




Spring 5-1-2023

Effects of Nonnative Plants on Space-Use in Eastern Box Turtles

Emily Ilene Crago
Winthrop University

Follow this and additional works at: <https://digitalcommons.winthrop.edu/graduatetheses>

 Part of the [Botany Commons](#), [Natural Resources and Conservation Commons](#), [Terrestrial and Aquatic Ecology Commons](#), and the [Zoology Commons](#)

Recommended Citation

Crago, Emily Ilene, "Effects of Nonnative Plants on Space-Use in Eastern Box Turtles" (2023). *Graduate Theses*. 148.

<https://digitalcommons.winthrop.edu/graduatetheses/148>

This Thesis is brought to you for free and open access by the The Graduate School at Digital Commons @ Winthrop University. It has been accepted for inclusion in Graduate Theses by an authorized administrator of Digital Commons @ Winthrop University. For more information, please contact digitalcommons@mailbox.winthrop.edu.

May 2023

To the Dean of the Graduate School:

We are submitting a thesis written by Emily Crago entitled “EFFECTS OF NONNATIVE PLANTS ON SPACE-USE IN EASTERN BOX TURTLES.”

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Science in Biology.

Dr. Kiyoshi Sasaki, Thesis Adviser

Dr. Jennifer Schafer, Committee Member

Dr. Salvatore Blair, Committee Member

Dr. Lauren Brasington, Committee Member

Dr. Takita Sumter, Dean, College of Arts and Sciences

Dr. Jack DeRochi, Dean, Graduate School

EFFECTS OF NONNATIVE PLANTS ON SPACE-USE IN
EASTERN BOX TURTLES

A Thesis
Presented to the Faculty
Of the
College of Arts and Sciences
In Partial Fulfillment
Of the
Requirements for the Degree
Of
Master of Science
In Biology
Winthrop University

May 2023

By
Emily Ilene Crago

ABSTRACT

Introduction of nonnative plants outside their natural range has caused widespread reduction in the abundance and diversity of native plant species. Nonnative plants typically form dense, often monotypic, thickets that affect the ability of animals to find food, reproduce, avoid predation risk, and thermoregulate. By doing so, nonnative plants have the potential to displace resident animals from areas otherwise suitable as animal habitat. However, limited studies have investigated whether resident animals avoid areas dominated by nonnative plants. This study investigated impacts of nonnative plants on eastern box turtles (*Terrapene carolina carolina*), a species that has been declining throughout their range. To determine if eastern box turtles avoid nonnative plants, I estimated habitat selection based on GPS fixes recorded for 16 individuals (6 males and 10 females) in an urban forest. Specifically, I determined if nonnative plants are avoided when turtles establish their home range (i.e., second order selection) and when they use their home ranges (i.e., third order selection). For females, the density of four of the six most common nonnative plant species was lower in turtle locations than available locations across the study area (i.e., second order selection) and those within home ranges (i.e., third order selection). For males, the density of only one nonnative plant species was lower in turtle locations than available locations across the study area (i.e., second order selection), and none of the species were different between turtle locations and available locations within their home ranges (i.e., third order selection). These results suggests that eastern box turtles avoid some (but not all) species of nonnative plants and that females are more sensitive to nonnative plants than males. The displacement of animals from highly invaded areas represents a functional loss of habitat. The reduction in available habitat area may lead to reduction in carrying capacity of invaded areas, and therefore, may have long-term impacts on population persistence.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank Dr. Kiyoshi Sasaki for his understanding, endless patience, and his phenomenal guidance throughout the process of this research. This project would not have been possible without his excellent mentoring, and I would not be the biologist I am today without him. Additionally, I would like to thank Winthrop University Research Council, IDeA Networks of Biomedical Research Excellence (INBRE), Sigma Xi, and the North American Box Turtle Conservation Committee for funding the following research.

I would also like to thank Dr. Lauren Brasington, Dr. Jennifer Schafer, and Dr. Salvatore Blair for their review of my writing, providing excellent feedback, and support. I would like to thank Fumiko Shirakura, Luke Reed, Ivon Valenciano-Tovar, and Tony Adorno-Colon for all their hard work in the field while data collection was in progress. The following results would not have been possible without all mentioned parties involved.

TABLE OF CONTENTS

Abstract.....	ii
Acknowledgements.....	iii
List of tables.....	v
List of figures.....	vi
Introduction.....	1
Methods	5
Study area	5
Vegetation survey	6
Vegetation mapping: kriging	6
Vegetation mapping: inverse distance weighting	7
Radio telemetry	8
Space use patterns	8
Habitat Selection	9
Results	10
Vegetation	10
Radio telemetry	10
Space use	10
Home range selection (second order selection)	11
Habitat selection within home range (third order selection).....	11
Discussion	12
Tables.....	16
Figures	17
Literature cited	26

