

Article

Non-Native Plants Influence Forest Vegetative Structure and the Activity of Eastern Temperate Insectivorous Bats

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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 the 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 to 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.

Keywords: acoustic monitoring; bat conservation; Chiroptera; non-native plants; prey availability; vegetation structure; wildlife–habitat relationships



Citation: Mark, M.; Drake, E.; Kerwin, K.; Maslo, B. Non-Native Plants Influence Forest Vegetative Structure and the Activity of Eastern Temperate Insectivorous Bats. *Forests* **2024**, *15*, 711. <https://doi.org/10.3390/f15040711>

Academic Editors:
Katarína Pastirčáková and
Rostislav Zemek

Received: 15 February 2024

Revised: 2 April 2024

Accepted: 14 April 2024

Published: 17 April 2024



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1. Introduction

Non-native plants can profoundly impact ecological communities by reducing native biodiversity and altering ecosystem function [1–3]. 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 [4–6]. 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 at other trophic levels [7–9]. For example, non-native plants compete with and suppress the growth of native plants, altering the pre-existing vegetative community [10,11]. Such changes can directly and indirectly reduce the survival and reproductive success of some native herbivorous insects, which subsequently impact

insectivores and their predators [12]. 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 [13–16].

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 [17,18]. Non-native shrubs typically increase understory clutter [17], 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 [19], non-native plants often force animals to adapt or suffer negative fitness consequences [16]. 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 [20,21]. 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 [22], 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 [22,23]. Ectotherms also avoid non-native vegetation at multiple spatial scales, suggesting that non-native plants do not provide the required habitat components [24]. 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 [25]. 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.) [26,27]. All bat species native to eastern North America are insectivorous and require forests for roosting, reproduction, and/or foraging [28–30]. When selecting foraging habitats in forested landscapes, bats value both the high abundance of arthropod prey as well as the appropriate vegetative structure. However, studies show that neither of these factors alone can reliably predict bat presence or activity [31,32]. Non-native plants further obfuscate these dynamics by influencing both arthropod abundance and vegetative structure [5,12]. Although most of the 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 and create forest structures with open midstories and canopies. Such open habitats may facilitate flight and predator avoidance [25,33], ultimately increasing their use by bats.

Because many bats, including all temperate North American species, echolocate [34], passive acoustic monitoring has become a valuable tool for evaluating how bats are affected by factors such as non-native plants [35,36]. Bats produce echolocation pulses at a consistent rate to navigate and hunt [37,38]; thus, the number of pulses recorded can be a proxy for bat activity [39]. 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 it is found and consumed [40]. Therefore, the number of terminal buzzes recorded can be a proxy for foraging activity [41]. Acoustic monitoring studies have implicated low prey abundance caused by non-native plants in reduced bat activity [42]. Acoustic monitoring has also revealed that non-native structural clutter impacts open-space foraging bats but not clutter-loving foragers [43]. 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 [37,40]. 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 [44]. 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 [44,45]. 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 [46,47], 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 a 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 (which produce low-frequency pulses) would likely be more active in survey plots with a high percent non-native, which we predicted would be more structurally open, while the opposite would be true for clutter-loving bats (which produce high-frequency pulses).

2. Materials and Methods

2.1. 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. Jockey Hollow consists of 567 hectares of contiguous eastern temperate forest that is heavily influenced by past land uses [48]. 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 stilt grass (*Microstegium vimineum*, A. Camus) [49]. 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.) [48]. 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) [50].

Within the study area, we selected 23 circular plots, which we broadly classified into three habitat types, as follows: 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 [51] (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 [52] 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.

2.3. Acoustic Surveys and Bat Echolocation Analysis

From June to August 2020, we monitored survey plots for bats following the North American Bat (NABat) Monitoring Program protocols for stationary acoustic monitoring [39]. At the center of each survey plot, we placed a Pettersson D500X (Pettersson Elektronik AB, Uppsala, Sweden) acoustic detector equipped with a full-spectrum omnidirectional ultrasonic microphone. We mounted the microphone approximately 3 m off the ground and angled it approximately 45° upward into the airspace [41]. 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/h [41]. The detectors were active from 30 min before sunset to 30 min 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 [53]. 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 unknowns 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) [54]. 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 the 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 [41,55]. A terminal buzz can be heard as a distinct pitch change when played at 10× reduced speed and visualized as a short burst of accelerating pulses in the sonogram viewing window [41]. Although terminal buzzes can be identified using the sonograms produced by SonoBat, they often cannot be reliably classified into 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 unknowns.

