

Habitat influence on bat foraging activity in riparian areas in Western Montana

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UNDERC-West

Summer 2017

Abstract

Management of an ecosystem for conservation requires knowledge of the abiotic and biotic requirements of the species in question. Bat foraging behavior in forests has been associated with riparian areas due to higher prey densities and lower structural clutter. Grasslands lack clutter except in riparian areas, but bats still forage over water in these ecosystems. This study assesses multiple variables to determine what factors influence foraging site choice. The results suggest that there is a baseline size of stream and amount of vegetation required to support bat foraging. Beyond this baseline, the health of the ecosystem based on the macroinvertebrate communities is the main feature that determines the quality of the foraging site.

Introduction

To properly manage an ecosystem for conservation requires knowledge of the abiotic and biotic requirements of the species that compose it (Bellamy et al 2013; Fischer 2009). Identifying these habitat associations increases the efficiency of species specific conservation by focusing efforts on areas with certain favorable attributes (Fischer et al 2009). A variety of factors including the levels of competition, prey, temperature, precipitation, resources, mates and shelter can determine what types of habitats are fit for an animal species (Morrison et al 2012). Determining how animals use an area is valuable for managing its environmental resources because it tells us what features of the habitat it needs.

Bats are an extremely important group of organisms ecologically speaking. They make up about a fourth of all mammal species, making their order, Chiroptera, the largest mammal order. Worldwide, bat ecological role ranges from seed dispersal, pollination and insect consumption. In the temperate regions of North America all of the bat species are insectivorous and they consume an enormous quantity of insects (Fenton 1990; Holloway and Barclay 2000). Despite the importance of these species, they are misunderstood and often thought of poorly in the public eye (Adams 2003). Although this negative view is slowly changing, it remains ever important as humans transform more of the natural environment to learn more about these creatures. Bats have specific habitat requirements that need to be managed for.

Riparian areas have long been associated with increased insectivorous bat activity (Broders et al 2006, Fenton 1990; Grindal and Brigham 1999; Krusic 1995; Lloyd et al 2006; Morris et al 2010; Rautenbach 1996; Zimmerman and Glanz 2000). In forests, open areas like streams have less structural clutter to impede bat flight so they regularly use them as pathways for flying and foraging (Morris et al 2010; Krusic 1995; Broders et al 2006, Fenton 1990; Grindal and Brigham 1999; Lloyd et al 2006; Rautenbach 1996; Zimmerman and Glanz 2000). Aside from serving as flight paths, riparian areas have high prey insect concentrations and can serve as water sources for drinking (Lloyd et al 2006; Whitaker et al 2000; O'Donnell 2000; Taylor and O'Neill 1988). The degree to which these factors determine preference among riparian habitats is not fully understood. This is especially true in non-forest ecosystems that are likely used by bats in very different ways (Holloway and Barclay 2000). In more open habitats such as grasslands, larger vegetation is actually clustered around riparian areas, substantially increasing the clutter.

When considering bat conservation in a grassland, it is vital to know what attributes are important to provide bats with a suitable habitat to forage in. Vegetative clutter may not have a negative effect on bat activity in a grassland as it does in forests (Fenton 1990; Grindal and Brigham 1999). In fact, Everette et al 2001 suggests that in grasslands, bats actually rely on water-grassland interface for foraging habitat. Bats could be drawn to riparian vegetation because their prey use it as habitat to live, forage or reproduce (Grindal et al 1999). This potential reversal of the role of vegetation may result in an increase in the importance of other environmental factors (insect communities, water availability etc.) Accounting for multiple variables that potentially impact bat foraging behavior is necessary to give insight into the

conditions favored by insectivorous bats when choosing riparian foraging sites in a grassland ecosystem.

The aim of this study is to investigate how bats use riparian habitats and what factors determine their use. I compare the overall bat activity, foraging activity and diversity across sites with a gradient of stream widths, stream health (macroinvertebrate index [EPT]) and structural clutter in the canopy and understory along the streams. The overall activity, number of feeding buzzes and diversity should all increase with the size of the streams as more water is available to both the bats and their prey, especially in such a dry habitat (Whitaker 2000). Since trees in closed canopies are relatively scarce on the National Bison Range (NBR) and are clustered around important water sources, structural clutter should not deter the bats from foraging in an area because of the higher availability of multiple resources. Foraging may increase with clutter because the intensity of vegetation will increase near food and water sources. Additionally, clutter provides a more complex habitat and makes a site more attractive to a wider range of species (Brooks 2009). Healthier streams, as measured by the aquatic macroinvertebrate communities, should have a higher abundance and diversity of prey and therefore will draw a higher abundance and diversity of bats. These streams will attract more bats with overall increased health and a more robust and diverse insect community.