LIST OF TABLES

Table 1.	16
---------------	----

LIST OF FIGURES

Figure 1. 17

Figure 2. 18

Figure 3. 19

Figure 4. 20

Figure 5. 21

Figure 6. 22

Figure 7. 23

Figure 8. 24

Figure 9. 25

INTRODUCTION

Globalized trade has intentionally and unintentionally transported thousands of species outside of their native range defined by natural dispersal limitations (Ollier and Bertelsmeier 2022). Some of these species have spread rapidly, threatening biodiversity across the globe (Vilà et al. 2011). Globally, species invasions are thought to have contributed to 54% of all extinctions (Bellard et al. 2016a). Currently, 1,352 (27%) of all tetrapods are considered to be threatened by invasive species, mostly by fungi, animals, and plants (Bellard et al. 2016b). With continued spread and increase in abundance of nonnative species (Pyšek et al. 2020; Seebens et al. 2021), understanding the invasion impacts and underlying mechanisms of impacts remains critical for predicting impacts and informing efficient management (Stewart et al. 2021).

Thousands of plant species have been introduced to areas outside of their native range around the world. Of which, 13,168 species have become naturalized, establishing self-sustaining populations (van Kleunen et al. 2015), and more than 1,000 species have become invasive, spreading, and increasing in abundance in their new habitat (Turbelin et al. 2017) even in protected areas (Miller et al. 2021). Nonnative plant species typically form dense, often monocultural stands by suppressing the establishment and the growth of native plant species through competition and allelopathic chemicals, exploiting untapped resources by native species, altering species interactions, and altering abiotic conditions (Qu et al. 2021). As the dominant primary producer in their new habitat, nonnative plants can affect animal communities not only by generating bottom-up effects through changes in the food base, but also by altering a suite of biotic (e.g., predation pressure) and abiotic (e.g., microclimate) characteristics of their habitat on which resident animals depend (Jones et al. 1994; Crooks 2002; Hayes and Holzmüller 2012).

Studies examining the impacts that nonnative plants have on animals have increased substantially over the last few decades (Schirmel et al. 2016). Most of these studies have focused on population- or community-level impacts, revealing widespread changes (increase or decrease)

in the abundance and diversity of animals (Pyšek et al. 2012; Schirmel et al. 2016; Fletcher et al. 2019). However, while these studies provide direct measures of the state of populations or diversity, which are of primary interest to conservation and management of native wildlife, revealing population- and community-level changes provides limited utility in uncovering the mechanisms underlying population and community change. Mechanisms of impacts at population- or community-level change can be discerned by examining effects and processes at the individual level (Crystal-Ornelas and Lockwood 2020).

Animal behavior is important for understanding and predicting the impacts of human-altered environment on wildlife (Sole et al. 2013). The first response of individuals to an environmental change is often behavioral. The type of behavioral response (e.g., avoidance, attraction, or neutral) has the potential to affect survival and reproduction of individuals, and ultimately, key demographic parameters (e.g., birth, death, migration rate). Understanding behavioral responses could therefore provide insight into the mechanisms through which human-altered environment affects population persistence and community dynamics. Studies of behavioral impacts on human-altered environment are increasingly being recognized as important for informing conservation and management (Berger-Tal et al. 2011; Greggor et al. 2016). However, studies on the impacts of nonnative plants on animal behavior remain limited (Stewart et al. 2021).

Eastern box turtles (*Terrapene carolina carolina*) have been experiencing population declines over the past several decades (Dodd 2001) and are listed as ‘vulnerable’ in the IUCN Red List (van Dijk 2011). Eastern box turtles are a terrestrial species inhabiting primarily mixed and hardwood forests in the eastern United States. Habitat loss resulting from the conversion of forests to anthropogenic land cover is considered a major threat (Nazdrowicz et al 2008; Graham et al. 2022). Furthermore, the eastern United States harbors more nonnative plants than other regions of the United States (Iannone et al. 2015; Oswalt et al. 2015), potentially contributing to box turtle declines through habitat change.

Eastern box turtles primarily use forests but may use fields (Stickel 1950; Fredericksen 2014). They generally select areas with dense ground vegetation and woody debris (Greenspan et al. 2015; Harris et al. 2020; Parlin et al. 2017). There appear to be no difference in habitat use between female and male turtles, except during nesting season. Females typically nest in grassland, savanna, forest edge, and canopy gaps from May to early July (Congello 1978; Willey and Sievert 2012; Refsnider et al. 2023). Eastern box turtles are omnivorous and consume a wide range of food items, such as plants, mushrooms, and invertebrates (Figueras et al. 2021). Home range size vary among individuals and geographic locations, ranging from 0.2 to 113.1 ha, with females exhibiting larger home range sizes (Habeck et al. 2019; Roe et al. 2020).

Impacts of nonnative plants on eastern box turtles are equivocal. McKnight (2011) found that eastern box turtles frequently use dense patches of multiflora rose (*Rosa multiflora*). However, Attum et al. (2016) found that eastern box turtles avoided habitat dominated by Amur honeysuckle (*Lonicera maackii*), as this species forms dense patches which limits sunlight availability (Collier et al. 2002). Also, McEvoy and Durtsche (2003) found eastern box turtles were only in habitat not dominated by Amur honeysuckle. Maes and Walton (2012) found only a few turtles in habitat dominated by autumn olive (*Elaeagnus umbellata*) and Amur honeysuckle. Discrepancy among these studies may be due to the difference in species (and associated growth form) in question or analytical approaches. A paucity of studies of impacts of nonnative plants on eastern box turtles (and animals in general) precludes identification of general pattern in impacts of nonnative plants (Stewart et al. 2021).