2.4. Arthropod Surveys

Concurrent with each acoustic survey, we deployed a blacklight insect bucket trap (Leptraps, LLC, Georgetown, KY, USA) within 10 m of each survey plot. This distance is sufficiently close to the survey plot to appropriately characterize the arthropod community without influencing bat activity [56,57]. Traps consisted of 15 W T8 blacklight bulbs (PestWest, Sarasota, FL, USA), drawing arthropods into a catch bucket lined with Vaportape

II insecticidal strips (Hercon, Emigsville, PA, USA) 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 by order. We calculated the Shannon diversity index of all arthropod orders at each site using the *vegan* package in R [58]. 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, i.e., Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Trichoptera [59].

2.5. Statistical Analysis

We performed all statistical analyses using R v3.3.0+ [60]. We manipulated data using the *dplyr* package [61] and created plots using the *ggplot2* package [62]. 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 1000 replicates in the *boot* package [63]. To test the hypothesis that non-native plants affect arthropod prey, we performed linear mixed-effects models (LMERs) in the *lme4* package [64] using non-native vegetation percentage as the predictor and either prey abundance or total arthropod order diversity as the response. We included the month as a random effect to account for potential declines in arthropod abundance and diversity as the year progresses from spring to fall [65]. We also conducted a generalized linear model (GLM) in the *stats* package [60] 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 by 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 [66] 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 [67] to conditionally average all candidate models within 2 ΔAICc scores of the top model [68]. 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 scores of the top model.

Table 1. Candidate model set to test competing hypotheses about predictors of bat activity in northern New Jersey.

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 (dictated by midstory clutter)		X			
Ground cover			X		
Non-native percentage				X	
Prey availability					X
No predictors (null model)					

3. Results

3.1. Vegetation and Arthropod Surveys

The percent of non-native vegetation in each plot ranged from 0 to 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 2).

