Responses of bats and associated nocturnal food webs to bark beetle kill

2021 Lois Webster Fund Project Report, the Audubon Society of Greater Denver

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Summary

Major findings

1) Forest dwelling bats are on average using beetle killed forests more than unaffected sites.

2) Some partitioning of bat species by foraging guilds is occurring. This is especially apparent for open habitat foraging bats like big brown (*Eptesicus fuscus*), silver haired bats (*Lasionycteris noctivagans*), and hoary bats (*Lasiurus cinereus*).

3) Successional patterns following kill events appear to be driving bat activity patterns including increased volumes of coarse woody debris for forest foraging bats and decreases in basal area appear to be driving bat activity patterns for forest, edge, and open habitat foraging bats.

4) High percent beetle kill in sites with high volumes of newly fallen snags are negatively correlated with 8/9 bat species in this system. Prior age and density of the stand before the kill event may be important factors driving how bats are responding to successional changes.

Abstract

Climate change has caused increased frequency and severity of disturbance events globally, including widespread bark beetle outbreaks in North America and Europe. In North America, billions of trees across millions of acres have been killed. Bats, apex predators in many food webs, offer a top-down perspective of changing ecosystems as loss of bat species richness and abundance is known to cause increased insect abundance and herbivory in tropical and temperate forests and agricultural fields. I used a food web approach to quantify how forest stand disturbance and recovery through secondary succession following severe beetle outbreaks alters food web dynamics by measuring vegetative changes within successional stages of forest stands, collecting and identifying nocturnal insects, and deploying acoustic detectors to quantify bat richness and activity (calls/night) in Red Feather Lakes, Colorado. The results of this research revealed differences in nightly activity levels of bat species in forests undergoing succession compared to unaffected forest and meadow sites. Vegetation characteristics associated with forests recovering from a severe beetle kill event include increased coarse woody debris and decreased basal area, and analyses reveals these bottom-up effects are influencing bat activity patterns for some species. This study has helped document the impacts climate change has on bats in high elevation ecosystems and can inform management and conservation strategies for vulnerable species, including *Perimyotis subflavus* and *Corynorhinus townsendii*, found in beetle-affected high elevation forests habitats that are expected to become increasingly important refuges with climate change.

Methods

Project Location: This study was conducted in the Red Feather Lakes area Roosevelt National Forest, Larimer County, Colorado. Sites ranged in elevation from 2,650 to 2,800 meters. Habitats that were surveyed included

“Unaffected” = forest stands with < 20% overstory mortality from mountain pine beetles

“Early” = forest stands in early successional stages up to 3 years since beetle kill event

“Late” = forest stands in late successional stages (4+ years since beetle kill event

“Meadow” = meadow habitats

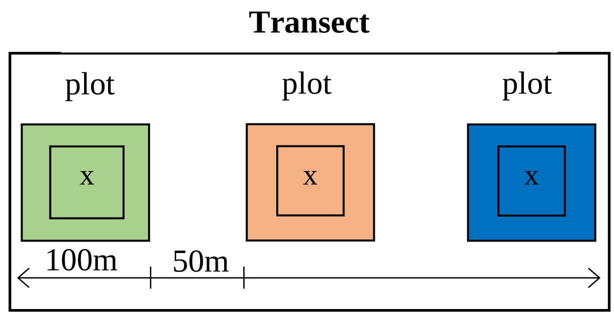

Figure 1. Each large square represents a 1-hectare plot recently affected by severe beetle kill (blue), 4+ years since (orange) severe kill, and an unaffected stand or a meadow site (green). Inlaid squares represent the detector range ($90m^2$). These habitat types were not sampled consistently following this arrangement in 2020 but will be implemented in 2021. In 2020, some transects included two sites in later successional stages or a meadow site.

Objective: The objective of this research is to quantify the effect of changes in vegetative characteristics (secondary succession) on bat activity patterns, and habitat characteristics that are indicators of secondary succession following a severe beetle kill event include several variables listed in Table 1. The primary characteristics found to explain bat activity patterns are:

a. Volume of coarse woody debris (Figures 3-5)
b. Mean basal area (Figures 6)

Timeline

June 1st to September 6th, 2021: Detectors were relocated among 4 transects throughout the sampling period and detectors were kept in rotation until average nightly temperatures remained below 40 degrees (~September 6th). 12 sites were sampled for three or four 7-night periods resulting in 315 detector nights (3 sites x 7 nights x 4 site replicates x 3.75 sessions (some transects sampled 4 times). Vegetation surveys were completed during the day and insect sampling occurred for 2 nights during the 7-night sampling period resulting in 90 insect nights (2 nights x 3 sites x 4 replicates x 3.75 sessions). All necessary permits were approved.

