanooga National Military Park. We monitored bat activity at each site once for 20 minutes between 21.15 and 02.00 hours (3–10 sites per night) (Schirmacher et al. 2007, Johnson et al. 2008). We used active monitoring, sweeping the detector to sample over the water source until a bat was detected. We attempted to capture as much of the echolocation pass sequence as possible by orienting the detector to follow the detected bat's flight. Sampling was not conducted during periods of heavy rain, high wind (≥ 20 kph), or cold temperatures (< 10°C), as these conditions may negatively affect bat activity (Erickson & West 2002). Bat echolocation passes, or a series of echolocation pulses or calls emitted by bats as they navigate and search for food, were analyzed with Analook 4.7j software (Corben 1999b). The senior author identified all echolocation passes to avoid variation in identification accuracy among personnel (O'Farrell et al. 1999) and only identified echolocation passes containing ≥ 3 pulses. We qualitatively identified echolocation passes of non-*Myotis* bats by comparing structures and frequencies of echolocation passes recorded at sampling sites to a library of identified echolocation passes of hand-released bats captured throughout the southeastern United States (Fenton & Bell 1981). We identified *Myotis* species based on frequency and slope characteristics of echolocation passes (O'Farrell 1999, Britzke & Murray 2000, Murray et al. 2001, Britzke et al. 2002).

Riparian conditions

We measured 18 variables at each acoustic monitoring site that we believed influenced presence of bats either directly or indirectly based on previous studies (Table 1). Each waterway was categorized as lentic or lotic (variable = Lotic). The surface of the water was qualitatively classified as pool, run, riffle, or rapid because some bat species have been found to avoid rapids and riffles of lotic waterways (Flow) (Mackey & Barclay 1989). We measured the width of each water source with a laser range finder (Leica Camera Inc., Solms, Germany) or tape measure (Width) (Seidman & Zabel 2001). Water depth was categorized (Depth; 0–15 cm, 16–90 cm, > 90 cm). Substrate was classified according to approximate aggregate size, including clay/mud, sand, gravel, cobble, or bedrock (Substrate). We measured the temperature of the water's surface with a thermometer (Temp). Turbidity was categorized (Turbidity; clear, semi-turbid, turbid). Because some bats avoid structural clutter (e.g., vegetation, tree limbs) when foraging over water (Mackey & Barclay 1989), we estimated the amount of clutter over water sources that could potentially impede bat flight by separating streams into 20 1 m segments; 10 upstream and 10 downstream from the sampling site. Each segment received a score of one if clutter was present < 3 m from the water's surface or zero if otherwise, resulting in a potential score of 0–20 for each sample site (Shrub). We estimated percent (0, 25, 50, 75, or 100) overstory forest canopy cover at 5 locations

Table 1. *Relation between 2 dimensional nonmetric multidimensional scaling (NMDS) axes and riparian variables measured at acoustic sampling sites (n = 300) in northwestern Georgia, 2000–2002.*

Variable	Variable definition	NMDS Axis 1	NMDS Axis 2	r^2	P
Depth	Depth at center of waterway	0.981	-0.193	0.050	<0.001
Flow	Pool, run, riffle, or rapid	0.991	-0.129	0.046	0.002
Lotic	Waterway was lentic or lotic	0.841	0.541	0.034	0.005
% Canopy	Percent canopy cover over waterway	0.446	0.895	0.024	0.021
Water	Percent open water within 56.4 m of sampling site	0.650	-0.760	0.025	0.021
Turbidity	Clear, semi-turbid, or turbid	0.995	-0.101	0.024	0.032
Elevation	Elevation at sampling site	-0.948	-0.317	0.020	0.053
Wetland	Percent wetland area within 56.4 m	0.854	-0.519	0.016	0.090
Developed	Percent developed area within 56.4 m	-0.839	0.545	0.013	0.141
Width	Width of waterway	0.597	-0.802	0.011	0.204
Snags	Number of snags within 50 m of sampling site	-0.228	-0.974	0.010	0.220
Shrub	Amount of shrubs or tree limbs over water surface	-0.997	0.083	0.010	0.224
Exfobark	Number of trees with exfoliating bark within 50 m	0.349	-0.937	0.009	0.235
Ag	Percent agriculture area within 56.4 m	-0.317	0.948	0.009	0.262
Temp	Surface water temperature at streambank	-0.430	-0.903	0.008	0.326
Open	Percent open area within 56.4 m	0.976	0.216	0.004	0.531
Forest	Percent forested area within 56.4 m	0.122	-0.993	0.002	0.672
Substrate	Clays/mud, sand, gravel, cobble, or bedrock substrate	0.403	0.915	0.001	0.818

(5 m spacing): 1 at the sampling site, 2 upstream and 2 downstream from the sampling site, and averaged the values (% Canopy). We tallied the number of dead trees (Snags) and trees with exfoliating bark (Exfobark) within 50 m of each sampling site.