The goal of this study was to understand the impact of nonnative plants on eastern box turtles. To determine if eastern box turtles avoid nonnative plants (1) the spatial distribution of nonnative plant density were determined, (2) characterized the space use pattern of eastern box turtles, and (3) estimated habitat selection by eastern box turtles in Winthrop Woods, a 28-ha forest in the Piedmont ecoregion of the southeastern United States. Habitat selection is a process by which animals choose a specific area to use among a set of available areas. It is thought to be

hierarchically ordered choices made by animals (Johnson 1980): selection of a geographic range (i.e., first order selection), selection a general area to live—a home range—within its range (i.e., second order selection), and selection different patches for a specific type of activity, such as foraging and nesting, in its home range (i.e., third order selection) (Johnson 1980). In this study, habitat selection was estimated for second and third order selection. To address the potential sex-specific responses, the space use and habitat selection of males and females were examined separately. Sex-specific responses may arise because of inherent differences in their life history requirements, usually associated with reproduction (Chen and Lue 2008; Fredericksen 2014). Eastern box turtles are classified as vulnerable / apparently secure (S3S4) in South Carolina (South Carolina Natural Heritage Program 2023).

Winthrop Woods are invaded by multiple nonnative plants. The most conspicuous species forming largely monocultural patches include autumn olive (*Elaeagnus umbellata*), Chinese privet (*Ligustrum sinense*), bigleaf periwinkle (*Vinca major*), Japanese stiltgrass (*Microstegium vimineum*), Chinese wisteria (*Wisteria sinensis*), and golden bamboo (*Phyllostachys aurea*). Autumn olive is native to Asian and was introduced to the United States in the 1830s (Miller et al. 2010). Autumn olive fixes nitrogen (Gardner 1958) and produces allelopathic chemicals (Miller et al. 2010). It can grow up to 6 m and spread and dominate forest understory (Oliphant et al. 2017). Chinese privet is native to Asia and was introduced to the United States in 1852 (Enloe et al. 2018). It forms monotypic thickets and reduces understory vegetation and diversity (Cash et al. 2020). This shade tolerant species colonizes areas via root sprouts and seed dispersal by birds (Miller et al. 2010). Bigleaf periwinkle is native to southern Europe and northern Africa and was introduced to the United States for landscaping and medicine in the 1700s (Bossard et al. 2000; Miller et al. 2010). It is a scrambling or trailing vine and forms dense mats on the forest floor (Miller et al. 2010), which can shade out native plants (Bossard et al. 2000). Bigleaf periwinkle has been shown to affect body mass and reproduction of a reptile, possible due to change in microclimate associated with the dense growth of periwinkle (Downes

and Hoefer 2007). Japanese stiltgrass is native to Asia and was introduced to the United States in 1919 (Fairbrothers and Gray 1972). It forms dense mats on the forest floor and can outcompete or suppress other plant species (Leicht et al. 2005; Oswalt et al 2007). Chinese wisteria is native to Asia and was introduced to the United States for landscaping in 1816 (Wells and Brown 2000). This liana species forms dense thickets that shade out other plants and strangles other woody plants (Hawthorne et al. 2015). Golden bamboo was introduced in 1882 (U.S. Department of Agriculture 2012) and forms dense monotypic thickets (U.S. Department of Agriculture 2012). Invasions of bamboo can cause decreases in plant biomass (Nelson et al. 2001). Understanding behavioral responses to these nonnative plants will help us identify species for management and predict effects of management practices (Hale et al. 2020).

METHODS

Study area

This study was conducted at Winthrop Woods, which is located in the Piedmont ecoregion of Rock Hill, South Carolina. Winthrop Woods is situated within the Winthrop University Recreational and Research Complex and is bordered by residential area, open fields, and a two-lane road. Winthrop Woods is a mixed coniferous and deciduous forest dominated by oaks (*Quercus* spp.), eastern red cedar (*Juniperus virginiana*), sweetgum (*Liquidambar styraciflua*), and white ash (*Fraxinus americana*) (Department of Biology - Recreational & Research Complex ... c2023). The Recreational and Research Complex was once a farm supplying produce (e.g., vegetables, dairy, and poultry) to the university community until 1956 (Olson 1983; Unknown 1932/1937). The use of land for farming ceased by 1980 with the construction of athletic and recreational facilities. According to surveys in 1976, a half of what used to be an old field, pasture, or outdoor pig pens had regressed to a stand of tree saplings with dense understory with Japanese honeysuckles (*Lonicera japonica*), plums (*Prunus* spp.), and

briers (*Smilax* spp.) (Woodland Management Plan 1976). The remaining area was mostly composed of hardwood species of 30–80 years old (Woodland Management Plan 1976) (Figure 1).