Sampling Design

Transect Layout:

1. Three stationary SM Mini Bat (Wildlife Acoustics) acoustic detectors placed equidistant along a 400 meter transect to record for 7 nights. Detectors were then relocated to a new transect. Four transects in total were sampled. We placed transects so that habitat types would not vary more than the 3 designated habitat types but would represent the landscape that bats in this forest were encountering (Figure 1).
2. Each detector was centered on a 1-hectare habitat type.
3. Vegetation (overstory and understory) was characterized using two 30 x 1-meter belt transects centered on the detector. Belt transects were chosen

Acoustic analysis

Bat calls were recorded using the new Song Meter Mini Bat detectors (Wildlife Acoustics) we purchased with the support from The Lois Webster Fund. Calls were identified to species using SonoBat 4.2 Software, and identification analyses used a 90% call matching threshold to identify a call to species. To determine general bat activity patters, average calls per night per species for individual sites and various successional stages were summarized in R.

Results

Habitat Data

All habitat variables I quantified in each plot have been summarized (Table 1). All variables are listed below; however, I only show some relationships that were interesting in this report.

Table 1. Variables collected to quantify vegetative characteristics that are expected to change following a severe (>50%) overstory mortality event including a bark beetle outbreak.

No.	Variable	Details	Related Figure(s)
1	Percent ground cover by type	shrub, forb, grass, sapling/seedling, moss/lichen, fine woody debris, bare ground	Figure 10
2	Average volume of coarse woody debris	Including average volumes of coarse woody debris by decay class (1-5)	Figures 4-6
3	Average height of saplings	Including by species composition	Figure 10
4	Basal area		Figures 7-9
5	Tree density	To address if several small stands crowing "aerial" space for bats (basal area may not indicate well)	Figure 10
6	Overstory height	Including species composition	Figure 10
7	Time since beetle kill	Including mean, max, and mode using USFS protocols estimating remaining color and percentage of needles and branches	Figure 10
8	Flight corridor width		Figure 10
9	Canopy cover		Figure 10
10	Primary productivity	Estimated using tree cores	

Bat Activity Patterns

Bat activity (calls/night) was relatively high across the summer, with a few nights (<5) having no recordings because of severe weather. Five species were never detected in some sites, but all species were detected in all site types (unaffected, early successional stages, late successional stages, and meadow habitats). Figure 2 provides a broad view of bat activity by successional stage from 0.5 to 3 years since killed (0.5 = recently attacked but not yet showing signs of needle loss), 4+ years since kill (by 4 years most of the needles are gone and by 5 years the major branches are gone). We included meadow sites in the 2020 study and unaffected (<20% kill) and meadow sites in 2021. A two-factor ANOVA showed significant differences in average nightly calls between site types (p= 0.00752) and a significant difference in species activity patterns between site types (p = 0.0000351).

The long-legged myotis, *Myotis volans* or "Myvo", was the most active species across all habitat types which was unexpected. Typically, little brown bats (*Myotis lucifugus/* "Mylu") are the most active species in this area. It is possible that the wet and mild start to the summer provided optimal conditions for *Myotis volans:* a species that has decreased capture rates along the Northern Front Range during drought years (Adams 2010). The fringe myotis (*Myotis thysanodes* or "Myth") is also more active than expected and this could also be tied to the mild and wet conditions in the Red Feather Lakes area throughout much of the summer (Adams and Hayes 2008).

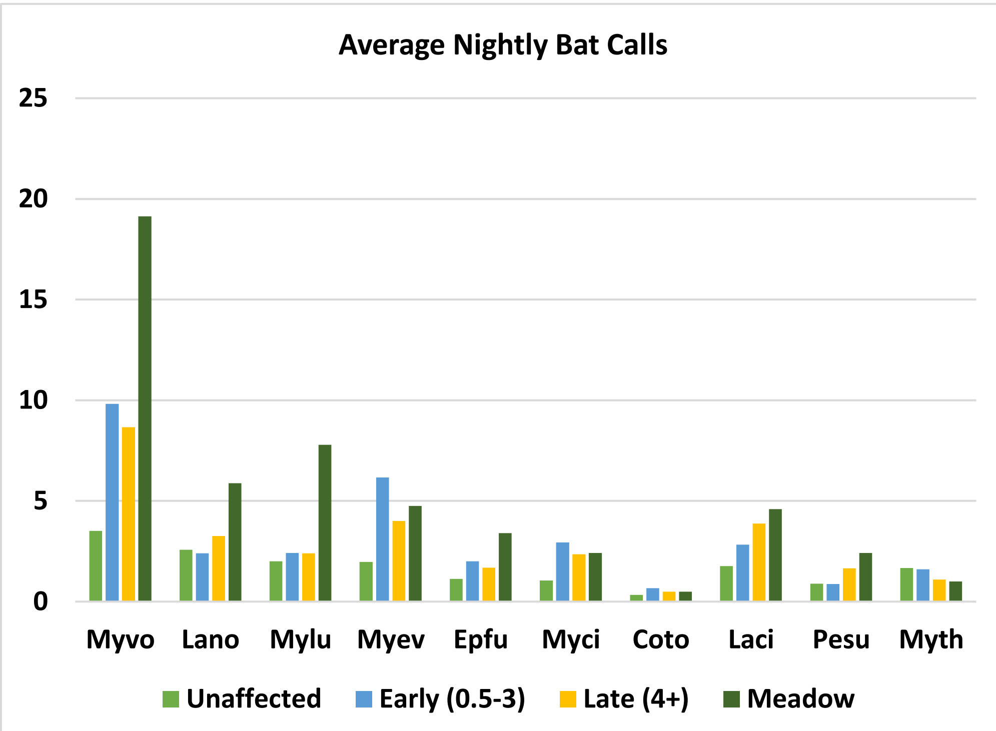

Figure 2. Average calls recorded per species per night within each habitat type.