Methods

Study Site

This study was conducted on the Flathead Indian Reservation and the National Bison Range in the Moiese Valley of western Montana from June 26th 2017-August 1st 2017. A variety of streams were selected based on their width, vegetation levels and stream health (Figure 1).

The stream areas were relatively calm without riffles that would impact bat echolocation and therefore foraging suitability of the site. All of the streams were found at or close to the base of the valley and therefore had similar elevations.

The Reservation and Bison Range are bunchgrass prairie ecosystems that get about 33 cm of rain per year. The riparian areas where sampling took place were concentrations of vegetation mainly in the form of shrubs and trees largely absent from the surrounding landscape.

Vegetation sampling

Two 100 meter transects were used for the vegetation sampling at each of the 7 sites. The transects ran parallel to relatively straight stretches of the waterways and stayed between 1 meter and 3 meters from the water's edge. These vegetation metrics will be used together to represent the structural/vegetative clutter along each of the sampling sites.

Canopy cover

A densitometer was used to measure the canopy cover at 40 points at each stream site. At ten points every ten meters along both transects and at ten points parallel to the transects ten meters away.

Density board

The understory vegetation was sampled using a 0.2 meter by 2 meter density board.

Every 10 meters along the transects the percent vegetative cover was estimated from 10 meters away, perpendicular to the transect.

Point-centered quarter tree density sampling

At 10 randomly selected points at least 4 meters apart along the transects at each site, the point-centered quarter (PCQ) method was used to find the tree density along the streams.

Insect sampling

Human landing catch (HLC)

Each night of sampling for echolocation, a human landing catch assay (HLC) was performed for 10 minutes at the start of each sampling period to find the mosquito density at each site (Kenea et al 2017). The mosquito density was used to represent a portion of the prey density at each of the streams.

Aquatic macroinvertebrates

Aquatic insects were sampled at each site with a dip net over the course of 5 minutes. The invertebrates were counted and identified back at the lab and the percent of the entire sample made up of Ephemeroptera, Plecoptera and Tricoptera was determined (percent EPT). This sampling is used as an index of the overall stream health according to the macroinvertebrate populations (Ferreira et al 2014).

Bat activity and foraging

An Anabat II detector (Titley Scientific) was used to measure the activity and foraging levels at each site. The detectors were 5 meters from the water's edge positioned facing upwards over the stream at an angle from 30-45 degrees. The recordings were analyzed using AnaLookW (Titley Scientific). Since most bat foraging occurs within two hours of sunset, the sampling periods were two hours long starting at sunset each night (Maxell et al 2015). The bat activity

was measured by the number of passes per two hour period; passes being a series of 2 or more consecutive echolocation pulses.

When flying, bats produce periodic pulses of echolocation in order to survey the environment and locate prey. After finding their prey, they approach them and emit feeding buzzes to determine their precise location (Fenton and Bell 1979; Griffin et al 1960; Humes et al 1999). Feeding buzzes are characterized as a clear increase in the rate of a pulses in a bat call (Fenton 1990; Grindal et al 1999; Figure 2). These feeding buzzes can be used to measure predation events and therefore quantify foraging levels. The foraging activity was quantified as the number of feeding buzzes per night.

Over the course of 14 nights, 1394 bat passes were recorded. These passes include 110 feeding buzzes (7.89 percent of total). Due to the volume of passes recorded, the calls were separated only by morphospecies to find the richness and Shannon diversity rather than each one identified to species.

Statistics

For each of the overall activity (number of passes), foraging activity (number of feeding buzzes), richness and diversity a multiple regression was performed using R version 3.3.0. A stepwise AIC was used to select the variables that most accurately model the variable in question. The regressions display the presence and relative strength of the relationships between bat foraging habits and the environmental factors (stream width, stream health (percent EPT), percent canopy cover, tree density, understory density, mosquito activity) selected by the stepwise AIC that best predict them.

Results

In order to meet the assumptions for a multiple regression, the residuals of each of the 4 data sets were tested for normality. All four sets of residuals were normally distributed (Shapiro-Wilk normality test; bat activity $W = 0.98308$ p-value = 0.9912, foraging activity $W = 0.94296$ p-value = 0.4963, diversity $W = 0.90486$ p-value = 0.1559, richness $W = 0.96694$ p-value = 0.8553).