Vegetation survey

I surveyed vegetation from June–August 2021 in Winthrop Woods and adjacent areas in 776, 5-m radius plots along east-west transect set up about 20 meters apart (Figure 2). In each plot, I identified all plants to genus or species and determined their abundances. Abundance of herbaceous species was recorded as an estimate of the percentage of ground cover, while the abundance of woody species was determined as the number of stems. The ground cover was estimated visually and determined by averaging the cover values from two or three field crews.

Vegetation mapping: Kriging

To map the spatial variability in nonnative species abundances, I used kriging to interpolate the value of abundance over a continuous spatial field over the entirety of Winthrop Woods. Kriging is a geostatistical interpolation technique that predicts unknown values from observed data at known locations. In ordinary kriging, values of unsampled locations are estimated as a weighted sum of measured values from neighboring locations using the equation (Armstrong and Boufassa 1988):

$$\hat{Z}(x_0) = \sum_{i=1}^n \lambda_i Z(x_i)$$

where $\hat{Z}(x_0)$ is an estimation of abundance at location x_0 , $Z(x_i)$ a measured abundance value at location i in the neighborhood of location x_0 , and λ_i a weight for a measured value at the i th location, and n is the total number of sampled locations.

Weights are determined based on the spatial distance of the measured points and the distances between measured points and the predicted location (x_0). The spatial dependence is the

degree of similarity in measured values as a function of distance and can be quantified using a variogram, which plots semivariance according to distance. Semivariance, γ , is calculated as half the variance of the difference between observed values of a variable (abundance in this case) for all pairs of locations that are separated by a certain distance (d) using the equation:

$$\gamma(d) = \frac{1}{2n(d)} \sum_i^{n(d)} [z(x_i) - z(x_i + d)]^2,$$

where $z(x_i)$ is the density at location x_i and $n(d)$ is the number of pairs of sampling locations separated by a distance. A mathematical model is fitted to observed variogram, and the covariance matrix derived from the model is solved to obtain kriging weights (λ_i). Kriging was implemented using the `autoKrige` function in the R package *automap* (Hiemstra 2013).

Vegetation mapping: Inverse distance weighting

Predictive maps for small vegetation patches outside of the main woods were produced with inverse distance weighting (IDW). I used IDW for small patches outside of Winthrop woods instead of kriging because kriging had a large amount of prediction errors. IDW has the same general equation as the ordinary kriging but differs from kriging in that data points are weighted by an inverse function of the distance, d , raised to the power value p :

$$\lambda_i = \frac{d_i^{-p}}{\sum_{i=1}^n d_i^{-p}}$$

The value of p determines the rate at which the weights decrease with distance. The p was adjusted by visually cross validating the interpolation output with known distribution of a species. The IDW was implemented in using the `gstat` and `interpolate` functions in the *gstat* package in R (Pebesma 2004).

Radio Telemetry

Movement was monitored for 16 adults (6 male, 10 female) equipped with radio transmitters. These transmitters have a battery life that can last from 7 to 24 months (RI-2B, Holohil Systems Ltd., Ontario, Canada; or R1850, R1680, or R2020, Advanced Telemetry Systems, MN, USA). Ten turtles were captured and equipped with transmitters during a previous study in 2018 and 2019 (Graham et al. 2022). Eleven additional turtles were added for this study in 2020 and 2021. Individuals were visually located while walking throughout Winthrop Woods and its vicinity. All captured turtles were sexed based on sexually dimorphic characteristics, including concavity of the plastron, coloration, claw length, and relative position of cloaca (Burke 2011). All turtles were measured (straight line carapace length) and weighed with a spring scale (Pesola, AG, Barr, Switzerland) before attaching a transmitter. Transmitters were attached to the costal scute with a PC-7 nontoxic epoxy paste (Protective Coatings, Inc., Allenton, PA, USA). The turtles were held in captivity overnight to ensure curation of the epoxy. All individuals were released the next day at their original point of capture.

Turtles were located once a month during inactive seasons (November–April) and 2–3 times a week during active seasons (May–October) in 2020 and 2021 using a handheld radio receiver (R410) with a three-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN, USA). Each turtle's location was recorded with a handheld GPS unit (GPSMAP 64sc, Garmin, Ltd., Olathe, Kansas, USA). Animal handling procedures are approved by Winthrop University Institutional Animal Care and Use Committee (IACUC Control Number: 20003).

Space use

I used the dynamic Brownian bridge movement model (dBBMM) to estimate and visualize the space use patterns of eastern box turtles based on movement data collected by radio telemetry. I estimated the core area used by box turtles as 50% isopleth based on dBBMMs. The dBBMM predicts the probability of animal occurrence by accounting for the order of animal

locations (fixes), the distance and time elapsed between successive fixes, an estimate of the animal's mobility, and spatial uncertainty of each fix (Kranstauber et al. 2012). The animal's mobility (i.e., the Brownian motion variance) is estimated based on the degree of irregularity of the path of an animal between successive locations. The dBBMMs was implemented using the `Brownian.bridge.dyn` function in the package *move* in R (Kranstauber et al. 2019).