Foraging Guilds of Bats and Average Nightly Activity

There are ten species of bats that occur in the Front Range of Northern Colorado that are segregated into foraging guilds including forest, open, edge (and generalists), and above the canopy foraging species. For this study, we consider only forest, edge, and open foraging guilds because detectors should not be detecting foraging above the forest canopy, and we are primarily interested in activity patterns under canopy height. Bats associations with each foraging guild are as follows:

Forest Foragers:

- Western long-eared myotis (*Myotis evotis*) - **MYEV**
- Townsend's big-eared bat (*Corynorhinus townsendii*) – **COTO**
- Fringe myotis (*M. thysanodes*) - **MYTH**
- Long-legged myotis (*M. volans)** – **MYVO**
  * Forages in and out of forests ~ forest edges

Edge & Generalist Foragers:

- Western Small-footed myotis (*M. ciliolabrum*) – **MYCI**
- Little brown myotis (*M.* lucifugus) – **MYLU**
- Tricolored bats (*Perimyotis subflavus*) – **PESU**

Open habitat Foragers (characterized by direct aerial pursuit):

- Silver haired bat (*Lasionycteris noctivagans*)- **LANO*** can be associated with forest edge
- Hoary bat (*Lasiurus cinereus*) - **LACI**
- Big brown bat (*Eptesicus fuscus*)- **EPFU**

In Figure 3, the species are assembled from left to right according to their foraging guild. Interestingly, the forest foraging bats do not forage more in unaffected forests than forests affected by bark beetle kill ("early" and "late" sites). These sites provide more open foraging habitat (Figures 7-9), and it is likely that insect prey availability is higher in forest sites affected by bark beetle kill. Habitat characteristics that are highly associated with insect abundance and diversity include coarse woody debris (Figures 4-6). Edge/generalist foraging bats do not seem to respond to habitat type, but further analysis will be conducted to confirm this trend. Open habitat foraging bats do show increased activity in late and meadow habitats.

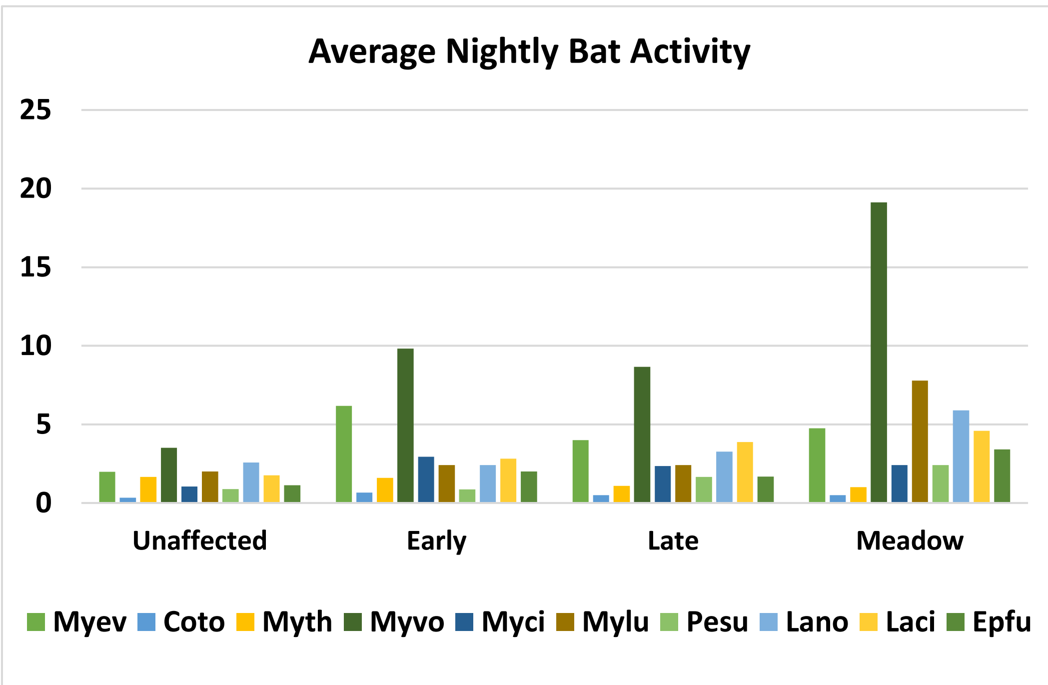

Figure 3. Meadow sites had more calls than other site types, which is unsurprising seeing that meadows tend to provide high abundance of food sources and open foraging habitats for bats restricted from foraging in more cluttered environments due to wing morphology constraints.

