



Habitat Use and Foraging Ecology of Bats in Morristown National Historical Park

Effects of Invasive Vegetation



Acoustic bat detector deployed in a forest canopy gap.

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Habitat use and foraging ecology of bats in Morristown National Historical Park: Effects of invasive vegetation

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Contents

	Page
Figures.....	iv
Tables	v
Appendices.....	vi
Abstract.....	vii
Acknowledgments.....	vii
Introduction.....	1
Methods.....	4
Study Area and Survey Locations	4
Vegetation Surveys.....	5
Acoustic Surveys and Bat Echolocation Analysis	8
Arthropod Surveys.....	9
Statistical Analysis.....	11
Results.....	13
Vegetation and Arthropod Surveys.....	13
Acoustic Surveys	13
Predictors of Bat Activity	14
Discussion	16
Implications for Forest Management.....	18
Literature Cited	19

Figures

Page

Figure 1. We conducted acoustic monitoring, conventional insect trapping, and vegetation surveys in 23 survey plots (30 m in diameter) in Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020.	5
Figure 2. Survey plot from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 dominated by the invasive Japanese barberry and native mature tulip trees (RUTGERS UNIVERSITY).	6
Figure 3. Survey plot from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 with low levels of invasive vegetation (RUTGERS UNIVERSITY).	7
Figure 4. A blacklight insect bucket trap setup from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 (RUTGERS UNIVERSITY).	10
Figure 5. The percentage of a plot, average of the ground and midstory layers, occupied by non-native vegetation was significantly and positively correlated with the (a) number of midstory trees and shrubs ($\beta = 0.01 \pm 0.006$ SE) in the entire plot and (b) percentage of the ground covered by vegetation ($\beta = 0.36 \pm 0.14$ SE) in four quadrats within the plot in Morristown National Historical Park, New Jersey, USA in summer 2020 (number of plots = 23).	13
Figure 6. The percentage of a plot (average of the ground and midstory layers) occupied by non-native vegetation had a significant positive effect on the number of (a) total bat passes; (b) terminal buzzes; and (c) total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020 as revealed by model-averaging the effect sizes of predictors from top-ranked generalized linear models ($< 2 \Delta AICc$ scores from the top model).	15

Tables

	Page
Table 1. Candidate model set to test competing hypotheses about predictors of bat activity in Morristown National Historical Park during the summer of 2020.	12
Table 2. Counts of arthropods collected in blacklight traps deployed at 23 plots in Morristown National Historical Park, NJ, USA in summer 2020.....	27
Table 3. Counts of passes recorded by acoustic detectors deployed at 23 plots in Morristown National Historical Park, New Jersey, USA in summer 2020.....	28
Table 4. Top models ($< 2 \Delta AICc$ scores from top model) for total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	30
Table 5. Effect sizes for predictors in top models for total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	30
Table 6. Top models ($< 2 \Delta AICc$ scores from top model) for total passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	30
Table 7. Effect sizes for predictors in top models for total passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	30
Table 8. Top models ($< 2 \Delta AICc$ scores from top model) for terminal buzzes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	31
Table 9. Effect sizes for predictors in top models for terminal buzzes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	31
Table 10. Top models ($< 2 \Delta AICc$ scores from top model) for total high frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	31
Table 11. Effect sizes for predictors in top models for total high frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.....	31

Appendices

	Page
Appendix A. Arthropod Counts	27
Appendix B. Bat Pass Counts	28
Appendix C. Top Model Results	30

Abstract

Temperate insectivorous bats value high prey abundance and appropriate vegetative structure when selecting foraging habitats. Forests, particularly in the eastern United States, provide prime foraging habitats for bats but can be heavily impacted by non-native plants, which may alter arthropod diversity and abundance, as well as vegetative structure. To investigate associations between non-native plants and insect abundance, vegetative structure, and consequently bat activity, we performed vegetation surveys, insect trapping, and acoustic monitoring at 23 forested plots in northern New Jersey, USA. We predicted that non-native vegetation would either positively influence bat activity by increasing structural openness (thus, facilitating flight) or negatively influence bat activity by lowering the abundance of putative prey. We also hypothesized that vegetative characteristics, and therefore non-native vegetation, impact bats differently depending on their foraging habitat preferences. The percent of non-native cover of the ground and midstory vegetative layers of our study plots ranged from 0–92.92% ($\bar{x} = 46.94 \pm 5.77$ SE) and was significantly correlated with structural vegetative characteristics, such as midstory clutter ($\beta = 0.01 \pm 0.006$ SE), but not putative prey abundance ($\beta = -0.81 \pm 2.57$ SE). Generalized linear models with only vegetative characteristics best predicted overall bat activity and foraging, which were greatest in areas with a high percent non-native vegetation and low midstory clutter. Although percent non-native vegetation and midstory clutter were also significant effects for bats that prefer to forage in open areas, neither vegetative characteristics nor prey abundance were significant effects for clutter-loving bats. Such findings suggest that vegetative structure is more important than prey availability for predicting overall insectivorous bat activity, but other factors, such as foraging strategy and life history traits, can impact how bat guilds respond to non-native vegetation. Therefore, more research is required to reveal additional mechanisms by which non-native plants impact bats.

Acknowledgments

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Introduction

Non-native plants can profoundly impact ecological communities by reducing native biodiversity and altering ecosystem function (Kettenring and Adams 2011; Mack et al. 2000; Fletcher et al. 2019). By modifying the biotic (e.g., prey availability) and abiotic characteristics (e.g., structure, light availability, and soil chemistry) of a native species' habitat, non-native plants may affect individual fitness and ultimately population or species persistence (Hall et al. 1997; Asner et al. 2008; Vitousek et al. 1987). Because impacts on individual species can radiate through food webs, non-native plants can also alter the availability, distribution, and quality of resources for consumers in other trophic levels (Drake et al. 2016; Dutra et al. 2011; McCary et al. 2016). For example, non-native plants compete with and suppress the growth of native plants, altering the preexisting vegetative community (Manchester and Bullock 2000; Mangla et al. 2008). Such changes can directly and indirectly reduce the survival and reproductive success of some native herbivorous insects, which subsequently impact insectivores and their predators (Bezemer et al. 2014). By potentially reducing native biodiversity, non-native plants can also diminish the ecosystem functions that native species perform, such as pollination and tree regeneration, which may consequently alter the succession dynamics of a landscape (Collier et al. 2002; Crooks 2002; McKinney and Goodell 2010; Stewart et al. 2021).