Habitat selection

To assess how nonnative plants affect home range selection (second order selection), I compared the density of nonnative plants at locations where turtles were located ("used locations") to those at randomly selected locations across Winthrop Woods ("available locations"). How nonnative plants affect turtle use of areas within their home ranges (third order selection) was assessed by comparing the density of nonnative plants at used locations with those at available locations randomly sampled within their home ranges. The home range for each individual was defined as the 100% minimum convex polygon (MCP) including all locations recorded for each individual. MCP was constructed using the `mcp` function in the *AdehabitatHR* package in R (Calenge 2006). I generated 100 random available points per used point for both second order and third order selection analyses.

I coded used locations as 1 and available locations as 0 and used this as a binary response variable to model habitat selection as a function of the density of nonnative plant species. By using generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function. To account for individual differences in second and third order selection, models were constructed in a way to allow intercepts and slopes to vary by individual, that is, with random intercepts and slopes. Males and females were analyzed separately because of the potential sex differences in behavioral response. GLMMs were implemented using the *glmmTMB* function in the R package *glmmTMB* (Magnusson et al. 2017).

RESULTS

Vegetation

Of 116 plant species detected in the study area, 36.2% (42) were nonnative species. Nonnative species covered ca. 70% of the study area (Winthrop Woods and peripheral shrub and wooded areas). The most widespread and abundant nonnative species were autumn olive and Chinese privet, followed by Chinese wisteria, Japanese stiltgrass, and bigleaf periwinkle (Figure 3). Golden bamboo was found only in a small discrete patch (Figure 3). Herbaceous species (Japanese stiltgrass and bigleaf periwinkle) occupied the perimeter of the woods, whereas lianas (wisteria) and shrubs (Chinese privet and autumn olives) had extended distributions in the interior of the woods.

Radio telemetry

I followed the 16 turtles a total of 1,048 times (mean \pm SD = 61 ± 7 times; range = 47–72 times) over 158 to 467 days (mean \pm SD = 353 ± 111 days). All individuals were tracked for at least one full active season (May–October; Table 1). Tracked males ($n = 6$) averaged 13.6 cm (SD = 0.6) in carapace length and 415.3 g (SD = 50.0) in mass. Tracked females ($n = 10$) averaged 12.2 cm (SD = 0.6) in carapace length and 382.7 g (SD = 70.2) in mass (Table 1).

Space use patterns

The core areas of the majority of females were situated outside dense growth of nonnative plants (Figure 4). The notable exception was a female (Wednesday), whose occurrence was largely confined to a dense patch of Chinese wisteria. Another female was found frequently in moderate to dense growth of Chinese privet. Similarly, to females, core areas of most males were located outside of dense growth of nonnative plants (Figure 5). The only exception was a male whose core area overlapped substantially with a dense patch of Japanese

stiltgrass. No turtles were located in the bamboo patch; therefore, bamboo was excluded from the subsequent habitat selection analyses.

Home range selection (second order selection)

For female, abundance of autumn olive ($z = -2.56$, $P = 0.001$), bigleaf periwinkle ($z = -3.95$, $P < 0.001$), and Chinese wisteria ($z = -2.02$, $P = 0.043$) were lower at turtle locations than available locations within the study area. These three species exhibited relative selection strength <1 , indicating avoidance of these species by female turtles in home range selection (Figure 6). There was little evidence for avoidance of Japanese stiltgrass ($z = -0.09$, $P = 0.927$) and Chinese privet ($z = -1.20$, $P = 0.230$) (Figure 6).

For males, abundance of autumn olive ($z = -2.16$, $P = 0.031$) and possibly bigleaf periwinkle ($z = -1.95$, $P = 0.051$) were lower in turtle locations than available locations within the study area. These two species exhibited relative selection strength <1 , indicating avoidance of these species by turtles in home range selection (Figure 7). There was little evidence of avoidance for Chinese privet ($z = 0.28$, $P = 0.782$), Chinese Wisteria ($z = -1.22$, $P = 0.224$), and Japanese stiltgrass ($z = -1.88$, $P = 0.061$) (Figure 7).

Habitat selection within home ranges (third order selection)

For females, abundance of the same nonnative plant species were lower in turtle locations than available locations within home ranges (autumn olive ($z = -3.31$, $P < 0.001$), bigleaf periwinkle ($z = -2.46$, $P = 0.014$), and Chinese wisteria ($z = -2.81$, $P = 0.005$). These three species exhibited relative selection strength <1 , indicating avoidance of these species by female turtles within their home ranges (Figure 8). There was little evidence for avoidance of Japanese stiltgrass ($z = -0.16$, $P = 0.871$) and Chinese privet ($z = -1.49$, $P = 0.136$) (Figure 8).

For males, there was little evidence for avoidance of autumn olive ($z = -0.70$, $P = 0.481$)

bigleaf periwinkle ($z = 0.44$, $P = 0.660$), Chinese privet ($z = -0.92$, $P = 0.357$), Chinese wisteria ($z = -1.42$, $P = 0.156$), and Japanese stiltgrass ($z = -1.47$, $P = 0.142$) only within areas inside of their home ranges (Figure 9).