Coarse Woody Debris

Coarse woody debris, or large relatively undecayed logs, are an important component of the life history of many insect orders, especially so for moths, flies, and beetles. Forest-foraging bats are either gleaners (MYEV, COTO) and will pick insects off debris/vegetation or are highly maneuverable slow aerial hawkers (MYVO, MYTH) which will pursue prey within the forest canopy. Low values of coarse woody debris represent meadow and unaffected sites, moderate values represent early successional sites (0.5 – 3 years since kill), and high values represent late successional sites (4+ years since kill) (Klutsch et al. 2009).

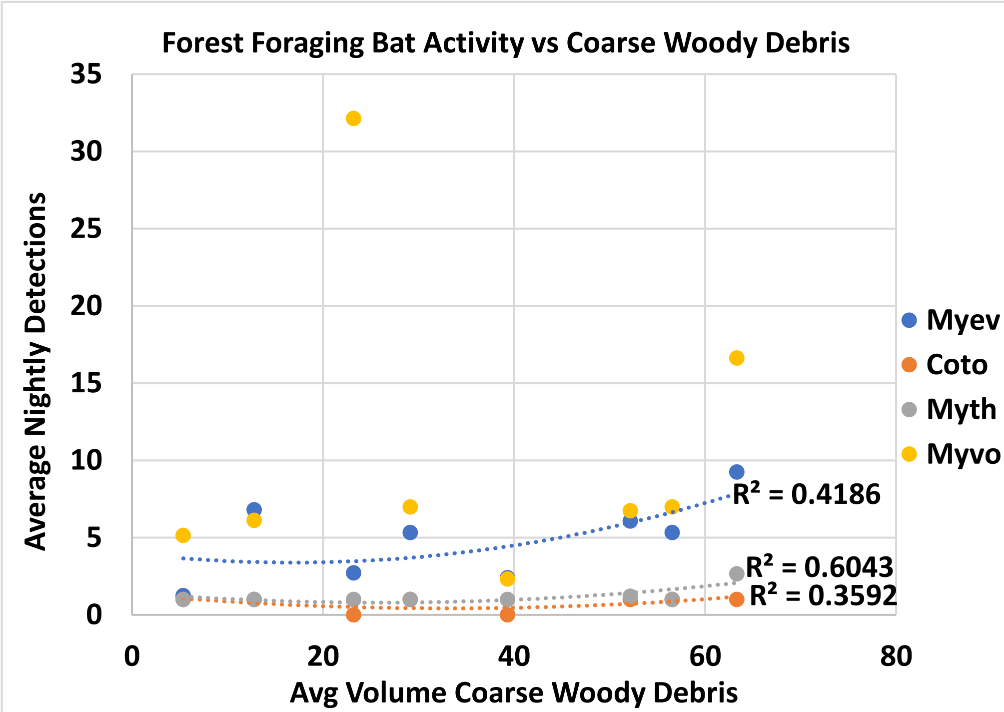

Figure 4. Fitted with polynomial trendlines and associated correlation coefficients for associations >0.30, which is typically considered ecologically relevant.

Edge and generalist foraging species are not expected to be affected by changes in successional stage but may respond to changes in prey availability associated with some vegetation characteristics tied to prey life history, such as coarse woody debris. MYCI, MYLU, and PESU all have relatively weak relationships with coarse woody debris (Figure 5; R^2 values $\leq$ 0.30). These species have a similar, albeit weaker, relationship to coarse woody debris as forest-foraging bats (Figure 4).