Forests, particularly those in the eastern temperate zone, are highly susceptible to invasions of non-native plants due to such human-induced stressors as forest fragmentation and soil disturbance (Maynard-Bean and Kaye 2019; Trammell et al. 2020). Non-native shrubs typically increase understory clutter (Maynard-Bean and Kaye 2019), which could affect how forest-dwelling wildlife use the landscape. Although non-native plants in some cases have been shown to have little impact on native fauna (Silaeva et al. 2021), non-native plants often force animals to adapt or suffer negative fitness consequences (Stewart et al. 2021). Indeed, native eastern North American butterflies, birds, and snakes have been shown to alter their habitat use in response to non-native plants, often resulting in increased mortality. The West Virginia white (*Pieris virginiensis*, Edwards), an imperiled native butterfly, preferentially oviposits on non-native garlic mustard (*Alliaria petiolate*, Cavara & Grande), despite the plant being toxic to its caterpillars (Augustine and Kingsolver 2018; Davis and Cipollini 2014). Neotropical migrant birds, such as Kentucky warblers (*Geothlypis formosa*, Wilson) and hooded warblers (*Setophaga citrina*, Boddaert), will not nest in areas dominated by non-native plants (Magee and Van Clef 2016), leading to decreased reproductive success. Further, nonmigratory birds that do build nests in non-native shrubs experience higher daily mortality and nest failure due to predation than birds using native shrubs (Magee and Van Clef 2016; Borgmann and Rodewald 2004). Ectotherms also avoid non-native vegetation at multiple spatial scales, suggesting that non-native plants do not provide required habitat components (Carter et al. 2015). Consequently, non-native plants can negatively impact native fauna by increasing mortality, reducing reproductive success, and diminishing habitat quality. Thus, understanding how and to what extent non-native plants impact native fauna requires studying multiple animal taxa.

Despite the growing body of research on the effects of non-native plants on native wildlife, temperate insectivorous bats are understudied in the invasion literature (Welch and Leppanen 2017). This is

problematic because North American bats rely heavily on forested landscapes and are experiencing significant population declines resulting from multiple threats (e.g., disease, wind energy production, etc.; Arnett et al. 2016; Cheng et al. 2021). All bat species native to eastern North America are insectivorous and require forests for roosting, reproduction, and/or foraging (Brigham 2007; Harvey et al. 2011; Wunder and Carey 1996). When selecting foraging habitats in forested landscapes, bats value both high abundance of arthropod prey as well as appropriate vegetative structure. However, studies show that neither of these factors alone can reliably predict bat presence or activity (Bender et al. 2021; Froidevaux et al. 2021). Non-native plants further obfuscate these dynamics by influencing both arthropod abundance and vegetative structure (Asner et al. 2008; Bezemer et al. 2014). Although most literature suggests that non-native vegetation negatively affects habitat structure for bats by acting as clutter that obstructs flight and impedes echolocation, non-native plants often suppress native tree and shrub seedlings, creating forest structures with open midstories and canopies. Such open habitats may facilitate flight and predator avoidance (Welch and Leppanen 2017; Brigham et al. 1997), ultimately increasing their use by bats.

Because many bats, including all temperate North American species, echolocate (Hutson et al. 2001), passive acoustic monitoring has become a valuable tool for evaluating how bats are affected by factors such as non-native plants (Frick 2013; Russo and Voigt 2016). Bats produce echolocation pulses at a consistent rate to navigate and hunt (Denzinger and Schnitzler 2013; Jones and Teeling 2006), thus the number of pulses recorded can be a proxy for bat activity (Loeb et al. 2015). Moreover, when a bat detects a prey item, it deviates from its consistent echolocation pattern and produces a terminal buzz, whereby the bat directs pulses toward the target prey at an increasingly rapid rate until found and consumed (Schnitzler and Kalko 2001). Therefore, the number of terminal buzzes recorded can be a proxy for foraging activity (Drake et al. 2023). Acoustic monitoring studies have implicated low prey abundance caused by non-native plants in reduced bat activity (Welch et al. 2016). Acoustic monitoring has also revealed that non-native structural clutter impacts open space foraging bats but not clutter-loving foragers (Beason et al. 2020). Bat guilds or species may be impacted by non-native plants differently due to variations in foraging strategy, physiology, and prey preferences, which are all often correlated (Denzinger and Schnitzler 2013; Schnitzler and Kalko 2001). Insectivorous bats can be characterized into two foraging guilds based on their echolocation pulses. Species that produce low frequency pulses (~16–33 kHz) typically forage in open habitats, such as above the forest canopy or in openings and corridors. Such low frequency echolocation is ideal for long-range prey detection (Aldridge and Rautenbach 1987). Oppositely, species that forage in cluttered habitats, such as in or below the forest canopy, generally produce high frequency pulses (~34–50 kHz) that facilitate short-range object detection (Aldridge and Rautenbach 1987; Wund 2006). Thus, it is possible that non-native plants that mediate changes in overall vegetative structure, either by creating clutter or more open landscapes, may have opposite effects on bats based on their preferences in foraging habitats.

Here, we explored the relationship between non-native plants and habitat use by bats in eastern temperate forests. Using bat activity as an indicator of habitat suitability (Bellamy et al. 2013; Wordley et al. 2015), we combined acoustic monitoring, conventional insect trapping, and vegetation surveys to investigate if bat activity is correlated with plot non-native percentage, which we defined

as the average non-native cover of the ground and midstory vegetative layers. We predicted that survey plots with high non-native percentage would also have open midstories and canopies, suggesting that non-native plants positively influence bat habitat by facilitating flight. Despite increased levels of overall bat activity, however, we also predicted that plots with high non-native percentages would exhibit reduced bat foraging activity relative to plots with low non-native percentages due to lower arthropod abundance and diversity. However, we hypothesized that non-native plants would affect bats differently depending on their foraging strategy: bats that prefer to forage in open areas (produce low frequency pulses) would likely be more active in survey plots with high percent non-native, which we predicted would be more structurally open, while the opposite would be true for clutter-loving bats (produce high frequency pulses).

Methods

Study Area and Survey Locations

We conducted our study within the Morristown National Historical Park—Jockey Hollow Unit (hereafter, Jockey Hollow) in Morristown, New Jersey, USA between June and August 2020 (Figure 1). Jockey Hollow consists of 567 hectares of contiguous eastern temperate forest that is heavily influenced by past land uses (Sneddon et al. 2008). Many of the lower elevation areas in Jockey Hollow are dominated by early-to-mid successional species, such as tulip poplar (*Liriodendron tulipifera*, L.), that form an open midstory and partially open canopy. These areas often experience severe deer browse, which limits the regeneration of native vegetation and facilitates the invasion of non-native plants that deer often selectively avoid, such as multiflora rose (*Rosa multiflora*, Thunb.), Japanese barberry (*Berberis thunbergii*, DC.), and Japanese stiltgrass (*Microstegium vimineum*, A. Camus; Wagner et al. 2014). Such non-native plants form a dense thicket and are locally abundant in the shrub layer, outcompeting resident native shrubs such as northern spicebush (*Lindera benzoin*, Blume) and American witch hazel (*Hamamelis virginiana*, L.; Sneddon et al. 2008). Previous biodiversity surveys of Jockey Hollow confirmed the presence of four of the nine bat species in New Jersey, including big brown bat (*Eptesicus fuscus*, Palisot de Beauvois), eastern red bat (*Lasiurus borealis*, Müller), little brown bat (*Myotis lucifugus*, Le Conte), and northern long-eared bat (*Myotis septentrionalis*, Trouessart; Pilipski 2002).