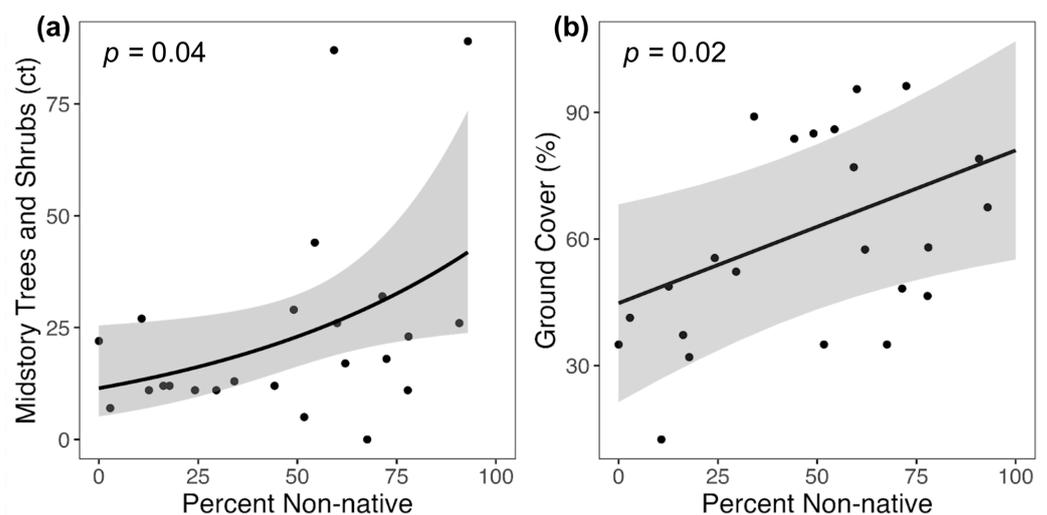


Figure 2. The percentage of a plot (average of the ground and midstory layers occupied by non-native vegetation) was significantly and positively correlated with the (a) number of midstory trees and shrubs ($\beta = 0.01 \pm 0.006$ SE) in the entire plot and (b) percentage of the ground covered by vegetation ($\beta = 0.36 \pm 0.14$ SE) in four quadrats within the plot in northern 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 and 1462 individuals ($\bar{x} = 861 \pm 85.5$ SE). The arthropod community was dominated by lepidopterans ($N = 8399$), coleopterans ($N = 4496$), and trichopterans ($N = 4318$), 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.

3.2. Acoustic Surveys

Over 46 recording nights, we collected 3614 usable bat passes, 303 of which contained terminal buzzes (Appendix B). Bat activity and foraging varied widely by survey plot, ranging from 5 to 684 total passes ($\bar{x} = 157 \pm 34.28$ SE) and from 0 to 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 3074 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, both of which produce high-frequency pulses.

3.3. 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 3a) and terminal buzzes ($\beta = 1.57 \pm 0.46$ SE; Figure 3b). 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.

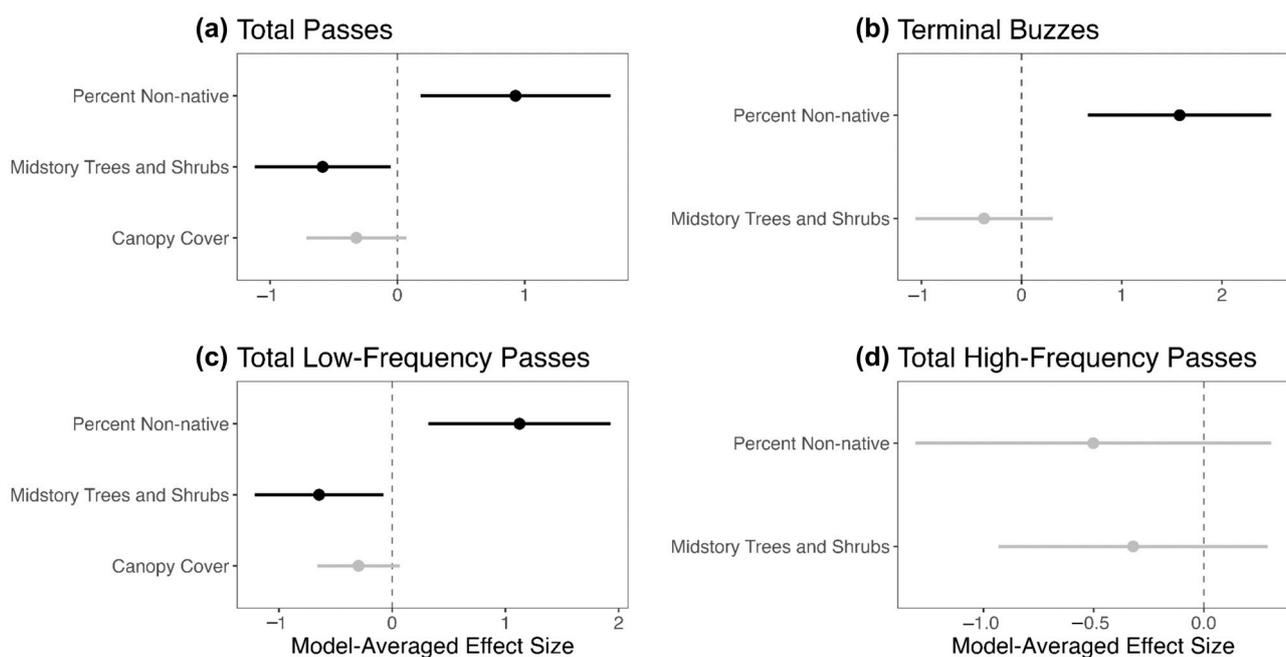


Figure 3. The percentage of a plot (average of the ground and midstory layers) occupied by non-native

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 northern 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 (the model-averaged effect size did not cross 0). Gray points and gray lines indicate effects that were not significant (the model-averaged effect size crossed 0).