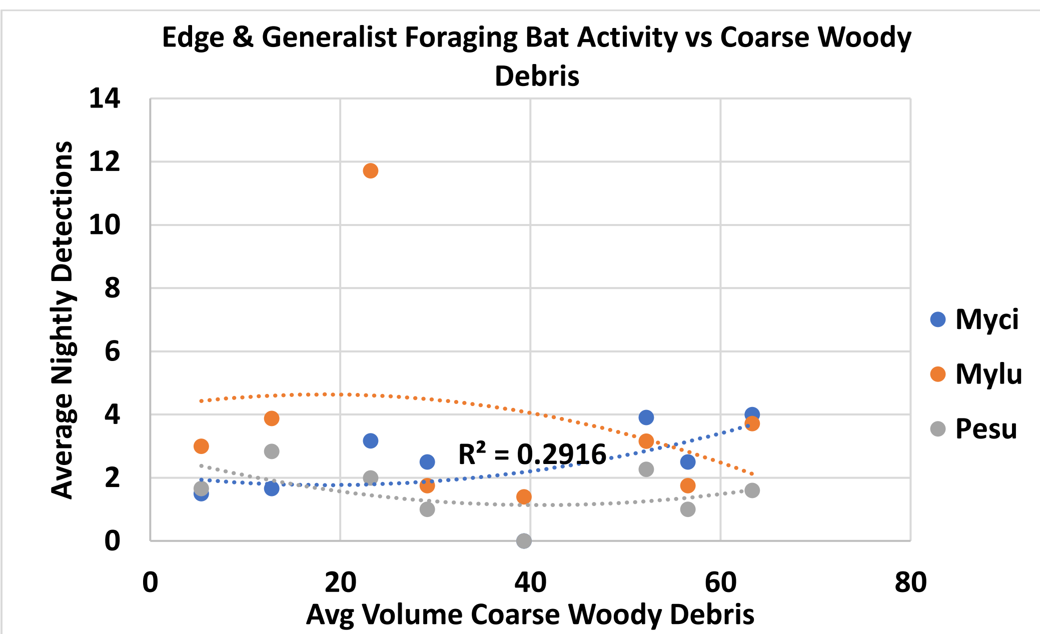

Figure 5. Fitted with polynomial trend lines. Correlations were only ~ relevant for MYCI.

Open foraging bats are typically most active in meadow sites. These species are also expected to have increased activity levels in late successional stages that have open understories with sapling regeneration at heights below 2 meters. I expected higher relative frequencies in later successional stages than were observed. Areas with high volumes of coarse woody debris may provide high prey availability but may still be too dense for these species to forage in, as they are significantly limited by their morphology from navigating cluttered spaces.

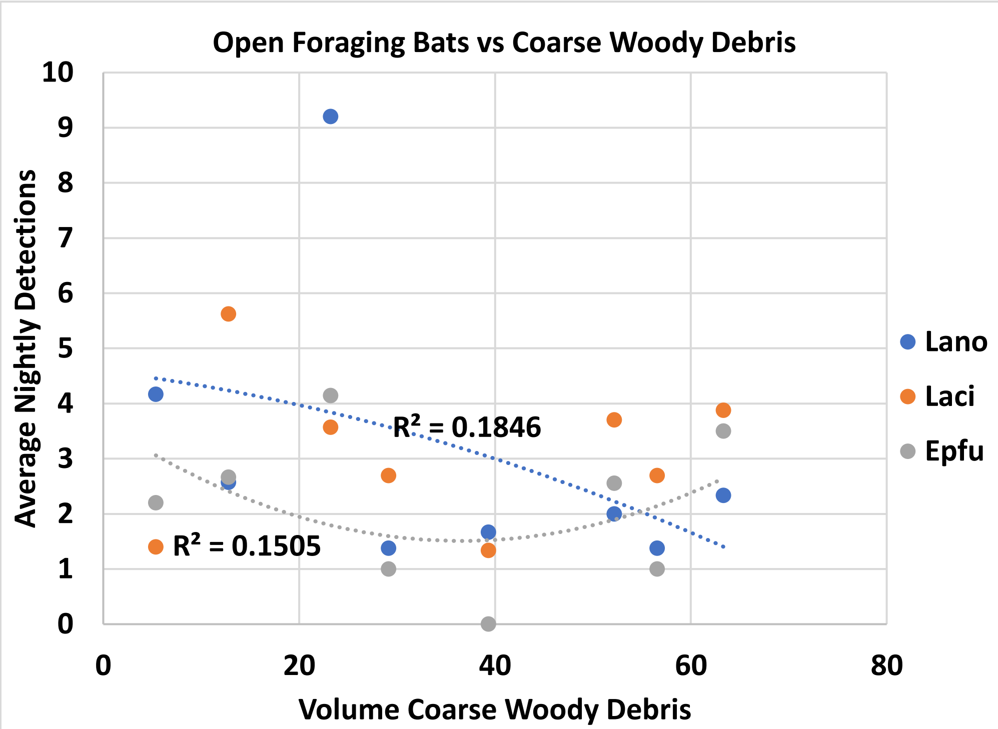

Figure 6. All open foraging bats show a weak relationship with changes in coarse woody debris (R^2). Data fitted with polynomial trends.

Basal Area

Basal area is an indicator of the overall amount of space that trees take up in a forest. With increases in basal area, I would expect that forest-foraging bats will increase in relative frequencies, edge and generalist foraging bats will have relatively little to no change, and open-foraging bats will decrease in relative frequency. Forests generally decrease in basal area once tree fall following a bark beetle kill event begins, and forests stands in later successional stages haver lower basal area than unaffected and early successional sites.

For forest foraging bats, changes in activity for MYEV and COTO are as expected, but MYVO activity decreases in denser forests that have higher basal area(Forest 7). MYVO is often considered a forest-edge specialist and as the largest Myotis, wing loading impacts maneuverability significantly in dense sites. There seems to be one data point that is driving this pattern for MYVO, and an outlier analysis will be conducted to see if removal is appropriate.