Within the study area, we selected 23 circular plots, which we broadly classified into three habitat types: open habitats (N = 6) included locations within canopy gaps; forested habitats (N = 13) included locations with closed canopies; and stream/corridors (N = 4) included locations containing former access roads or water bodies, which are known to influence bat activity (Rogers et al. 2006; Figure 1). We delineated survey plots at a diameter of 30 m, corresponding to the presumed range of the acoustic detectors within forest habitats. We located survey plots at least 200 m apart (Ketzler et al. 2017) to ensure that acoustic detectors in adjacent plots were not sampling the same bat individuals. Because we wanted to explore the relationship between non-native vegetation and bat activity, we selected survey plots that ranged in percent non-native cover and other habitat characteristics that could influence bat locomotion and foraging, such as canopy cover, tree density, and shrub density.

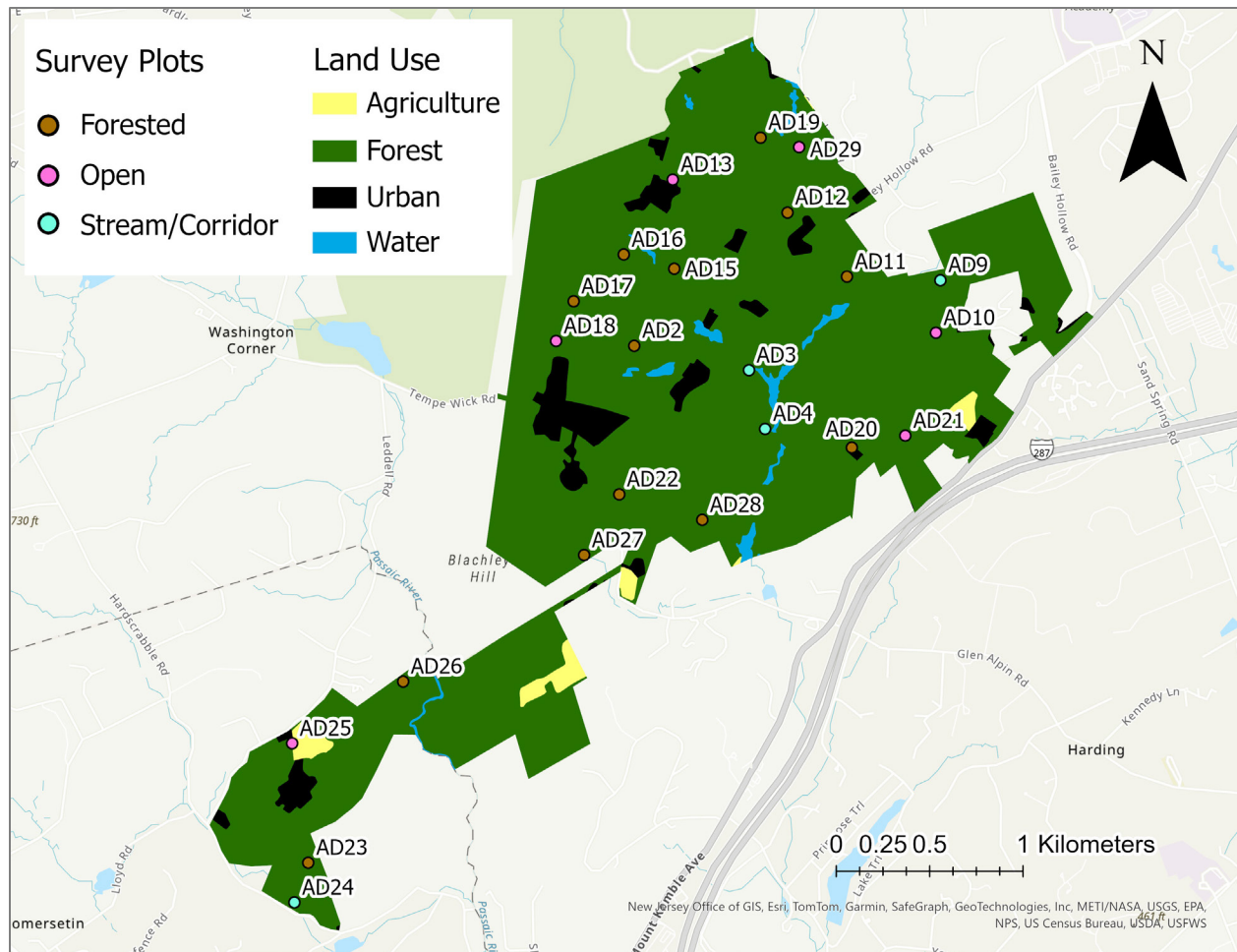


Figure 1. We conducted acoustic monitoring, conventional insect trapping, and vegetation surveys in 23 survey plots (30 m in diameter) in Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020. Brown markers indicate forested sites, pink markers indicate open sites, and blue markers indicate stream/corridor sites.

Vegetation Surveys

To determine how plant structure and nativity (i.e., native or non-native) influence bat activity, we conducted a vegetation survey at each site within a 15-m radius about the bat detector. Because structurally cluttered environments can hinder flight and reduce bat activity (Beason et al. 2020), we quantified measures of clutter at multiple vertical strata. We measured midstory clutter by counting the number of midstory trees and shrubs, defined as woody species 2–10 m in height, in the entire plot (Figure 2, Figure 3). We measured ground layer clutter by averaging the percent ground cover of four 1-m² quadrats placed 7.5 m from the detector in each of the four cardinal directions. We also documented what percentage of midstory trees and shrubs in the plot and the ground layer in the four quadrats were non-native.

To test the hypothesis that a closed canopy facilitates bat activity by reducing predation risk, we also measured canopy cover by averaging five spherical crown densiometer measurements recorded in each plot, one from the center of the plot and one from a random point in each cardinal direction.

Finally, we calculated the overall plot percent non-native to investigate a possible relationship between plant composition and bat activity. Because every site had a fully native canopy (i.e., no non-native canopy trees), we only considered the ground and midstory layers in our calculation. Therefore, we averaged the percent midstory non-native and four non-native ground cover percentages, one from each quadrat, to obtain the plot percent non-native.



Figure 2. Survey plot from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 dominated by the invasive Japanese barberry and native mature tulip trees (RUTGERS UNIVERSITY).



Figure 3. Survey plot from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 with low levels of invasive vegetation (RUTGERS UNIVERSITY).

Acoustic Surveys and Bat Echolocation Analysis

From June–August 2020, we monitored survey plots for bats following the North American Bat (NABat) Monitoring Program protocols for stationary acoustic monitoring (Loeb et al. 2015). At the center of each survey plot, we placed a Pettersson D500X (Pettersson Elektronik AB, Sweden) acoustic detector equipped with a full-spectrum omni-directional ultrasonic microphone. We mounted the microphone approximately 3 m off the ground and angled it approximately 45° upward into the airspace (Drake et al. 2023). At each survey plot, we recorded bat echolocation pulses for two consecutive nights that were forecasted to have little to no precipitation and wind speeds below 10 km/hr (Drake et al. 2023). Detectors were active from 30 minutes before sunset to 30 minutes after sunrise with a 500-kHz sampling frequency and medium trigger sensitivity to reduce nontarget noise recordings. Once triggered, detectors recorded for three seconds and stored recordings as .WAV files. Because we assumed that each recording was a succession of pulses, or a pass, produced by one individual as it flew near the detector, we quantified general bat activity and foraging activity by counting the total number of recorded passes and terminal buzzes respectively from a survey location over the two-night monitoring period.