Bat activity

The variables composing the most accurate model to describe the number of bat passes, as selected by the AIC, were percent EPT, mosquito density and tree density (Table 1). The model was run through a multiple linear regression and was able to describe the bat activity with significance (Adjusted R-squared: 0.6964, F-statistic: 10.94, df: 3 and 10 p-value: 0.001686; Table 2). The only variable in the model that could significantly explain the bat activity on its own was the percent EPT (T-value: 2.599, p-value: 0.000381; Table 2). While not statistically significant, the other variables (mosquito density and tree density), contribute to the model. These two remaining variables have a relationship with the bat activity several orders of magnitude lower than the percent EPT, leaving EPT as the main factor predicting the bat activity in the model (Figure 3).

Foraging activity

Similar to the bat activity, the variables composing the most accurate model to describe the number of feeding buzzes, as selected by the AIC, were percent EPT, mosquito density and tree density (Table 3). The model was run through a multiple linear regression and was able to describe the bat activity with significance (Adjusted R-squared: 0.6037, F-statistic: 7.601, df: 3 and 10, p-value: 0.006152; Table 4). The only variable in the model that could significantly

explain the bat activity on its own was the percent EPT (T-value: 4.438, p-value: 0.00126; Table 4). While not statistically significant, the other variables (mosquito density and tree density), contribute to the model. These two remaining variables have a relationship with the foraging activity several orders of magnitude lower than the percent EPT, leaving EPT as the main factor predicting the foraging activity in the model (Figure 4).

Diversity and richness

The variables composing the most accurate model to describe both the diversity and richness (canopy cover, mosquito density, stream width, tree density) were unable to significantly explain the either one (Diversity, Adjusted R-squared: 0.09495, F-statistic: 1.341, df: 4 and 9, p-value: 0.327; Richness, Adjusted R-squared: -0.003183, F-statistic: 0.9897, df: 4 and 9, p-value: 0.4604).

Discussion

The overall activity changes across sites can be attributed mainly to foraging behavior, rather than the bats using the waterways for travel since the surrounding grassland ecosystem is so free of clutter. This does not rule out the bats using the streams to drink, but the similarity of the foraging activity to the overall activity confirms that the bats are using these waterways to forage.

The lack of a relationship between the environmental characteristics and the richness and diversity of the bats that forage at each of the sites likely has to do with the scale of the study. Richness and diversity may be geographically determined because bats can travel far distances in a night, sometimes over 50 km (Buchler 1980; Fenton 1990). Because of this large flight range, and the relatively small area that the study was conducted in (~50 km x 50km), the bat

populations at each site did not greatly differ in their species composition. Each site was likely a similarly composed population of bats, but of a different size based on the environmental characteristics. In order to correct for this issue, a larger variety of sites across a larger geographical area would be necessary. Such a scale was not feasible for this study which is why the diversity of bat populations was not a primary focus.

For both the foraging and overall activity models the percent EPT, mosquito density and tree density were the best predictors (Table 2; Table 4). In past studies, the vegetation was found to have a much more profound impact on the activity (Morris et al 2010; Krusic 1995; Rautenbach 1996; Zimmerman and Glanz 2000). The tree density has only a slightly negative relationship to the activity indicating that even with an increase in clutter, the bats are not greatly deterred from foraging. Further reinforcing this idea is the lack of a relationship between bat activity and the other vegetative variables (canopy cover, understory vegetation). This was an expected outcome and provides evidence for the differential habitat requirements of bats when foraging in grasslands. Rather than looking for clear pathways to fly through while foraging, they are drawn to water sources with little regard to the clutter, even though it is mostly concentrated around water.

The environmental characteristic that appears to be driving the behavior of the bats is the percent EPT in the streams (Table 2; Figure 3). This result indicates that bat species are relying on healthier streams for their foraging. Healthier streams can support a higher diversity and abundance of insects, making a stream more suitable for forage. This powerful relationship is important, but not the whole story. The stream width and vegetation data, while not linearly correlated with activity, help to give a picture of the type of habitats used for forage. The lowest width streams that lack overstory vegetation have some of the lowest bat activity (Figure 3;

Figure 4). Beyond small streams that cannot support larger vegetation, the size and amount of clutter around streams does not affect the foraging levels.

This study was able to shed some light on the foraging behavior of insectivorous bats in grassland dominated ecosystems. It provides evidence supporting differential study of bat behavior in forests and grasslands. In fact, the driving factors that determine bat behavior may be wholly different between the two ecosystem types. The data from this study suggests that in grasslands there is a baseline size of stream and amount of vegetation necessary to support foraging and beyond that point the health and insect populations of a stream determine how attractive it is. Further study into these factors and the degree to which they contribute to the suitability of a foraging habitat will be key in the management of grasslands for bat conservation.