We determined the elevation (Elevation), and latitude and longitude of each sampling site with a GeoExplorer II global positioning unit (Trimble Navigation, Ltd., Sunnyvale, California) and entered them into a GIS. We used ArcMap 9.2 (ESRI 2006) to acquire and analyze land use/land cover types from the 2001 National Land Cover Database (NLCD; Homer et al. 2007). We determined the percent of 15 possible land use/land cover types in a 1 ha area (56.4 m radius) surrounding each sampling site (USGS 2003). An area of 1 ha was chosen to examine the land use/land cover types immediately surrounding each sampling site while retaining independence among sampling sites. We summed percentages of NLCD land cover classes into 6 new land cover types as follows: (1) developed open space + low intensity developed + medium intensity developed + high intensity developed (Developed); (2) open water (Water); (3) coniferous forest + deciduous forest + mixed forest (Forest); (4) barren land + unconsolidated shore + scrub or shrub + grassland (Open); (5) pasture or hay + crops (Ag); and (6) woody wetland + forested wetland + emergent herbaceous wetland (Wetland).

Statistical analysis

We examined ordination of acoustic sampling sites according to bat species assemblages with nonmetric multidimensional scaling (NMDS; Appendix A; McCune & Grace 2002). To conduct the analysis, we used the metaMDS function in the R vegan package (Oksanen et al. 2008, RDCT 2008). We performed NMDS only on acoustic sampling sites where bats were positively identified (300 of 338 sites). We compiled a data matrix with bat species (presence or absence) and riparian variables as columns and sites as rows. Bray-Curtis dissimilarity distances among sites were determined for the bat species presence/absence portion of the data matrix. Because some acoustic sampling sites had identical bat species assemblages, a small positive value (0.071) was automatically added by R to these sites to allow Bray-Curtis distances to differentiate among them. Nonmetric multidimensional scaling hierarchically orders sites by their Bray-Curtis distances, and seeks to determine and represent the optimum position of n entities in k-dimensional space. Moreover, NMDS optimizes the position of the entities by minimizing the measure of stress, which is the magnitude entities must be moved in k-dimensional space to preserve monotonicity, or the original hierarchical ordering of the sites. The starting location of the entities is constructed at random in k-dimensional space. The entities are then moved to preserve monotonicity, and stress is measured. This process is repeated several times within each k-dimensional space to ensure stress stability. The n entities can be perfectly represented (zero stress) in n-1 dimensions. To represent n entities in > n-1 dimensional space, it is likely that the entities would have to be moved to preserve monotonicity, consequently increasing stress. Although lower stress values equate to a better representation of entities and may require a larger number of dimensions, interpretability is sacrificed if too many dimensions are retained in order to minimize stress values (McCune & Grace 2002). For our study, we iteratively examined stress levels of 1–6 dimensional ordinations of the data. A maximum of 20 runs was conducted for each dimension. Within each run, stress was averaged over 5 iteration-intervals for a maximum of 200 iterations and examined for stability. We chose to proceed with the dimension that provided the best compromise between stress (< 20) and interpretability (Clarke 1993).

We used the envfit function in the R vegan package to determine if riparian conditions were correlated with the NMDS ordination axes based on 1000 permutations of the data (Oksanen et al. 2008, RDCT 2008). Prior to analysis, we used Spearman's rank correlation analysis to examine all riparian condition variables for collinearity, and considered any variable pair with a correlation (ρ) exceeding 0.7 to be significantly correlated. No variable pairs were significantly correlated. We considered riparian condition variables to be significantly correlated with NMDS ordination axes at the $P \leq 0.10$ level. We calculated partial correlation coefficients for each variable.