We analyzed all recordings using the SonoBat 4.4.5 software and the northeastern North America regional library (Szewczak and Szewczak 2017). We first used the file-scrubbing function in SonoBat to eliminate recordings that did not meet the default medium quality threshold. We then programmed the Batch Classification in SonoBat according to NABat guidelines to classify the remaining recordings that surpassed the acceptable quality threshold of 0.80. After this filtering process, recordings that were below the automatic classification threshold of 0.90, and therefore unidentifiable to species level, were labeled as high frequency or low frequency unknown in SonoBat. Recordings that surpassed the automatic classification threshold of 0.90 and contained at most 16 consecutive echolocation pulses were then automatically classified by SonoBat as one of the nine bat species found in New Jersey. Three bat species in New Jersey produce low frequency pulses, including big brown bat, hoary bat (*Lasiurus cinereus*, Palisot de Beauvois), and silver-haired bat (*Lasiurus noctivagans*, Le Conte; Szewczak et al. 2017). We summed the passes produced by these bats and the low frequency unknown classification to calculate the total number of low frequency passes. Six species in New Jersey produce high frequency pulses, including little brown bat, Indiana bat, eastern red bat, northern long-eared bat, evening bat (*Nycticeius humeralis*, Rafinesque), and tricolored bat (*Perimyotis subflavus*, Cuvier). We summed the passes produced by these bats and the high frequency unknown classifications to calculate the total number of high frequency passes.

We used the sonogram viewing window in SonoBat to manually verify automatic classifications and to detect terminal buzzes. To minimize false-positive detections, we manually vetted every pass and corrected erroneous automatic classifications made by SonoBat. Because of their often indistinguishable pulse characteristics, we combined little brown bat (*Myotis Lucifugus*) and Indiana bat (*Myotis SODalis*, Miller & Allen) classifications into a single LUSO category, which we subsequently treated as a single sonotype (Drake et al 2023; Szewczak and Harris 2013). A terminal buzz can be heard as a distinct pitch change when played at one-tenth speed and visualized as a short burst of accelerating pulses in the sonogram viewing window (Drake et al. 2023). Although terminal buzzes can be identified using the sonograms produced by SonoBat, they often cannot be reliably

classified to species because they are accompanied by changes in typical pulse characteristics. Accordingly, we manually classified all files containing a terminal buzz as either low or high frequency unknown.

Arthropod Surveys

Concurrent with each acoustic survey, we deployed a blacklight insect bucket trap (Leptraps, LLC, Georgetown, KY) within 10 m of each survey plot (Figure 4). This distance is sufficiently close to the survey plot as to appropriately characterize the arthropod community without influencing bat activity (Dodd et al. 2012; Froidevaux et al. 2018). Traps consisted of 15-W T8 blacklight bulbs (PestWest, Sarasota, FL), drawing arthropods into a catch bucket lined with Vaportape II insecticidal strips (Hercon, Emigsville, PA) raised ~0.3 m above the ground. On the morning immediately following each two-day bat survey, we transferred the contents of the trap into an airtight plastic bag and stored them in a freezer at -20 °C until processing. We then soaked all arthropods in 95% ethanol before counting and sorting them to order. We calculated the Shannon diversity index of all arthropod orders at each site using the vegan package in R (Oksanen et al. 2022). We also calculated the order richness of all arthropods at each site. We calculated the abundance of potential arthropod prey at each site by taking the sum of the orders typically eaten by insectivorous bats in New Jersey: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Trichoptera (Maslo et al. 2022).



Figure 4. A blacklight insect bucket trap setup from Morristown National Historical Park—Jockey Hollow Unit, New Jersey, USA in summer 2020 (RUTGERS UNIVERSITY).

Statistical Analysis

We performed all statistical analyses using R v3.3.0+ (R Core Team 2022). We manipulated data using the dplyr package (Wickham et al. 2023) and created plots using the ggplot2 package (Wickham 2016). To ensure that all measured variables exerted similar influences on the models, we scaled and centered all predictor variables to have a mean of 0 and a standard deviation of 1. To obtain standard error values, we calculated bootstrapped means using 1,000 replicates in the boot package (Canty and Ripley 2016). To test the hypothesis that non-native plants affect arthropod prey, we performed linear mixed effects models (LMERs) in the lme4 package (Bates et al. 2014) using non-native vegetation percentage as the predictor and either prey abundance or total arthropod order diversity as the response. We included month as a random effect to account for potential declines in arthropod abundance and diversity as the year progresses from spring to fall (Wang et al. 2023). We also conducted a generalized linear model (GLM) in the stats package (R Core Team 2022) using percent non-native as the predictor and total arthropod order richness as the response. We used ANOVA in the stats package to confirm that prey abundance and total arthropod order diversity differed significantly with survey month (June, July, August).

To elucidate the relationships between non-native plants and habitat structure, we performed LMERs using non-native percentage as the predictor and either canopy cover or ground cover as the response. We included habitat type as a random effect to account for differing vegetative communities and structures in open, forested, and stream/corridor habitats. We also conducted a GLM using a quasipoisson family to determine if percent non-native was correlated with midstory clutter. We used percent non-native as the predictor, and midstory trees and shrubs as the response for this GLM.

We performed GLMs in the MASS package (Venables and Ripley 2013) using a negative binomial family to determine the relative effects of vegetative structure, vegetative nativity, and prey availability on bat activity and foraging. We generated fifteen candidate models to test biologically relevant hypotheses about bat behavior (Table 1). To determine which predictors were most strongly associated with bat activity, we used the MuMIn package (Barton 2022) to conditionally average all candidate models within 2 ΔAICc scores of the top model (Burnham and Anderson 2002). This yielded model-averaged coefficients for each of the top predictors, calculated by averaging over the models where the predictor appeared, which we then compared to assess their magnitude and direction on bat activity. To determine the relative effects of the predictors on bats that use differing foraging strategies, we performed two GLMs as described above, one for total low frequency bat passes and one for total high frequency bat passes. We again averaged all candidate models within 2 ΔAICc of the top model.

Table 1. Candidate model set to test competing hypotheses about predictors of bat activity in Morristown National Historical Park during the summer of 2020.

Bat activity depends on:	Predictors *				
	Canopy Cover	Midstory Trees and Shrubs	Ground Cover	Percent Non-native	Prey Abundance
All predictors (global model)	X	X	X	X	X
Habitat structure and composition	X	X	X	X	–
Habitat structure	X	X	X	–	–
Flight clearance (impacted by non-native plants) and predator avoidance	X	X	–	X	–
Flight clearance, prey availability, and predator avoidance	X	X	–	–	X
Flight clearance and predator avoidance	X	X	–	–	–
Midstory structure	–	X	–	X	–
Ground structure	–	–	X	X	–
Prey availability (impacted by non-native plants)	–	–	–	X	X
Canopy structure	X	–	–	–	–
Flight clearance (directed by midstory clutter)	–	X	–	–	–
Ground cover	–	–	X	–	–
Non-native percentage	–	–	–	X	–
Prey availability	–	–	–	–	X
No predictors (null model)	–	–	–	–	–

* An “X” indicates that a predictor was used for modeling that bat activity metric, and an endash (–) indicates that it was not.