DISCUSSION

This study revealed negative spatial associations between nonnative plants and eastern box turtles. Such associations suggest that eastern box turtles avoid areas heavily invaded by most of the nonnative plant species. However, given that this study was not a controlled experiment, a causal interpretation needs caution. A negative spatial association between abundance of nonnative plants and turtle habitat use can result from an independent response of plants and turtles to a common environmental condition. That is, eastern box turtles may avoid the same environmental condition that promotes proliferation of nonnative plants. This scenario, however, is unlikely. Eastern box turtles, especially females, frequent in canopy gaps or open canopy areas (Agha et al. 2018; Flitz and Mullin 2006). The microenvironment in open areas promotes establishment and growth of many nonnative plant species (Brym et al. 2014; Daniels and Larson 2019). Furthermore, an experimental study found that eastern box turtles colonized areas where nonnative plants were removed (Carter et al. 2015), which supports a causal role of nonnative plants in affecting habitat selection.

At the scale of home range selection, locations used by eastern box turtles had lower density of nonnative plant species than available areas, suggesting that eastern box turtles avoid dense growth of nonnative plants in home range selection. Avoidance of Amur honeysuckle is documented in an eastern box turtle population (Attum et al. 2016). Avoidance of nonnative plants likely account for the previous reports that eastern box turtles were not found in areas dominated by Amur honeysuckle (McEvoy and Durtsche 2003) and that only a few individuals were found in areas dominated by Amur honeysuckle and autumn olive (Maes and Walton 2012).

Within home ranges, density of nonnative plants was lower in locations used by turtles than available locations, suggesting avoidance of nonnative plants within home ranges. In contrast, evidence of avoidance was not detected for Amur honeysuckle within the home range (Attum et al. 2016). The discrepancy may be attributable to the difference in plant species involved. In this study, Amur honeysuckle was a minor component in the study area, and therefore, not analyzed. For non-specialist herbivores, the growth form of plants is likely more relevant than the species identity. Because the growth form of Amur honeysuckle is similar to that of autumn olive, avoidance of Amur honeysuckle is expected. Alternatively, the discrepancy may be attributable to the difference in analytical approach between the studies. In Attum et al. (2016), males and females were lumped for analysis, and samples were mostly composed of males. In this study, within-home range selection was only evident in females. Thus, any responses that females might have had would be masked in Attum et al. (2016).

The evidence of avoidance of nonnative plant species was overall more prevalent in females than males. Females and males may be affected differently by habitat change caused by nonnative plants because they often have different habitat requirements. Female turtles need to produce eggs and find nesting sites that provide favorable thermal conditions. Females may avoid areas with high density of nonnative plants because extensive shading by dense growth of nonnative plants may create an unfavorable thermal environment. Female turtles generally move to canopy gaps or open canopy habitat during nesting season, which takes place from May to June (Flitz and Mullin 2006; Willey et al. 2012; Fredericksen 2014). Frequent basking (Carrière et al. 2008) and maintenance of high body temperatures by gravid females (Chen and Lue 2008; Millar et al. 2012; Chandler et al. 2020) are documented for other species of turtles. Maintenance of high body temperatures is thought to promote egg development (Sarkar et al. 1996), embryogenesis, and energy assimilation for energy demanding reproduction in gravid females (Lefevre and Brooks 1995). Non-gravid females may also maintain high body temperatures for energy demanding preparation of ovarian follicles for the next reproductive year (Nutting and

Graham 1993). In habitat subjected to prescribed burning, female eastern box turtles shift their home ranges to areas where fire has made open understory covers, which provided higher temperatures and greater amounts of solar radiation (Roe et al. 2020). This suggests that females are more likely than males to respond to structural alterations that alter thermal environments.

Negative associations between nonnative plants and eastern box turtles were detected for autumn olive, bigleaf periwinkle, Chinese wisteria, and golden bamboos, but not Japanese stiltgrass and Chinese privet. How animals respond to nonnative plants may depend on the type of habitat alteration caused by nonnative plants and the density of nonnative plants (Ceradini and Chalfoun 2017). For ectothermic animals, change in thermal property of habitat caused by dense growth of nonnative plants is hypothesized to be a common mechanism underlying the impacts of nonnative plants (Garcia et al. 2019). Autumn olive, bigleaf periwinkle, Chinese wisteria, golden bamboos, and Chinese privet form dense stands and lower temperatures of the surrounding air under their canopies (Bilcke et al. 2006; Campanello et al. 2007; Carter et al. 2015), potentially creating a suboptimal thermal environment (Valentine et al. 2007; Hacking et al. 2014). However, associations between turtle habitat use and Chinese privet were neutral on average, with a possible negative association in females. An ambiguous response to Chinese privet may be because the density of Chinese privet was not high compared to the other species. Cash et al. (2020) suggests that low to moderate density of privet likely has little effects on animals.