The trends for low-frequency passes were nearly identical to those for total passes. The top model for total low-frequency passes included the number of midstory trees and shrubs ($\beta = -0.64 \pm 0.29$ SE) and non-native percentage ($\beta = 1.12 \pm 0.41$ SE), both of which had a significant effect on low-frequency passes (Figure 3c). There were no significant predictors of total high-frequency bat passes (Figure 3d). Detailed GLM results are in Appendix C.

4. Discussion and Conclusions

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 to foraging.

Contrary to our predictions and the findings of previous studies [69,70], 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 [12,71]. 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 [72,73]. 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 [74,75]. Non-native plants can also be highly suitable for native insects and actually increase arthropod fitness [76]. 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 in a native plant can exploit a closely related plant that produces similar chemical compounds [73]. We did not classify arthropods into 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 on bat use of forest habitats. First, North American bats are generalist insectivores, feeding on a wide array of arthropods [59,77], 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) [78], spotted lanternflies (*Lycorma delicatula*, White; McHale et al., unpublished data), and emerald ash borers (*Agrilus planipennis*, Waterhouse) [79]. Thus, bats may cope with decreased abundances of native prey by consuming non-native species, which often occur in high abundances [80,81]. 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 the 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 a 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 the 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 [82]. 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 conducted 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, responsible for over half of our recorded passes, is the most common bat in New Jersey [83]. We attribute the 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 the little brown and northern long-eared bats [84,85]. Alternatively, many areas within Jockey Hollow are dominated by non-native vegetation and have low densities of midstory trees and shrubs, both of which seem 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 [43,86,87]. 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 [43]. Both non-native plants and deer browse can hinder the survival of native seedlings, which could eventually decrease plant richness and woody species recruitment [88,89]. 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 seem 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 [90,91]. 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 the highest conservation concern.

Author Contributions: Conceptualization, B.M. and K.K.; Methodology, K.K.; Data curation, M.M., E.D. and K.K.; Formal analysis, M.M.; Writing, M.M., E.D. and B.M.; Project administration, B.M.; Funding acquisition, B.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Park Service Cooperative Research and Training Grant [number P20AC00480].

Data Availability Statement: Raw data associated with this paper are stored within the Rutgers Libraries Data Portal, which maintains all Rutgers-produced datasets. Data can be freely accessed through this portal.

Acknowledgments: Special thanks to Park Biologist Bob Masson, Park Law Enforcement, for facilitating field surveys, and to Justin Martinez and Kelly Faller for assisting with data collection. We also thank Mark Ford, Samantha Hoff, Joy O'Keefe, and Susan Loeb for their constructive feedback on previous drafts.

Conflicts of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A

Table A1. Counts of arthropods collected in blacklight traps deployed at 23 plots in northern New Jersey, 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	Opiilones	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

Table A2. Counts of passes recorded by acoustic detectors deployed at 23 plots in northern New Jersey, USA, in summer 2020.

Plot	Terminal Buzzes	Total 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/sodalitis</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

Table A2. Cont.

Plot	Terminal Buzzes	Total 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>
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
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

Table A3. Top models (<2 Δ AICc scores from top model) for total low-frequency passes recorded in northern New Jersey, USA, in summer 2020.

Model	AICc	Δ AICc 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 A4. Effect sizes for predictors in top models for total low-frequency passes recorded in northern 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 A5. Top models (<2 Δ AICc scores from top model) for total passes recorded in northern New Jersey, USA, in summer 2020.

Model	AICc	Δ AICc 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 A6. Effect sizes for predictors in top models for total passes recorded in northern 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 A7. Top models (<2 Δ AICc scores from top model) for terminal buzzes recorded in northern 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 A8. Effect sizes for predictors in top models for terminal buzzes recorded in northern New Jersey, USA, in summer 2020.

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

Table A9. Top models (<2 Δ AICc scores from top model) for total high-frequency passes recorded in northern 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 A10. Effect sizes for predictors in top models for total high-frequency passes recorded in northern New Jersey, USA, in summer 2020.

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

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