Results

Vegetation and Arthropod Surveys

The percent of non-native vegetation in each plot ranged from 0–92.9% ($\bar{x} = 46.94 \pm 5.77$ SE) and had a significant positive relationship with both midstory trees and shrubs ($\beta = 0.01 \pm 0.006$ SE) and ground cover ($\beta = 0.36 \pm 0.14$ SE; Figure 5).

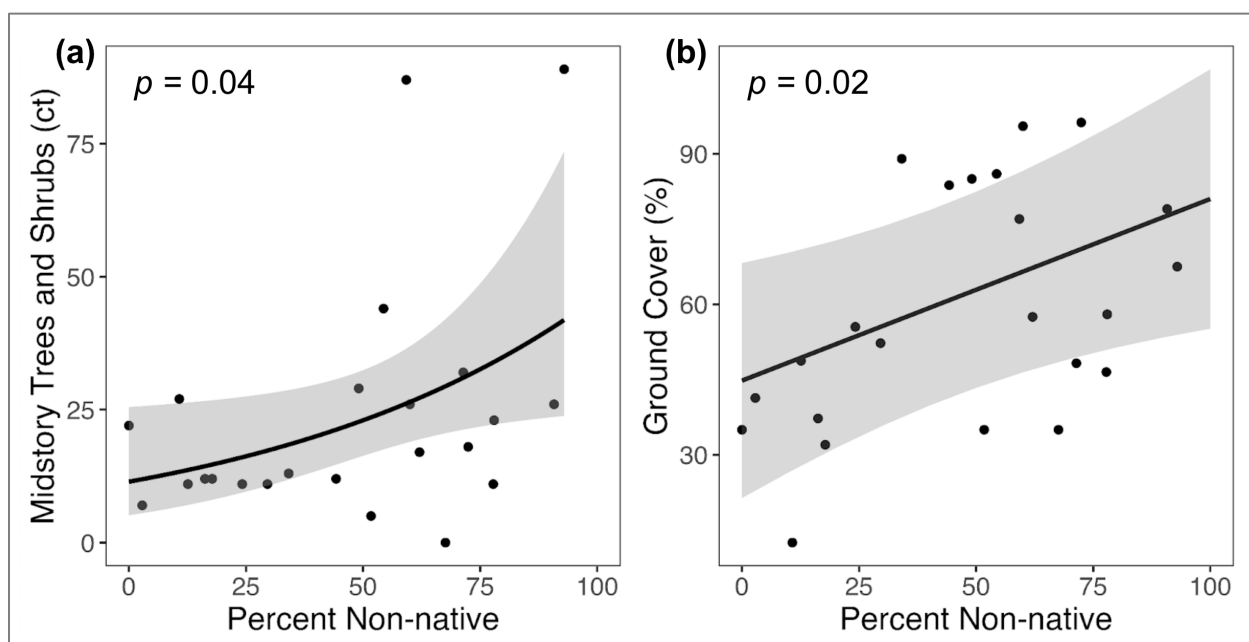


Figure 5. The percentage of a plot, average of the ground and midstory layers, occupied by non-native vegetation was significantly and positively correlated with the (a) number of midstory trees and shrubs ($\beta = 0.01 \pm 0.006$ SE) in the entire plot and (b) percentage of the ground covered by vegetation ($\beta = 0.36 \pm 0.14$ SE) in four quadrats within the plot in Morristown National Historical Park, New Jersey, USA in summer 2020 (number of plots = 23). Points depict the original data, solid lines depict the fitted model, and shaded areas depict 95% confidence intervals.

Of the 20,474 total arthropods captured, we considered 19,825 (96.8%) to be potential prey for insectivorous bats (Appendix A). Putative prey abundance varied across survey plots, ranging between 96–1,462 individuals ($\bar{x} = 861 \pm 85.5$ SE). The arthropod community was dominated by lepidopterans ($N = 8,399$), coleopterans ($N = 4,496$), and trichopterans ($N = 4,318$), but hemipterans ($N = 734$) and hymenopterans ($N = 615$) were also well-represented at our plots. Coleopterans, dipterans, hymenopterans, and lepidopterans occurred at every survey location. Prey abundance ($\beta = -0.81 \pm 2.57$ SE), total arthropod order diversity ($\beta = -0.001 \pm 0.001$ SE), and total arthropod order richness ($\beta = -0.001 \pm 0.001$ SE) were not significantly correlated with non-native percentage.

Acoustic Surveys

Over 46 recording nights, we collected 3,614 usable bat passes, 303 of which contained terminal buzzes (Appendix B). Bat activity and foraging varied widely by survey plot, ranging from 5–684 total passes ($\bar{x} = 157 \pm 34.28$ SE) and 0–80 terminal buzzes ($\bar{x} = 13 \pm 3.75$ SE) recorded over the

two-night monitoring period. Because we treated LUSO as a single sonotype, we recorded all “eight” bat species found in New Jersey. Big brown bats were recorded most frequently (51.7%), followed by low frequency unknowns (18.2%) and hoary bats (11.4%). We recorded 3,074 total low frequency passes (85.0%) and 540 total high frequency passes (14.9%). We recorded only three northern long-eared bat passes and two tricolored bat passes, which both produce high-frequency pulses.

Predictors of Bat Activity

The top models for total bat passes and terminal buzzes were midstory structure (number of midstory trees and shrubs and percent non-native) and non-native percentage, respectively. Percent non-native had a significant positive effect on both total passes ($\beta = 0.92 \pm 0.38$ SE; Figure 6a) and terminal buzzes ($\beta = 1.57 \pm 0.46$ SE; Figure 6b). Midstory trees and shrubs had a significant negative effect on total passes ($\beta = -0.58 \pm 0.27$ SE), but not terminal buzzes ($\beta = -0.37 \pm 0.34$ SE). Although canopy cover was a covariate in two of the top-ranked models for total passes, it was not a significant predictor. Prey abundance and ground cover were not included in any top-ranked models and were therefore not significant predictors of overall bat activity or foraging.

The trends for low frequency passes were nearly identical to those for total passes. The top model for total low frequency passes included number of midstory trees and shrubs ($\beta = -0.64 \pm 0.29$ SE) and non-native percentage ($\beta = 1.12 \pm 0.41$ SE), which both had a significant effect on low frequency passes (Figure 6c). There were no significant predictors of total high frequency bat passes (Figure 6d). Detailed GLM results are in Appendix C.