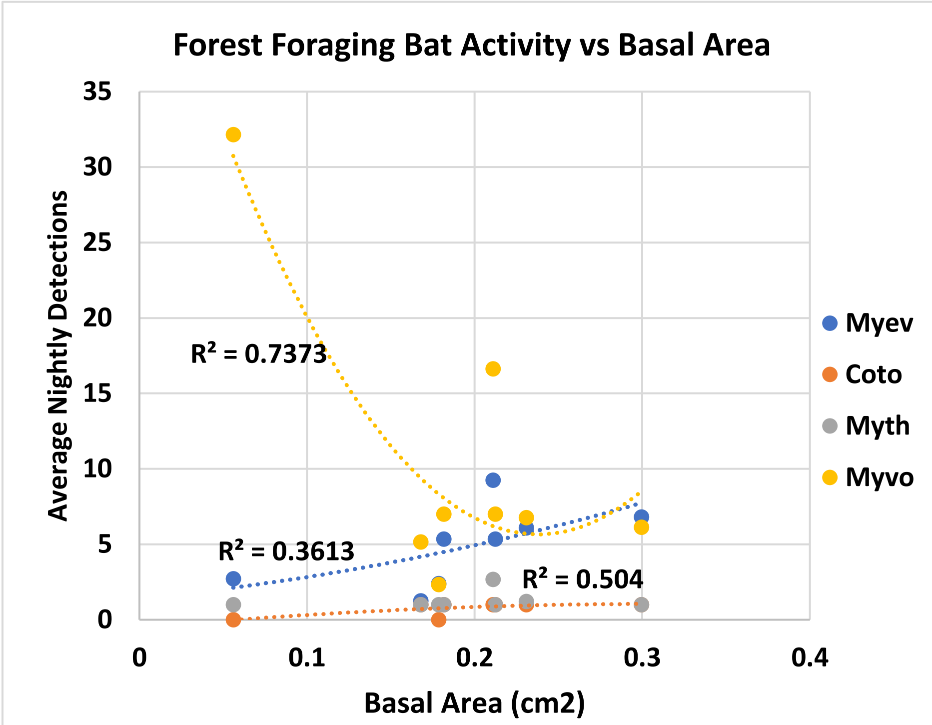

Figure 7. Low values of basal area are meadow sites and high values are unaffected stands and stands in early successional stages. Fitted with polynomial trend lines.

Edge and generalist foraging bat species, MYLU and PESU, had higher activity rates in dense forests compared to moderately dense forests. PESU was more active in dense forests than in open habitats, which might be an artifact of competition with relatively high activity rates of all bat species foraging in meadow sites (Figure 8).

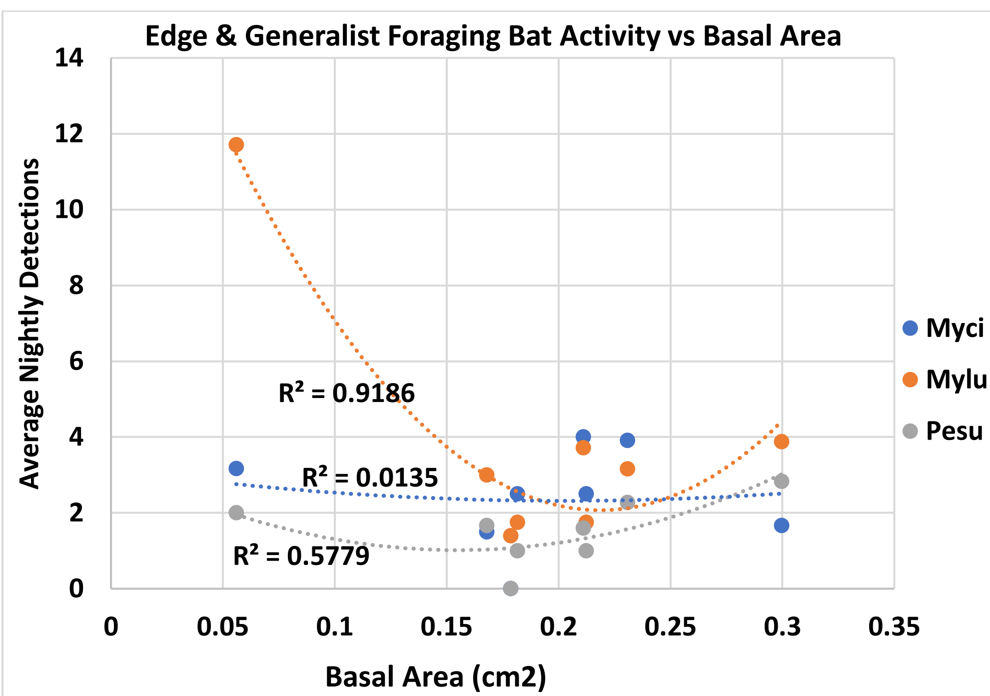

Figure 8. Little change was expected with increases in basal area and dense forests are expected to make foraging much less efficient for bats in this group. Fitted with polynomials trend lines.

Open foraging bats are expected to decrease activity with increasing basal area. This pattern holds true generally, but for LACI there is a spike at the higher range of basal area in activity patterns(Figure 8). LACI is highly associated with open habitats and consumes mostly moths and beetles. It is possible insect abundance and composition patterns might explain these patterns. LANO has slow maneuverable flight and can sometimes be associated with forests, but this species is typically found foraging in the open over woodland ponds and streams.