To determine if riparian condition affected bat species richness, we used a regression tree analysis performed in R mvpart package (McCune & Grace 2002, Oksanen et al. 2008, RDCT 2008). We used a regression tree instead of a classification tree approach in order to detect trends in species richness based on riparian variables rather than attempting classification of absolute species richness values. We used all acoustic sampling sites (n = 338) in the analysis, including sites where only unidentifiable bats or unidentifiable *Myotis* spp. were recorded. We considered bat species richness to be one (1) at sites where only unidentifiable bats, unidentifiable *Myotis* spp., or undetermined *L. borealis*/*P. subflavus* were

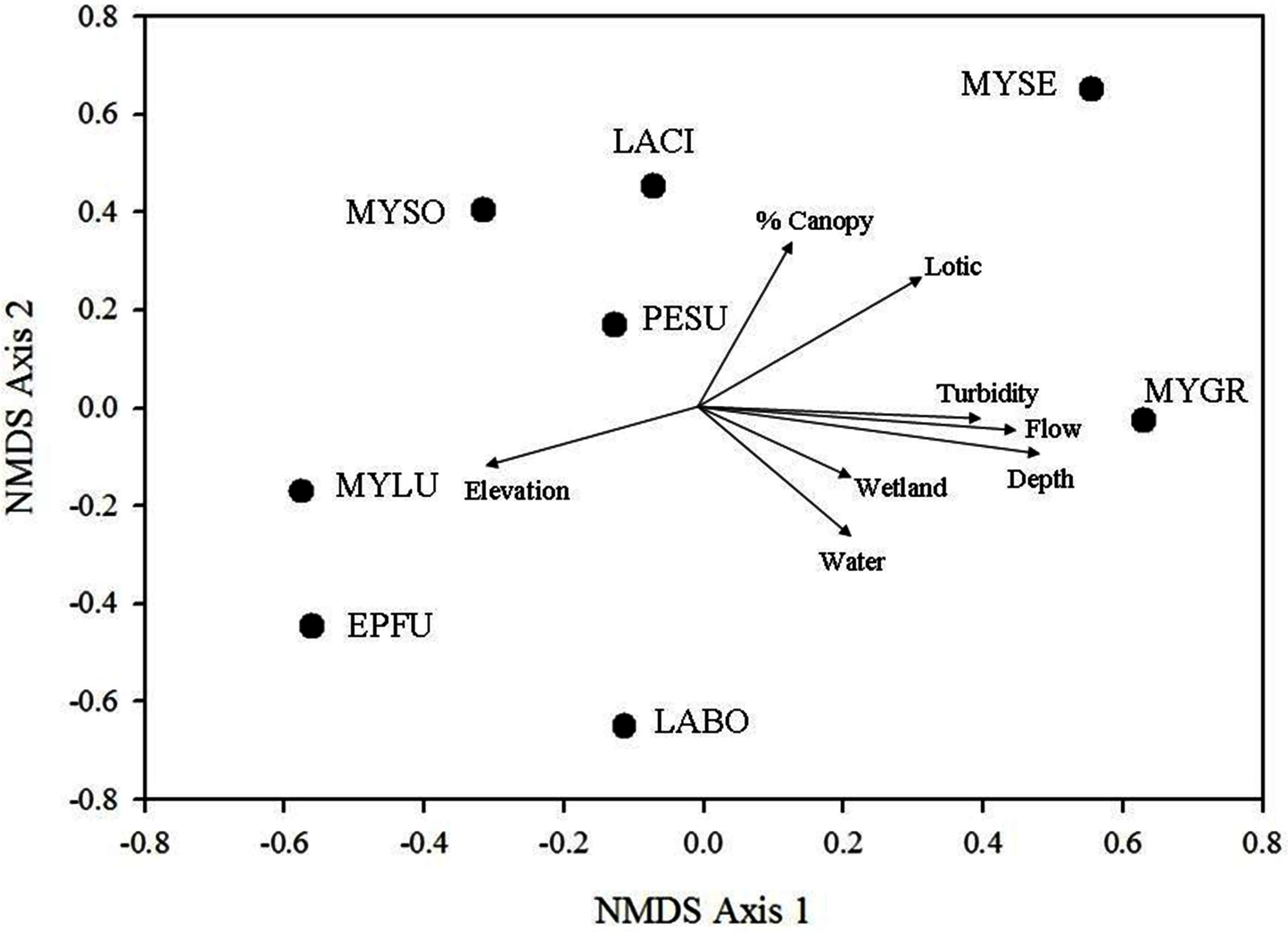

Fig. 2. *Association between nonmetric multidimensional scaling (NMDS) ordination axes of bat species and riparian conditions in northwestern Georgia, 2000–2002. Directions of arrows indicate increasing variable value.*
EPFU = Eptesicus fuscus*; LABO* = Lasiurus borealis*; LACI* = Lasiurus cinereus*; MYGR* = Myotis grisescens*; MYLU* = Myotis lucifugus*; MYSE* = Myotis septentrionalis*; MYSO* = Myotis sodalis*; PESU* = Perimyotis subflavus.

recorded because we were uncertain of exactly how many bat species were present at these sites. It would be incorrect to consider these sites as having no bat species present, making interpretation of the results problematic. If only unidentifiable *Myotis* spp. and undetermined *L. borealis*/*P. subflavus* were recorded, species richness was two (2) for the site. We performed 50 multiple cross validations on 10 random subsets of the data. The procedure was performed 5 times to ensure stability of the results in terms of tree size and cross-validation error rate. We determined classification tree size, i.e., number of leaves, by selecting the largest tree with a cross-validation error within one standard error of the minimum (Faraway 2006).

Results

Acoustic monitoring