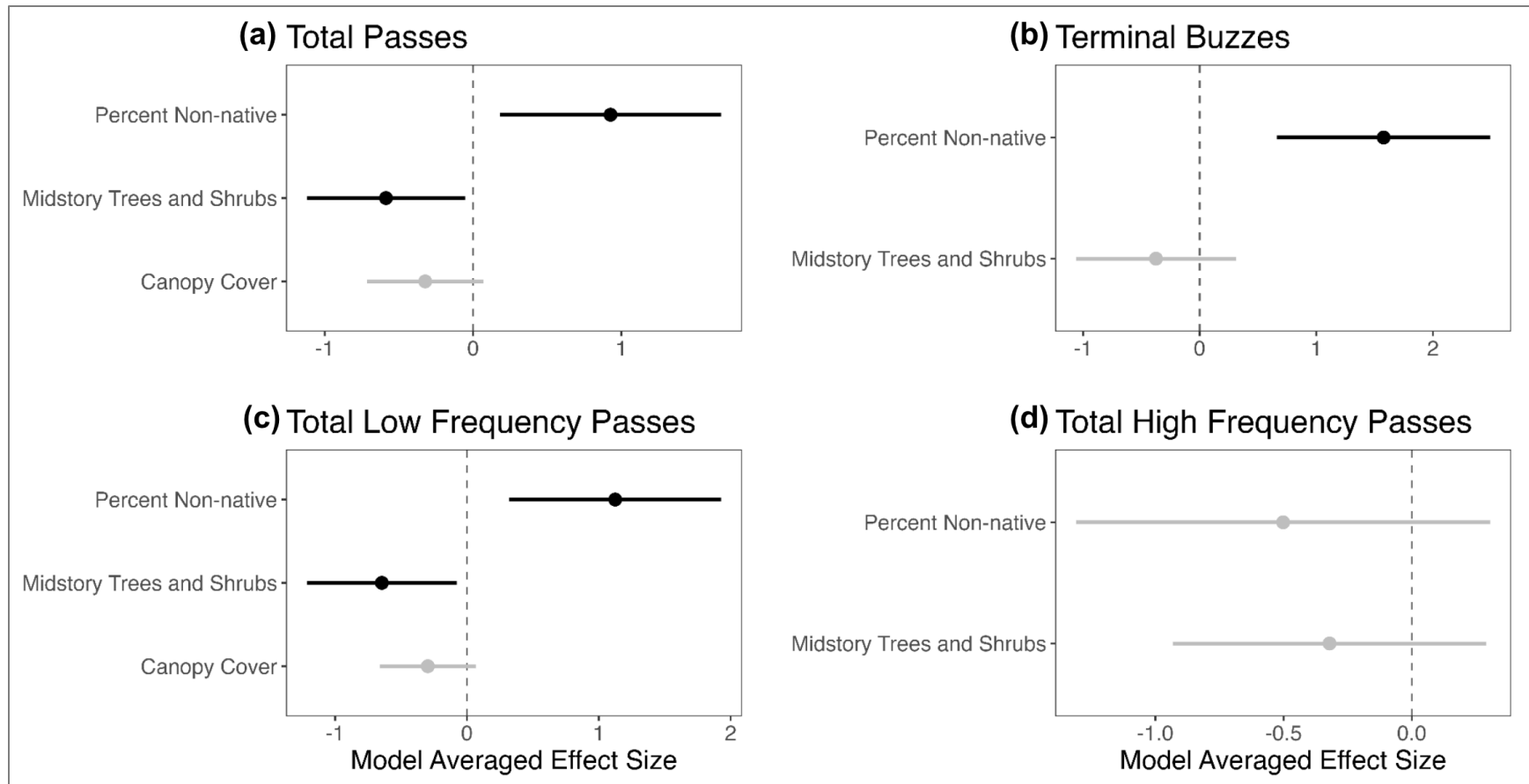


Figure 6. The percentage of a plot (average of the ground and midstory layers) occupied by non-native vegetation had a significant positive effect on the number of (a) total bat passes; (b) terminal buzzes; and (c) total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020 as revealed by model-averaging the effect sizes of predictors from top-ranked generalized linear models ($< 2 \Delta AICc$ scores from the top model). No measured predictor had a significant effect on (d) total high frequency passes. Lines depict 95% confidence intervals. Black points and black lines indicate significant effects (model averaged effect size does not cross 0).

Discussion

Overall, our research suggests that non-native vegetation does not have a completely negative impact on forest habitat use by bats. This conclusion is driven by two important findings. First, the percentage of non-native vegetation at a plot had the largest and most positive effect on both total passes, a proxy for overall bat activity, as well as terminal buzzes, a proxy for foraging activity, indicating that bats were more active in plots with higher percentages of non-native plants. Second, non-native percentage was not significantly correlated with putative prey abundance, which itself did not have a significant effect on overall bat activity or foraging activity. Together, such results suggest that bats value habitat structure more than prey availability when using foraging habitats and that non-native plants may benefit bats by creating habitat structures more conducive for foraging.

Contrary to our predictions and the findings of previous studies (Olckers and Hulley 1991; Samways et al. 1996), putative prey abundance and total arthropod order diversity and richness were not correlated with plot percent non-native. This could suggest that either non-native plants altered arthropod species composition without changing diversity and richness, or that arthropod communities were similar amongst all plots regardless of percent non-native. The former could occur if a diverse and species-rich community of non-native arthropods replaced the pre-existing native community. It is well documented that non-native plants can be toxic to and reduce the abundance of native arthropod species (Bezemer et al. 2014; Sunny et al. 2015). Because most herbivorous insects are specialists that have coevolved with one or a few plant lineages, native arthropods are likely unequipped to combat the chemical and physical defenses of non-native plants (Bernays and Graham 1988; Tallamy 2004). Therefore, non-native insects, especially those that have coevolved with a specific non-native plant, may fill niches opened by the loss of native insects, leading to no net reductions in overall arthropod abundance.

Alternatively, it is possible that the introduction of non-native plants to our study area had little to no effect on the pre-existing arthropod community. Some native insects demonstrate plasticity in host plant preference and could prefer to use non-native vegetation (Fielding and Conn 2011; Parker and Hay 2005). Non-native plants can also be highly suitable for native insects and actually increase arthropod fitness (Harvey et al. 2010). In such cases, native insect abundance could even increase post-invasion, although this was not detected in our study. In addition, many plants introduced to North America are closely related to native species (e.g., the non-native *Lonicera japonica* is a congener of *L. sempervirens*, L., an eastern North American native), increasing the likelihood that an herbivore that specializes on a native plant can exploit a closely related plant that produces similar chemical compounds (Tallamy 2004). We did not classify arthropods to species; therefore, the mechanisms driving our results are not known.

A non-significant change in arthropod abundance, regardless of the insect community composition, logically results in few impacts to bat use of forest habitats. First, North American bats are generalist insectivores, feeding on a wide array of arthropods (Maslo et al. 2022; Clare et al. 2009), suggesting that bats can tolerate small changes in arthropod availability. Thus, changes in insect diversity are likely inconsequential to bats, so long as there are ample numbers of prey items to make foraging

activities beneficial. Furthermore, bats may not discriminate between native and non-native insects. Indeed, bats have been shown to consistently consume such non-native insects as brown-marmorated stink bugs (*Halyomorpha halys*, Stål; Maslo et al. 2017), spotted lanternflies (*Lycorma delicatula*, White; McHale et al., unpublished data), and emerald ash borers (*Agrilus planipennis*, Waterhouse; Münzer et al. 2016). Thus, bats may cope with decreased abundances of native prey by consuming non-native species, which often occur in high abundances (Brockerhoff and Liebhold 2017; Murman et al. 2020). It is important to note that we caught arthropods in every survey plot, indicating that even plots with the lowest recorded arthropod abundances may have had ample prey to sustain bat foraging.