Acknowledgements

I would like to thank the Hank family for their generous contributions that make UNDERC possible. I also would like to thank the Confederated Salish and Kootenai tribes and the National Bison Range for allowing us to conduct research on their property and for being so accommodating. I would like to thank Gary Belovski for not only making UNDERC possible but making it so great. I also want to thank Kate Barrett and David Flagel for their help on this project, especially with statistics. Thanks to Dominic Acri, Angela Dunsmoor-Connor, Elizabeth Marjorie Berg, Kimberly Sutton, Daniel de Jesus, Kate Barrett and Meredith Kadjeski who all came out with me at night to record bat calls. Meredith and Angela also let me use their insect data that made this project possible.

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Tables

Table 1: Stepwise AIC used to select the most accurate model for the number of bat passes. Percent EPT, mosquito density and tree density produce the best model and prediction for the bat activity

Predictors	AIC score
EPT+ Mosquito density + Tree density	113.42
EPT+ Tree density	113.90
EPT+ Mosquito density	114.14
EPT+ Mosquito density + Tree density+ Stream width	114.28
EPT+ Mosquito density + Tree density+ Canopy cover	114.58
EPT+ Mosquito density + Tree density+ Understory vegetation	115.17
Mosquito density + Tree density	129.89
Selection: Feeding buzzes ~ EPT+ Mosquito density + Tree density : AIC value: 113.42	

Table 2: Multiple regression statistics for the regression chosen by the stepwise AIC to model the bat passes. The regression is a significant predictor of the number of bat passes with percent EPT, mosquito density and tree density, but only the percent EPT of the streams significantly predicts the number of passes on its own.

	<i>Coefficients</i>	<i>Std error</i>	<i>T-value</i>	<i>p-value</i>
EPT	324.86057	62.05114	2.599	0.000381*
Mosquito	-0.54975	0.39491	-1.215	0.194071
Tree density	-0.08582	0.05859	-1.070	0.173700
Regression	Adjusted R-squared: 0.6964, F-statistic: 10.94, df: 3 and 10 p-value: 0.001686			

Table 3: Stepwise AIC used to select the most accurate model for the number of feeding buzzes. Percent EPT, mosquito density and tree density produce the best model and prediction for the foraging activity.

Predictors	AIC score
EPT+ Mosquito density + Tree density	51.098
EPT+ Mosquito density + Tree density+ Stream width	51.265
EPT+ Mosquito density + Tree density+ Canopy cover	51.348
EPT+ Mosquito density	51.495
EPT+ Tree density	51.570
EPT+ Mosquito density + Tree density+ Understory vegetation	52.809
Mosquito density + Tree density	64.337
Selection: Feeding buzzes ~ EPT+ Mosquito density + Tree density : AIC value: 51.1	

Table 4: The multiple regression statistics for the foraging activity. The regression approaches significance, but only the percent EPT of the streams is close to being a significant predictor on its own.

	<i>Coefficients</i>	<i>Std error</i>	<i>T-value</i>	<i>p-value</i>
EPT	29.742892	6.701308	4.438	0.00126 *
Mosquito	-0.059271	0.042648	-1.390	0.19476
Tree density	-0.008647	0.006327	-1.367	0.20167
Regression	Adjusted R-squared: 0.6037 F-statistic: 7.601, df: 3 and 10, p-value: 0.006152			

Figures

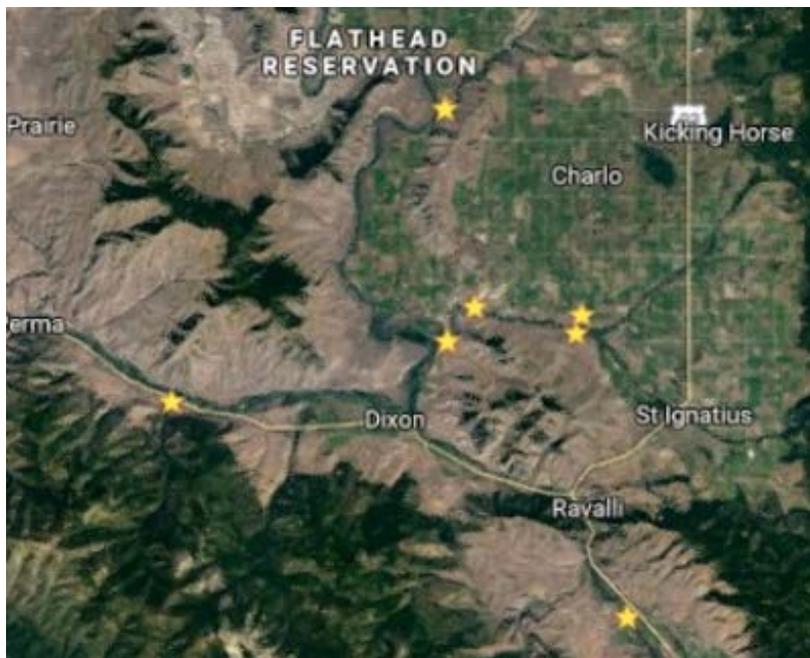


Figure 1: Map of seven stream sites on the Flathead Indian Reservation. The four sites on the National Bison range include: Pauline creek, two Mission creek sites and a small unnamed tributary to the Mission creek. The other three sites are Magpie creek, Crow creek and the Jocko River.