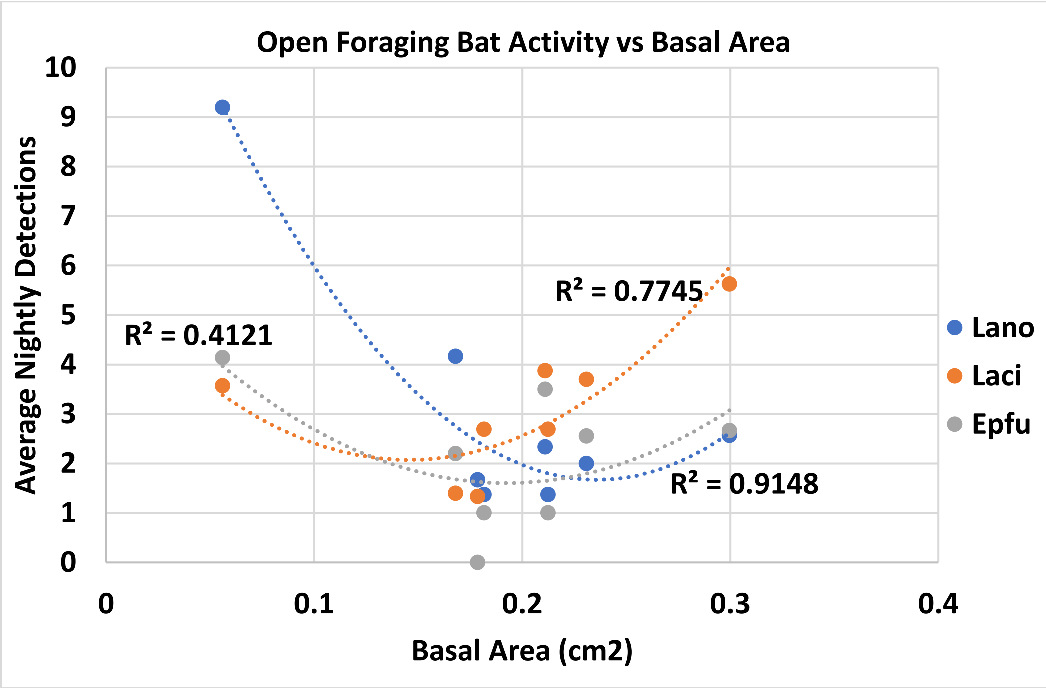

Figure 9. Open foraging bats fitted with a polynomial trend. Prey availability and composition patterns might be influencing the slight rise in activity at sites with higher basal area.

NMS Ordination

I conducted a non-metric multidimensional scaling ordination (NMS) using the average nightly detections of each species for each site (triangles). The white lines overlaid on the left most portion of the graph is a joint plot of the species responses (species codes below). The inlaid graph on the right includes all habitat features collected and described above as a joint plot (white lines) overlaid on the same ordination space. The length of the white lines from the joint plots demonstrates the magnitude of the relationship, and the orientation demonstrates the direction of the relationship with each axis.

This ordination suggests mostly open habitat foraging bat species, LACI, LANO, EPFU, and TABR (included because of a potential population), are strongly associated with habitat features associated with axis 2 including positively related to high percent cover of grasses and forbs and strongly negatively associated with basal area. All sites were associated with beetle kill, therefore these species must be responding positively to forest undergoing successional changes including canopy opening following severe beetle kill events. Nearly all species are negatively associated with axis 1, which is driven by extremely low average nightly detections in sites associated with high percent beetle kill and high volume of coarse woody debris in decay class 2 (fallen and recently beetle-killed trees). The photos below the ordination depict sites with these characteristics associated with either end of axis 1. Insect data may reveal that prey populations are suppressed for some time since recently downed trees may prohibit understory release from occurring (Photo 2). Additionally, young even aged stands that experienced high degrees of blowdown may prohibit efficient foraging for bats compared to older stands that were attacked by beetles early in the outbreak and have fallen trees that are well decayed (Photo 1).