We found that percent of non-native vegetation was also significantly and positively correlated with ground cover and the number of midstory trees and shrubs, but not correlated with canopy cover. Such findings suggest that non-native plants may proliferate in and alter the vegetative structure of the ground and midstory layers. Because North American insectivorous bats primarily use the midstory and canopy strata of forests, changes in ground-level structure likely have few direct impacts on bat activity. On the other hand, the increased number of midstory trees and shrubs, and therefore midstory clutter, associated with a higher degree of vegetative invasion could impact bat maneuverability and foraging.

In addition to percent non-native, the number of midstory trees and shrubs also had a significant, albeit negative, effect on overall bat activity. Such results indicate that bats were more active in plots with higher percent non-native and lower midstory clutter, which is interesting given our finding that percent non-native was positively associated with midstory trees and shrubs. Logically, bats should be less active in plots with high percent non-native due to the association with increased midstory clutter. However, our model results may indicate that bats were either: 1) partitioning their time between sites with only high percent non-native or only few midstory trees and shrubs; or 2) using sites that had high percent non-native and low midstory clutter. Regarding the latter, we did survey heavily invaded plots that had fewer than 25 midstory trees and shrubs. In such plots, it is possible that non-native vegetation was concentrated at the ground layer, resulting in a high calculated plot percent non-native despite there being few, mostly native, midstory trees and shrubs. Additionally, midstory clutter did not have a significant effect on terminal buzzes, which could suggest that habitat structure affects bat locomotion more so than foraging. While foraging bats likely compromise their own habitat preferences for the habitat preferences of their prey, commuting bats may have fewer tradeoffs to consider and more often travel down paths of least resistance (Verboom 1998). The discrepancy in the relationships between percent non-native, number of midstory trees and shrubs, and bat activity may also suggest that non-native plants may facilitate bat activity in ways that do not alter habitat structure, such as by improving habitat quality (e.g., providing roost sites). Further research should be done to determine the mechanisms by which non-native plants affect bats.

Although none of our measured predictors significantly affected total high frequency passes, both percent non-native and the number of midstory trees and shrubs significantly affected total low frequency passes, much like the model for total passes. This similarity is likely explained by the dominance within our dataset of bats that produce low frequency pulses. The low frequency

echolocating big brown bat was responsible for over half of our recorded passes, and is the most common bat in New Jersey (New Jersey Department of Health 2014). We attribute model results for total low frequency passes, which comprised less than 15% of all passes recorded, to an inadequate sample size. There are several explanations for why we recorded so few low frequency passes. First, white-nose syndrome has significantly reduced populations of previously common species that produce high frequency pulses, such as little brown and northern long-eared bats (Maslo et al. 2015; O’Keefe et al. 2019). Alternatively, many areas within Jockey Hollow are dominated by non-native vegetation and have low densities of mid-story trees and shrubs, which both seemed to facilitate the activity of bats with low frequency pulses. Therefore, the noticeably low number of high frequency passes recorded is not surprising but does prevent us from concluding if non-native plants or habitat structure affect bats at Jockey Hollow differently depending on their foraging preferences.

Implications for Forest Management

Managers often recommend removing non-native plants in both forested and urban landscapes because it can significantly increase insectivorous bat activity (Beason et al. 2020; Lintott et al. 2015; Smith and Gehrt 2010). However, our results suggest that in the short-term, non-native plants might not be detrimental to bats and may even benefit them by maintaining open flight space beneath the forest canopy. However, we are uncertain about how bats are impacted in the long term by non-native shrubs, especially in conjunction with deer browse. In the United Kingdom, the presence of a non-native rhododendron and red deer (*Cervus elaphus*, L.) negatively affected insectivorous bats that prefer to forage in open spaces (Beason et al. 2020). Both non-native plants and deer browse can hinder the survival of native seedlings, which could eventually decrease plant richness and woody species recruitment (DiTommaso et al. 2014; Stinson et al. 2006). As native trees die, these habitats may transition to having cluttered midstories and little to no canopy, which could negatively impact bats.

Our findings demonstrate that there are complex relationships between native and non-native species that warrant further study. Because bats seemed to highly value habitat structure when choosing where to travel and forage, management activities that remove non-native plants while maintaining structural attributes preferred by bats are likely to sustain bat activity. Therefore, reducing midstory clutter and removing non-native shrubs could create travel corridors that facilitate foraging for bats with low frequency pulses, the most common species detected at Jockey Hollow. Unfortunately, we collected insufficient data to draw conclusions about what structural habitat attributes significantly influenced high-frequency bat activity. Such an evidence base is needed to facilitate habitat-based bat conservation, particularly for bats impacted by other threats such as white-nose syndrome and wind energy infrastructure (Frick et al. 2017; Hoyt et al. 2021). Because our model results were largely driven by big brown bats, we cannot advocate for a single management solution for increasing the activity of all bats. It is likely that a variety of management techniques that promote or maintain structurally heterogeneous habitats will support the greatest bat diversity. Further studies targeting bats with high frequency pulses can reduce the uncertainty surrounding the impacts of non-native plants on bats of highest conservation concern.

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Appendix A. Arthropod Counts

Table 2 shows the counts of arthropods collected during this study.

Table 2. Counts of arthropods collected in blacklight traps deployed at 23 plots in Morristown National Historical Park, NJ, USA in summer 2020.

Plot	Total Arthropod Abundance	Putative Prey Abundance	Shannon Diversity Index	Araneae	Blattodea	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Mantodea	Megaloptera	Neuroptera	Odonata	Opiliones	Orthoptera	Plecoptera	Siphonaptera	Trichoptera
AD2	753	739	1.34	4	0	91	58	0	18	373	0	0	3	0	4	2	1	0	199
AD3	1620	1462	1.54	1	0	80	676	15	22	365	0	0	130	0	0	0	27	0	304
AD4	702	694	1.33	0	0	104	17	6	28	296	0	1	0	0	0	0	7	0	243
AD9	1422	1373	1.55	11	4	195	46	130	62	688	0	0	2	0	0	0	32	0	252
AD10	1233	1218	1.35	2	4	589	18	65	29	365	0	1	2	0	3	0	3	0	152
AD11	610	561	1.59	4	3	122	17	27	11	278	0	0	0	0	32	3	7	0	106
AD12	100	96	1.50	0	0	10	9	1	11	50	0	0	0	0	4	0	0	0	15
AD13	507	501	0.76	2	0	5	3	5	10	85	0	0	0	0	0	4	0	0	393
AD15	1218	1145	1.45	0	0	314	10	28	16	493	0	1	37	0	0	0	35	0	284
AD16	275	275	1.04	0	0	16	43	1	7	185	0	0	0	0	0	0	0	0	23
AD17	789	784	1.45	0	0	275	27	44	23	285	0	0	0	2	1	2	0	0	130
AD18	641	636	1.64	4	0	187	67	59	29	202	0	0	1	0	0	0	0	0	92
AD19	1463	1452	1.05	0	0	654	13	55	52	678	0	0	1	1	0	1	4	4	0
AD20	1035	1029	1.11	0	0	159	20	11	50	674	0	0	6	0	0	0	0	0	115
AD21	1182	1174	1.02	0	6	361	41	80	2	690	2	0	0	0	0	0	0	0	0
AD22	1047	1039	1.28	0	0	124	36	14	24	366	0	0	4	0	0	0	4	0	475
AD23	1423	1387	1.56	1	10	469	55	58	89	528	0	0	2	1	4	3	15	0	188
AD24	852	704	1.63	1	0	292	10	28	9	177	0	0	23	0	0	0	124	0	188
AD25	453	453	1.66	0	0	54	36	70	41	150	0	0	0	0	0	0	0	0	102
AD26	174	172	0.80	0	0	18	1	1	1	134	0	0	0	0	2	0	0	0	17
AD27	1475	1438	1.17	0	0	128	19	11	9	701	0	0	11	0	0	1	25	0	570
AD28	897	893	1.39	0	0	191	17	25	42	384	0	0	1	0	0	0	3	0	234
AD29	603	600	1.26	0	0	58	24	0	30	252	0	0	0	0	0	1	2	0	236