We conducted acoustic monitoring at 338 sampling sites, including 31 sites at ponds and lakes, 170 sites at streams (≤ 4th order) and 137 sites at rivers (≥ 5th order). We recorded 12018 echolocation passes in summers 2000–2002, and identified *P. subflavus* at 246 sites, *M. grisescens* at 126 sites, *L. borealis* at 67 sites, *E. fuscus* at 45 sites, *M. lucifugus* at 38 sites, *M. septentrionalis* at 23 sites, *L. cinereus* at 6 sites, and *M. sodalis* at 2 sites. Due to call sequences that were comprised of too few pulses or were of insufficient quality, we were unable to identify to species *Myotis* at 166 sites, and *L. borealis*/*P. subflavus* at 6 sites. At 16 (7.5%) sampling sites, no echolocation passes were recorded.

Statistical analysis

Solutions for NMDS ordinations at 1–6 dimensions were achieved within 18 runs of the data. Final stress values for all dimensions ≥ 2 were < 20. The stress value of the 2-dimensional NMDS ordination stabilized at 17.17 after 3 runs of the data. Among the 8 recorded species, only *M. septentrionalis* and *M. grisescens* were positively associated with NMDS axis 1; all other species showed a negative association.

Lasiurus borealis, *E. fuscus*, *M. lucifugus*, and *M. grisescens* were negatively associated with NMDS axis 2. *Myotis septentrionalis*, *L. cinereus*, *M. sodalis*, and *P. subflavus* were positively associated with NMDS axis 2 (Fig. 2).

Of the 18 riparian variables that we measured, 8 were correlated ($P \leq 0.10$) with the 2-dimension species space axes (Table 1). However, individually, all variables poorly explained ($r^2 \leq 5.0\%$) variation in species space. All riparian variables except Elevation were positively associated with NMDS axis 1. All riparian variables except % Canopy and Lotic were negatively associated with NMDS axis 2 (Fig. 2).

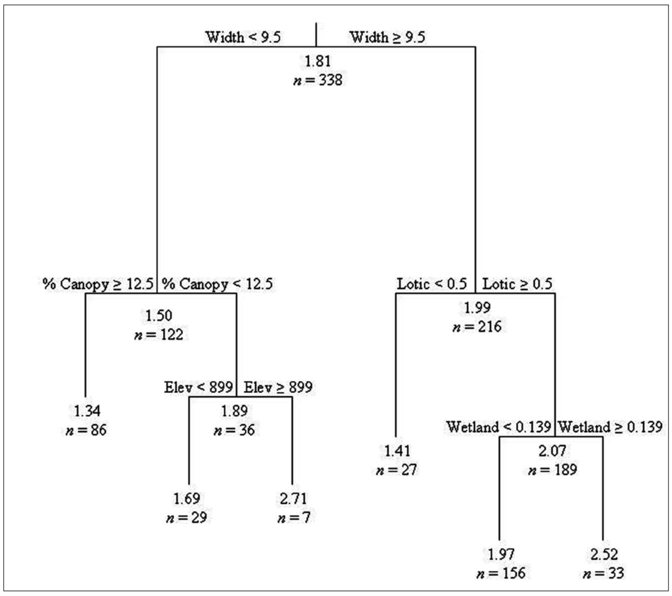

Fig. 3. *Bat species richness predicted by riparian condition at acoustic monitoring sites (n = 338) in northwestern Georgia, 2000–2002.*