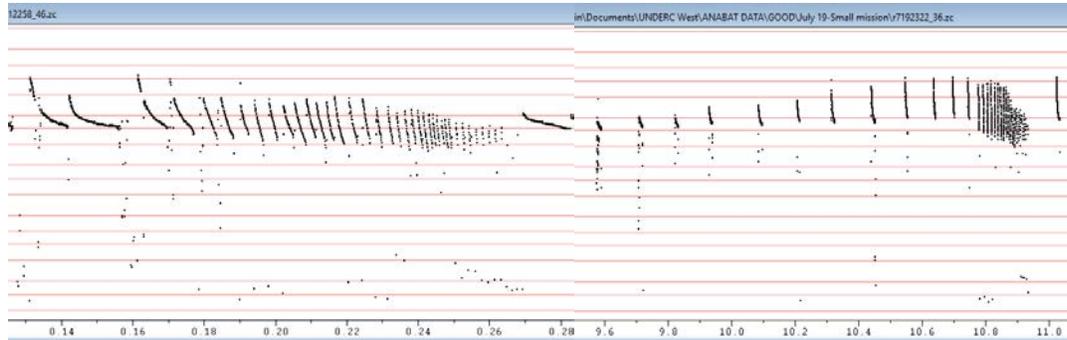


Figure 2: Two examples of clear feeding buzzes, identified by the rapid increase in frequency of pulses marking a feeding attempt. Sonograms compressed by AnaLookW for ease of viewing.