The response to Japanese stiltgrass was highly variable among individuals; some individuals showed no association, whereas others showed positive or negative association with Japanese stiltgrass. The eastern box turtles are reported to be frequent in Japanese stiltgrass patches (Orr et al. 2020). Similar frequent use of Japanese stiltgrass patches were also noted in my study. Alternatively, the use of Japanese stiltgrass patches may be promoted by enhanced prey availability. Invertebrate abundance increased with increasing Japanese stiltgrass abundance (Landsman et al. 2021). The apparent lack of avoidance for Japanese stiltgrass may be associated with their small extent of invasion and variable density within invaded patches. Animals likely

have access to adjacent uninvaded or less dense areas without traveling far, which may allow animals to avoid any negative effects of Japanese stiltgrass. How the impacts of nonnative plants change with their extent and density is identified as a priority question for predicting and managing the impacts of nonnative plants on animals (Stewart et al. 2021).

The avoidance of most nonnative plant species examined in this study indicates that eastern box turtles are prone to be displaced from areas dominated by nonnative plants, reducing the habitat area available to the turtles. With much of the turtle habitat being invaded by nonnative plants, the presence of nonnative plants may be a factor fueling the declines of eastern box turtles. An apparent sensitivity of females to nonnative plants raise concern about the population persistence in invaded habitat. Thus, the conservation and management of eastern box turtles will likely hinge on the reduction or removal of nonnative plants, with a priority on autumn olive (*Elaeagnus umbellata*), bigleaf periwinkle (*Vinca major*), golden bamboo (*Phyllostachys auera*), and Chinese wisteria (*Wisteria sinensis*). Management of these species should be accompanied by restoration of native plant communities because eastern box turtles are typically associated with relatively dense ground-level vegetation (Stickle 1950).

TABLES

Table 1. Morphometric and tracking summary for eastern box turtles (*Terrapene carolina carolina*) monitored in Winthrop Woods, Rock Hill, South Carolina through the summer of 2020 to the fall of 2021.

Turtle	Sex	CL (cm)	BM (g)	Tracking period (Number of days)	Number of locations
Blinky	M	13.9	432.6	07/18/2020 - 10/28/2021 (467)	69
Cyprus	F	12.2	452.6	05/10/2021 - 10/28/2021 (171)	58
Donnie	F	13	407.6	09/12/2020 - 10/28/2021 (411)	69
Elvira	F	12.4	397.6	10/02/2020 - 10/28/2021 (391)	64
Euphrates	F	12.8	497.6	05/10/2021 - 10/28/2021 (171)	54
Jason	M	12.4	327.6	10/16/2020 - 10/28/2021 (377)	62
Johnny	M	12	367.6	09/28/2020 - 10/28/2021 (395)	62
Kerry	F	12.7	442.6	10/02/2020 - 10/28/2021 (391)	65
Lilac	F	11.4	258.6	05/10/2021 - 10/23/2021 (166)	56
Mikey	M	13.3	457.6	09/12/2020 - 10/28/2021 (411)	48
Red	M	13.5	447.6	09/12/2020 - 10/28/2021 (411)	69
Sam	F	11.8	397.6	10/16/2020 - 10/23/2021 (372)	64
Small Leg	M	12.7	458.6	09/29/2020 - 10/28/2021 (394)	67
Small Stuff	F	12.8	307.6	07/18/2020 - 10/28/2021 (467)	63
Sprinter	F	11	317.6	07/18/2020 - 10/28/2021 (467)	72
Wednesday	F	12	347.6	10/16/2020 - 10/28/2021 (377)	59

Notes: M, male; F, female; CL, carapace length; BM, most recent body mass.

FIGURES

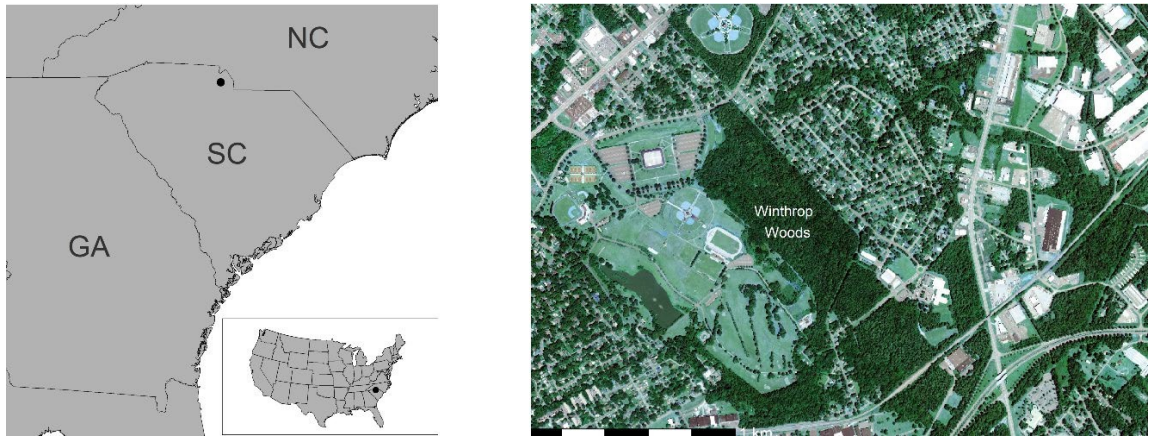


Figure 1. Geographic location of the study area in South Carolina, USA (left panel). Satellite image of Winthrop Woods located within Winthrop University Recreational Complex in the city of Rock Hill, South Carolina (right panel).