Lasiurus borealis, *E. fuscus*, and *M. lucifugus* were associated with high-elevation lentic waterways with sparse canopy cover. *Myotis septentrionalis* were associated with low-elevation lotic waterways with dense canopy cover. *Myotis grisescens* were associated with low-elevation, turbid, deep lotic waterways with adjacent wetlands. *Lasiurus cinereus* and *M. sodalis* showed a negative association with high amounts of water and wetland areas, but sample sizes for these species were 6 and 2 respectively, indicating that these results should not be considered robust. *Perimyotis subflavus* were the most ubiquitous species recorded, resulting in a nearly central location on the NMDS plot. However, there was some indication of negative association between *P. subflavus* presence and amount of water and wetland areas (Fig. 2).

Regression tree analysis indicated that up to 6 leaves were within 1 cross-validation error of the minimum and were meaningful in determining species richness according to riparian variables (Fig. 3). The model error was 0.83, indicating that 17% variation in species richness was explained by the regression tree. Relatively high (> 2) species richness was associated with 2 riparian conditions; small, high-elevation water sources with sparse canopy cover, and large streams and rivers with adjacent wetland areas (Fig. 3).

Discussion

The bat community that we observed was somewhat consistent with expectations, but was absent of *N. humeralis*, *C. rafinesquii*, *L. noctivagans*, and *M. leibii*. *Nycticeius humeralis* probably are more common on the Coastal Plain to the south, and were rarely documented during mist net surveys at the Chickamauga and Chattanooga National Military Park within our study area (Menzel et al. 2000, Ford et al. 2004). *Lasionycteris noctivagans* likely occur in northwestern Georgia only as seasonal transients or as winter residents (Menzel et al. 2000). *Corynorhinus rafinesquii* and *M. leibii* are considered rare throughout their respective geographic ranges and, in northwestern Georgia, are most likely occur near rock outcrops and talus slopes associated with the Lookout Mountain massif, where our surveys did not intensively focus (Menzel et al. 2000). Moreover, acoustic sampling is not appropriate for detecting *C. rafinesquii* because their low-intensity echolocation calls are difficult to detect (Menzel 2003). Notwithstanding the few species that we did not record, our surveys documented a species assemblage that was partitioned to some degree according to riparian condition.