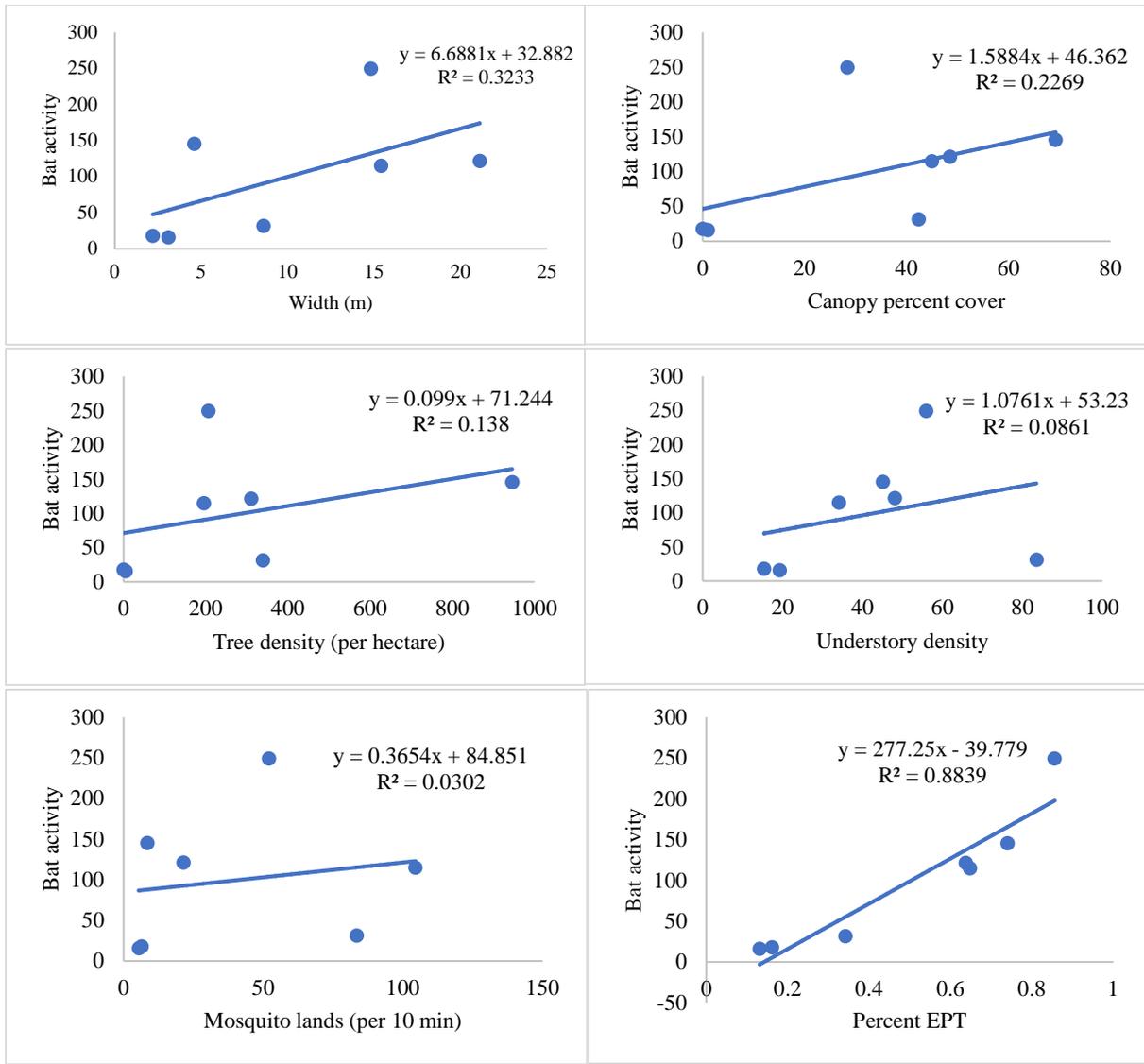


Figure 3: Relationships between the environmental variables (stream width, stream health (percent EPT), percent canopy cover, tree density, understory density, mosquito activity) and the bat activity as measured by the average number of bat passes per night in the two hour sampling period at each site. Percent EPT is the only variable with a significant relationship to bat activity.