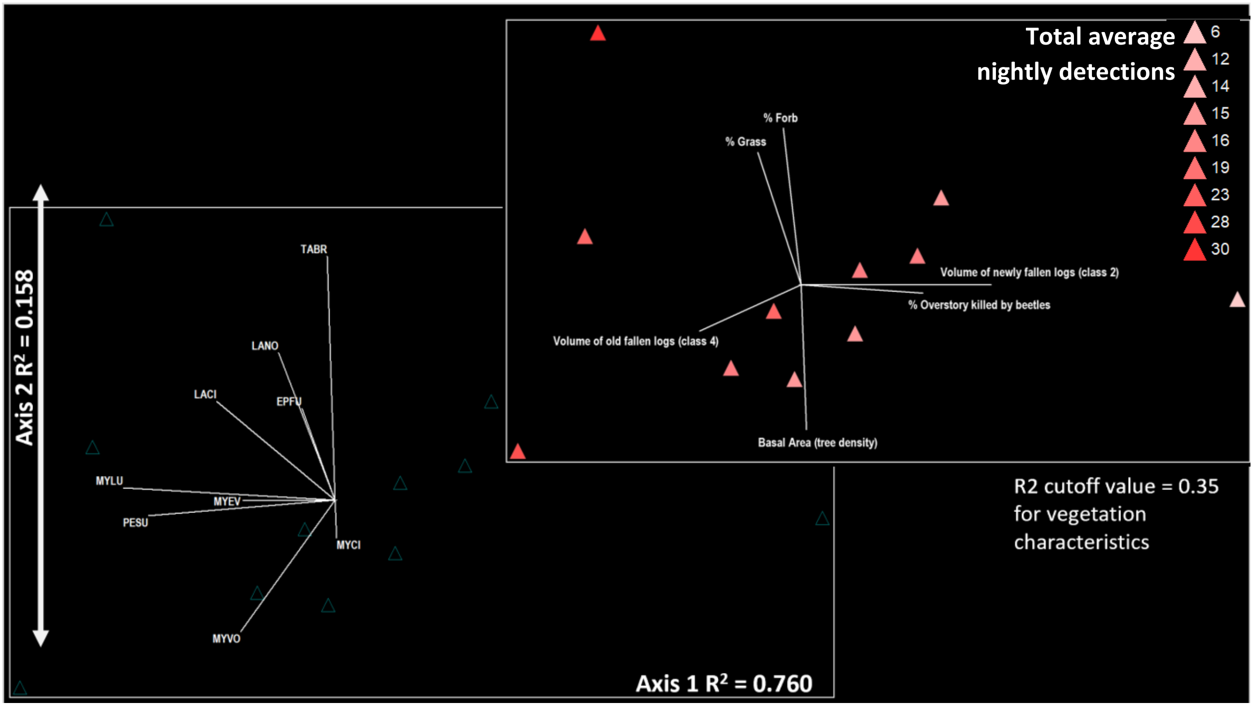

Figure 10. NMS ordination for average nightly detections of each species (lines with species codes on left, TABR = *Tadarida brasiliensis*. Upper right inlaid graph shows how moderate to strongly correlated habitat features are associated with each axis (R^2 cutoff was 0.35). The magnitude and direction of relationships is shown by the length and direction of the line. MYTH and COTO were identified as outliers (> 3 std from mean) and were removed. Foraging guilds and species codes are on page 5.

Figure 11. Photos demonstrating different successional patterns in stands following severe beetle kill depending on stand age class and structure before the kill event. **Photo 1**: Beetles impacted large diameter trees in early stages of the outbreak and moved into dense young, even-aged stands towards shown in **Photo 2** at the end of the outbreak and killed a larger portion of the overstory. Sites like this (photo on right) are susceptible to wind blow down.

Additional Considerations

The objective of this research is to use a bottom-up approach to quantify the effects of changes in vegetative structure on bat diversity and a top-down approach to quantify the effects of predation by bats on insect populations. I would expect that habitat characteristics, through bottom-up effects, would explain variation in bat relative frequencies and variation would be similarly explained within foraging guilds. Any variation not captured by habitat data might be explained by insect abundance (biomass) and composition (Kalka et al. 2008, Muller et al. 2012). For example, volume of coarse woody debris is an important component of the life history for many insect orders that are typical bat prey (moths, beetles, flies, true bugs). This could lead to greater bat activity for all species and especially for species with dietary preferences (i.e. moths specialists). Insect data, which include identification to family level of thousands of specimens, and associated research questions are not yet ready to incorporate in this report, but I will share that information in a follow up report when ready. Forest foraging bat species response patterns to coarse woody debris reveal prey availability may help to explain additional variation in this data set and will help us better understand bat responses to forests recovering from beetle kill events.

Outreach with Partners

Presentations

On January 20th, I will be giving a presentation on the findings of this research and address questions about bat conservation and management for the Wildlife Committee of the Crystal Lakes Water and Recreation Department. This is a mountain community adjacent to the field sites, and the site manager has allowed us to survey bats using mist nets and acoustic detectors on their private property.

The North American Symposium for Bat Researchers conference was cancelled due to concerns regarding Covid-19, however I will be applying to present my research this August with the Ecological Society of America.

Bat Walks

Partnering with the Colorado Bat Society, I gave a bat walk for the City of Fort Collins at Gateway Natural Area on September 16th. More than 40 participants attended ages 10-70. Another Bat Walk was planned in October for the City of Greeley, but the walk had to be cancelled due to weather.

Plans for 2022 Field Season

I plan on replicating this study again in summer 2022 and including new sites in the area. I will include varying age-classes of forest stands from before the majority of trees were killed by bark beetles to confirm my findings from the ordination analysis.

Please feel free to contact Amanda.Bevan@unco.edu for any questions or concerns you would like to discuss.

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