Despite the low variation in species-riparian relations explained by the variables we measured, several species met our expectations in the types of riparian areas wherein they were associated. *Myotis grisescens* were associated with deep, turbid streams and rivers in the valleys. Chickamauga Creek and the Oostanaula River previously have been identified as primary foraging areas for *M. grisescens* in northwestern Georgia (Johnson 2002). *M. grisescens* typically forage over larger waterways throughout their range, and may competitively exclude other *Myotis* species from these areas (LaVal et al. 1977). Indeed, the closest *Myotis* species to *M. grisescens* on the NMDS ordination was *M. septentrionalis*, which was associated more with waterways that had dense canopy cover, likely headwater streams. *M. septentrionalis* typically forage in intact forests and upland streams (Ford et al. 2005). However, contrary to our expectations, *M. septentrionalis* in northwestern Georgia were more commonly detected at lower elevations. In the Central Appalachian Mountains region, for example, *M. septentrionalis* are more prevalent in upland areas (Ford et al. 2005). In northwestern Georgia, the underlying sandstone geology and droughty soils of high elevation areas, i.e., the Lookout Mountain massif, do not provide the necessary conditions for an abundance of forested headwater streams and seeps (Wharton 1978). This is supported to some extent by the results of the regression tree analysis that indicate that higher species richness is associated with narrow, high-elevation waterways that have sparse canopy cover. *M. lucifugus* were at the opposite side of NMDS axis 1 from *M. grisescens* and *M. septentrionalis*, and were associated with high-elevation lentic waterways with sparse canopy cover. Foraging areas of *M. lucifugus* commonly are riparian areas with less canopy cover than those used by sympatric *M. septentrionalis* or *M. sodalis* (Ford et al. 2005, Schirmacher et al. 2007). Similar to *M. lucifugus*, *E. fuscus* and *L. borealis* foraged at high-elevation lentic waterways with sparse canopy cover. *Eptesicus fuscus* and *Lasiurus borealis* are commonly associated with open areas, including large pools and streams, when foraging (Ford et al. 2005, Schirmacher et al. 2007, Brooks 2009). However, it is unclear why these species were more commonly detected at high-elevation waterways, as we expected that they would be associated with low-elevation riparian areas (Ford et al. 2002, 2005). Perhaps the association is merely coincidently, considering the relatively weak explanatory power of elevation. *Perimyotis subflavus* were the most ubiquitous species detected in northwestern Georgia, resulting in a central location on the NMDS ordination. *P. subflavus* are considered a generalist species capable of efficiently foraging over both open and cluttered waterways of all types (Schirmacher et al. 2007). Low sample sizes of *M. sodalis* and *L. cinereus* limit strong inferences that can be drawn regarding the types of riparian areas they use in northwestern Georgia. *L. cinereus*, a rare summer resident of Georgia, typically forage in open areas, including large ponds and reservoirs (Menzel et al. 2000, Brooks 2009). *Myotis sodalis* typically forage in forests with intact canopies and near headwater streams (Menzel et al. 2005, Schirmacher et al. 2007). Given the wide range of riparian conditions used by the various bat species in northwestern Georgia, we believe our results not only support the importance of riparian areas as bat habitat in general, but also corroborate recommendations to maintain a variety of riparian areas to foster the full bat community (Lloyd et al. 2006, Williams et al. 2006, Ober & Hayes 2008). Results of the regression tree analysis indicate that two distinct types of riparian areas are associated with high bat species richness. Riparian areas at small, high-elevation waterways had high bat species richness. Also, these areas had sparse canopy cover, allowing use by open-area foragers, including *E. fuscus*, *M. lucifugus*, and *L. cinereus* (Brooks 2009). Water sources at high elevations may be an uncommon resource, increasing the importance of these areas to a wide range of bat species that may be forced to concentrate their activity in a relatively small area. Indeed, only seven of the sampling sites met these criteria, indicating that they are relatively uncommon riparian types in northwestern Georgia. High bat activity and species diversity has been documented at high-elevation wetlands and intermittent streams (Seidman & Zabel 2001, Francl et al. 2004, Lloyd et al. 2006). Also important to high species richness in northwestern Georgia were larger streams and rivers that had wetlands, i.e., inundated floodplains, adjacent to them. There may be an abundance of snags associated with these wetlands where bats can day- and night-roost (Carter 2006). Similar to some high-elevation waterways, many of the larger streams and rivers in the valleys also have sparse canopy cover, providing foraging conditions amenable to a higher overall number of bat species (Lloyd et al. 2006, Williams et al. 2006, Ober & Hayes 2008). These larger waterways, including the Oostanaula River and Chickamauga Creek, are known foraging areas of endangered *M. grisescens*, adding to their importance to bats (Johnson 2002). Although the regression tree explained 17% of variation in bat species richness, the results provide broader merit from a biological and conservation standpoint. By implementing conservation strategies for the *M. grisescens*, i.e., protecting larger streams and rivers, many bat species will benefit as a consequence. Therefore, protection of both small, open, high-elevation waterways and large streams and rivers and adjacent wetlands would be the most effective strategy to benefit the most bat species in northwestern Georgia.

A fuller understanding of the association between bats and riparian conditions would be gained by incorporating assessments of water quality and aquatic and aerial macroinvertebrates at sampling sites. Moreover, the NMDS and regression tree analyses that we used undoubtedly could be improved with the incorporation of data from a broader suite of ecological conditions. For example, urbanization may negatively impact water quality and arthropod resources for bats at riparian areas (Kusch et al. 2004, Kalcounis-Rueppell et al. 2007). More research is needed to determine the relation between arthropod resources and anthropogenic influences to form a more complete picture of the ecology of these riparian areas. Indeed, our models could be improved by a more complete analysis of the relation between riparian areas and bats with the addition of water chemistry and arthropod availability data to the existing dataset.

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