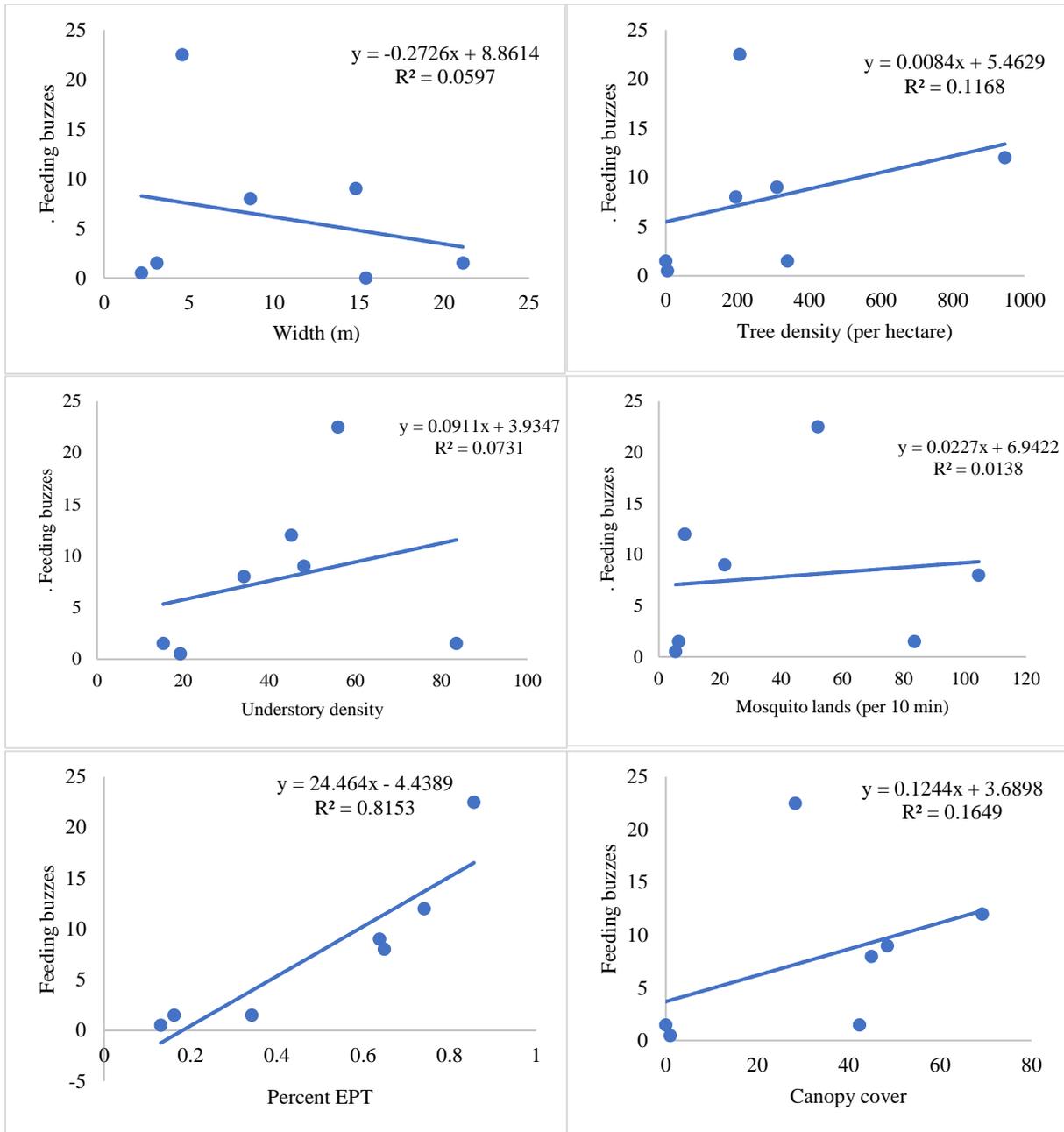


Figure 4: Relationships between the environmental variables (stream width, stream health (percent EPT), percent canopy cover, tree density, understory density, mosquito activity) and the foraging activity as measured by the average number of feeding buzzes per night in the two hour sampling period at each site. None of the variables have a significant relationship to foraging activity, but percent EPT approaches significance.

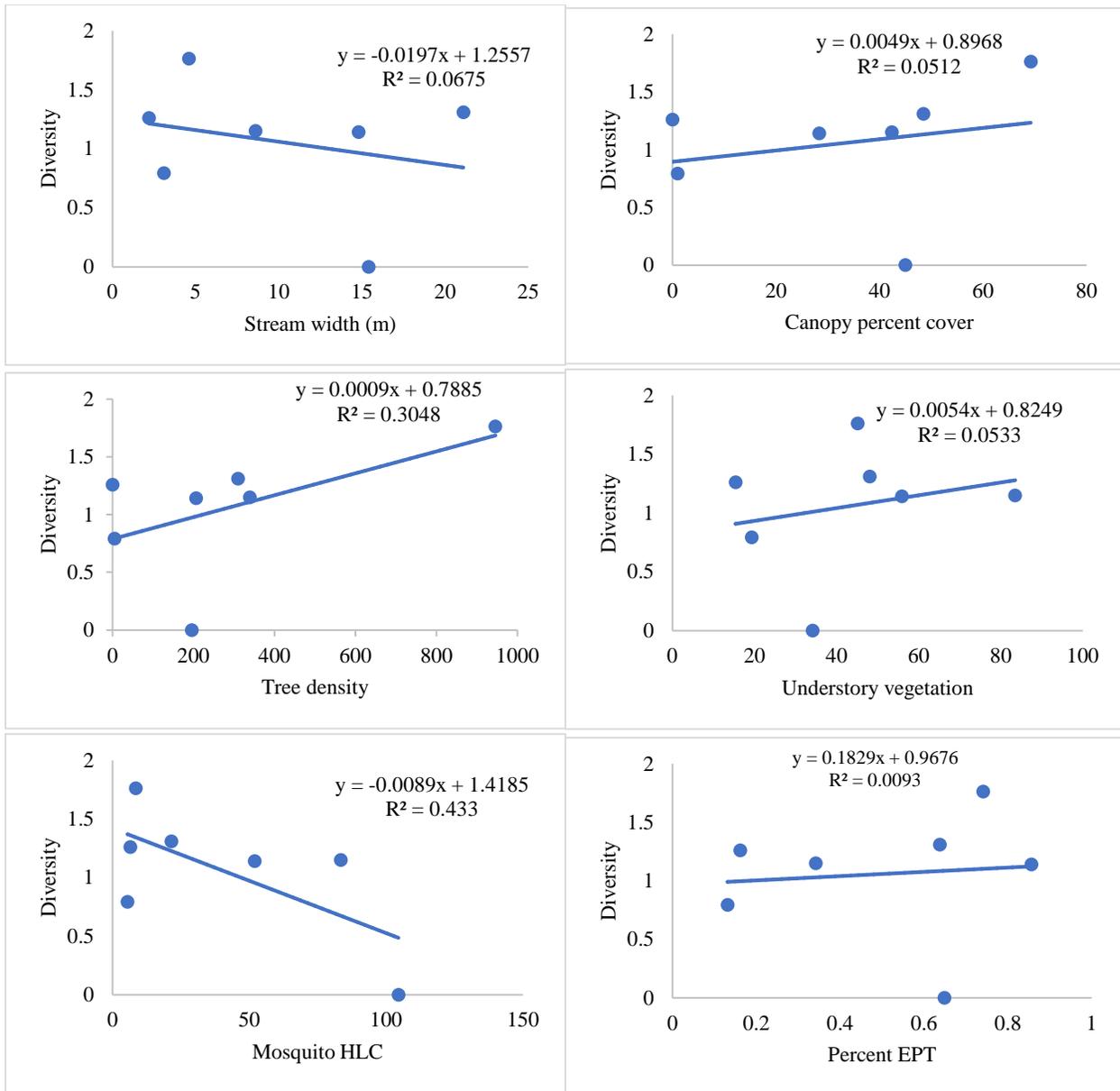


Figure 5: Relationships between the environmental variables (stream width, stream health (percent EPT), percent canopy cover, tree density, understory density, mosquito activity) and the average Shannon diversity of bat species per night in the two hour sampling period at each site.