Appendix B. Bat Pass Counts

Table 3 shows the bat pass counts recoded by detectors during this study.

Table 3. Counts of passes recorded by acoustic detectors deployed at 23 plots in Morristown National Historical Park, New Jersey, USA in summer 2020.

Plot	Terminal Buzzes	Total Bat Passes	Low-freq. Unknown	High-freq. Unknown	<i>E. fuscus</i>	<i>L. borealis</i>	<i>L. cinereus</i>	<i>L. noctivagans</i>	<i>M. lucifugus/sodalis</i>	<i>M. septentrionalis</i>	<i>N. humeralis</i>	<i>P. subflavus</i>
AD2	9	140	9	9	51	68	0	1	2	0	0	0
AD3	3	53	22	0	20	0	9	2	0	0	0	0
AD4	4	46	6	7	23	5	0	0	0	0	5	0
AD9	3	54	14	0	39	1	0	0	0	0	0	0
AD10	1	15	1	1	5	7	1	0	0	0	0	0
AD11	17	100	15	3	51	27	3	1	0	0	0	0
AD12	0	5	1	1	1	0	0	0	1	1	0	0
AD13	9	190	62	33	25	15	22	29	2	0	2	0
AD15	6	155	38	30	44	31	0	3	0	0	9	0
AD16	0	40	14	3	21	2	0	0	0	0	0	0
AD17	10	114	24	27	45	16	0	1	0	0	1	0
AD18	80	525	60	2	115	21	271	55	1	0	0	0
AD19	36	291	26	1	252	5	4	2	0	1	0	0
AD20	30	297	32	6	224	31	4	0	0	0	0	0
AD21	4	56	3	2	46	5	0	0	0	0	0	0
AD22	1	92	15	2	35	38	0	0	2	0	0	0
AD23	9	92	33	9	35	3	8	0	0	0	4	0
AD24	5	179	116	17	23	3	14	1	2	1	0	2
AD25	19	247	59	2	105	18	43	20	0	0	0	0
AD26	0	22	1	2	16	1	1	1	0	0	0	0

Table 3 (continued). Counts of passes recorded by acoustic detectors deployed at 23 plots in Morristown National Historical Park, New Jersey, USA in summer 2020.

Plot	Terminal Buzzes	Total Bat Passes	Low-freq. Unknown	High-freq. Unknown	<i>E. fuscus</i>	<i>L. borealis</i>	<i>L. cinereus</i>	<i>L. noctivagans</i>	<i>M. lucifugus/sodalis</i>	<i>M. septentrionalis</i>	<i>N. humeralis</i>	<i>P. subflavus</i>
AD27	4	60	7	5	41	1	5	1	0	0	0	0
AD28	16	157	23	12	90	7	18	4	0	0	3	0
AD29	37	684	80	20	564	2	9	9	0	0	0	0
Total	303	3614	661	194	1871	307	412	130	10	3	24	2

Appendix C. Top Model Results

Tables 4–11 show the top model results obtained by this study.

Table 4. Top models ($< 2 \Delta\text{AICc}$ scores from top model) for total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Model	AICc	ΔAICc from Top Model
1. Midstory Trees and Shrubs + Percent Non-native	270.23	0.00
2. Percent Non-native	270.94	0.71
3. Canopy Cover + Midstory Trees and Shrubs + Percent Non-native	271.60	1.36

Table 5. Effect sizes for predictors in top models for total low frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Predictor	Model 1	Model 2	Model 3
Midstory Trees and Shrubs	-0.66 ± 0.29 SE	—	-0.61 ± 0.28 SE
Percent Non-native	1.25 ± 0.39 SE	1.05 ± 0.38 SE	0.95 ± 0.39 SE
Canopy Cover	—	—	-0.29 ± 0.18 SE

Table 6. Top models ($< 2 \Delta\text{AICc}$ scores from top model) for total passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Model	AICc	ΔAICc from Top Model
1. Midstory Trees and Shrubs + Percent Non-native	279.58	0.00
2. Percent Non-native	280.21	0.62
3. Canopy Cover + Midstory Trees and Shrubs + Percent Non-native	281.45	1.87
4. Canopy Cover	281.50	1.91

Table 7. Effect sizes for predictors in top models for total passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Predictor	Model 1	Model 2	Model 3	Model 4
Midstory Trees and Shrubs	-0.59 ± 0.36 SE	—	-0.56 ± 0.26 SE	—
Percent Non-native	1.03 ± 0.36 SE	0.84 ± 0.35 SE	0.79 ± 0.37 SE	—
Canopy Cover	—	—	-0.23 ± 0.17 SE	-0.41 ± 0.18 SE

Table 8. Top models (< 2 Δ AICc scores from top model) for terminal buzzes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Model	AICc	Δ AICc from Top Model
1. Percent Non-native	162.52	0.00
2. Midstory Trees and Shrubs + Percent Non-native	164.35	1.83

Table 9. Effect sizes for predictors in top models for terminal buzzes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Predictor	Model 1	Model 2
Percent Non-native	1.54 $\pm$ 0.45 SE	1.65 $\pm$ 0.48 SE
Midstory Trees and Shrubs	—	-0.37 $\pm$ 0.34 SE

Table 10. Top models (< 2 Δ AICc scores from top model) for total high frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Model	AICc	Δ AICc from Top Model
1. Null model	196.73	0.00
2. Percent Non-native	198.18	1.45
3. Midstory Trees and Shrubs	198.32	1.58

Table 11. Effect sizes for predictors in top models for total high frequency passes recorded in Morristown National Historical Park, New Jersey, USA in summer 2020.

Predictor	Model 1	Model 2	Model 3
Percent Non-native	—	-0.50 $\pm$ 0.41 SE	—
Midstory Trees and Shrubs	—	—	-0.32 $\pm$ 0.31 SE

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