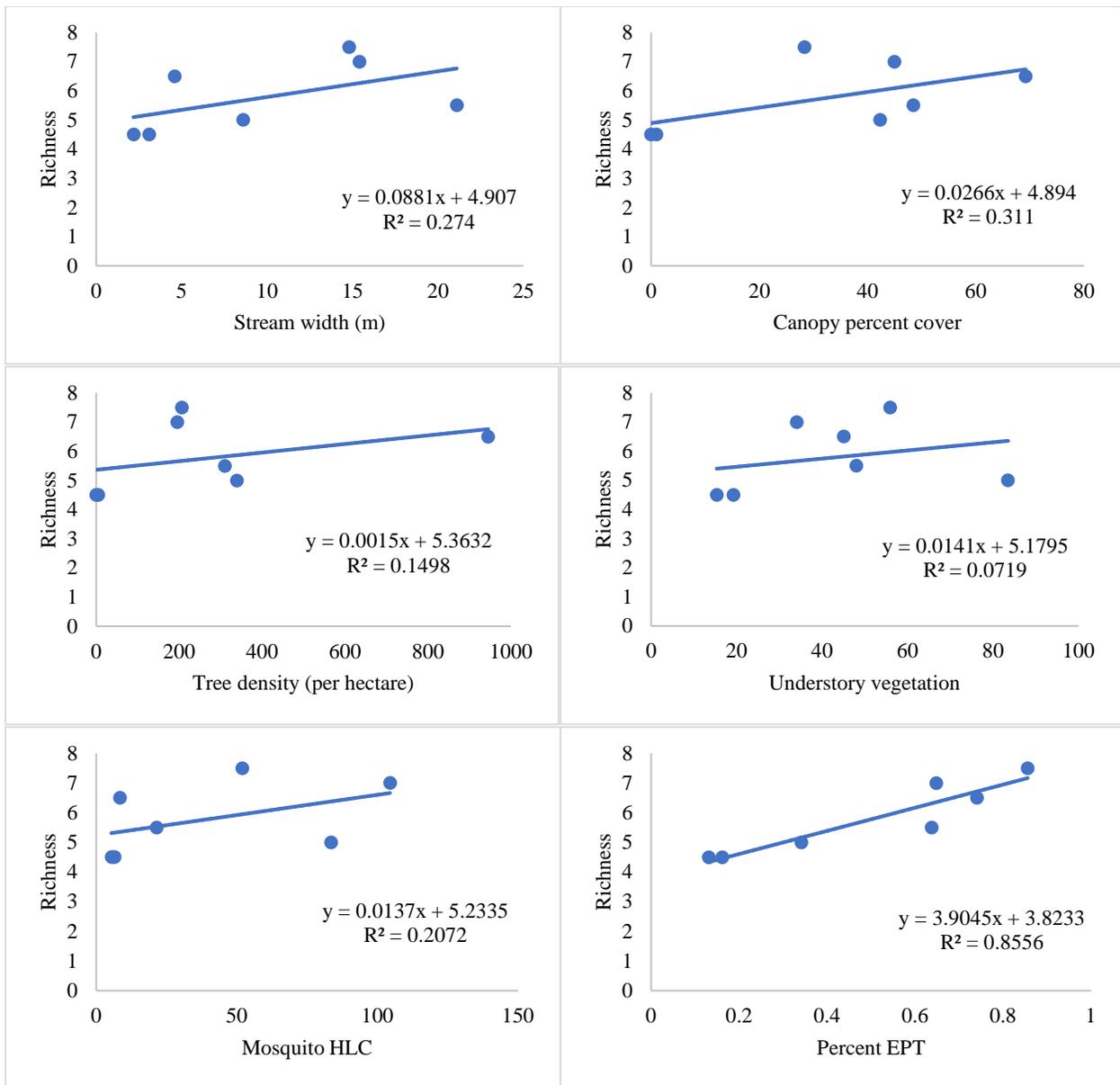


Figure 6: Relationships between the environmental variables (stream width, stream health (percent EPT), percent canopy cover, tree density, understory density, mosquito activity) and the foraging activity as measured by the average number of feeding buzzes per night in the two hour sampling period at each site.