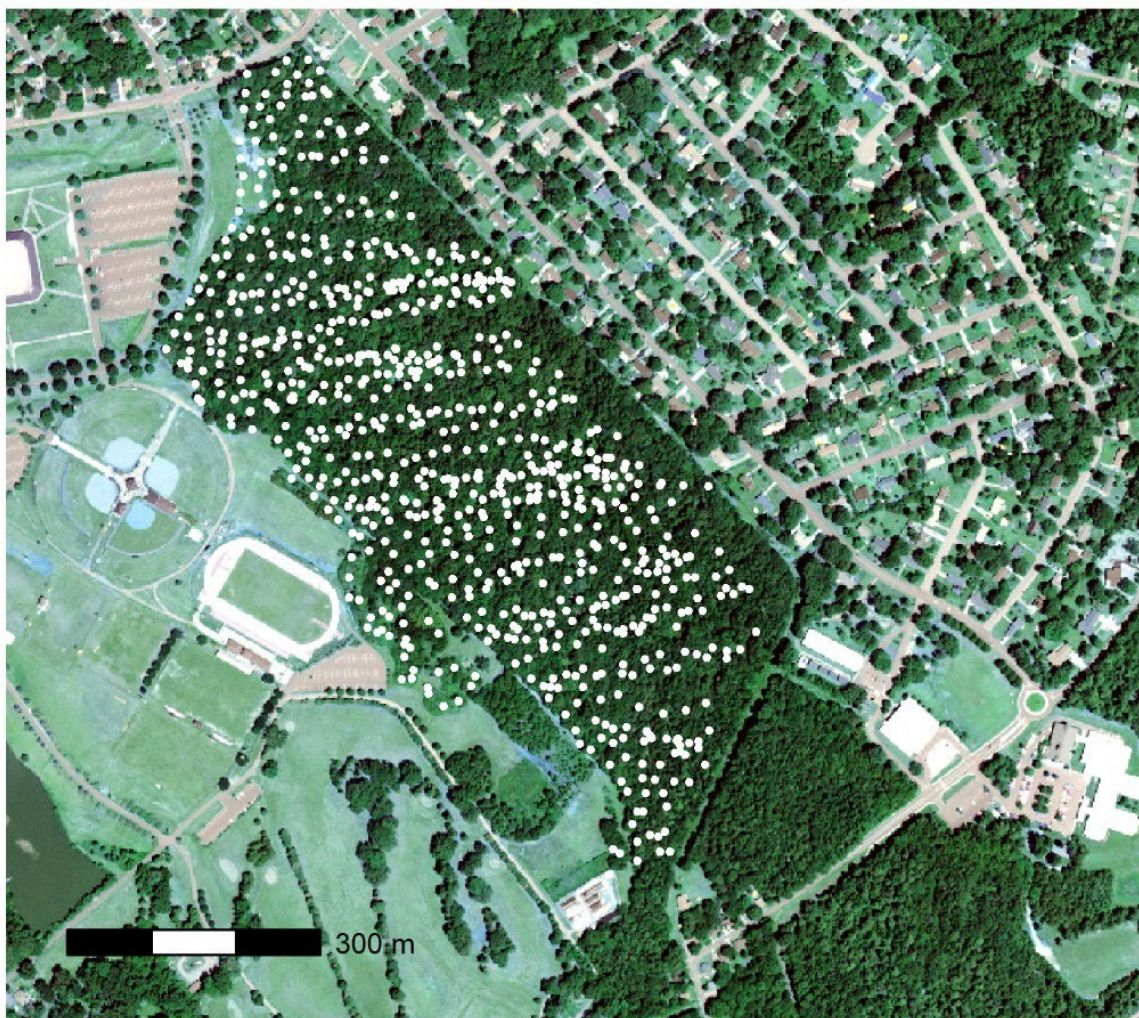


Figure 2. The distribution of 5 m radius vegetation plots (indicated with white dots) at Winthrop Woods, Rock Hill, South Carolina.



Figure 3. Interpolated distribution of densities of the most common nonnative plant species in Winthrop Woods and adjacent area in Rock Hill, South Carolina: (A) *Elaeagnus umbellate* (autumn olive), (B) *Ligustrum sinense* (Chinese privet), (C) *Microstegium vimineum* (Japanese stiltgrass), (D) *Phyllostachys auera* (golden bamboo), (E) *Vinca major* (bigleaf periwinkle), and (F) *Wisteria sinensis* (Chinese wisteria). The color gradient of pink to red depicts the increase in species density (per 100 m²) for the species in the order listed above: 40, 80, and >120 stems; 150, 250, and >350 stems; 40, 60, and >80%; 40, 60, and >80%; 40, 60, and > 80%; and 100, 150, >200 stems.

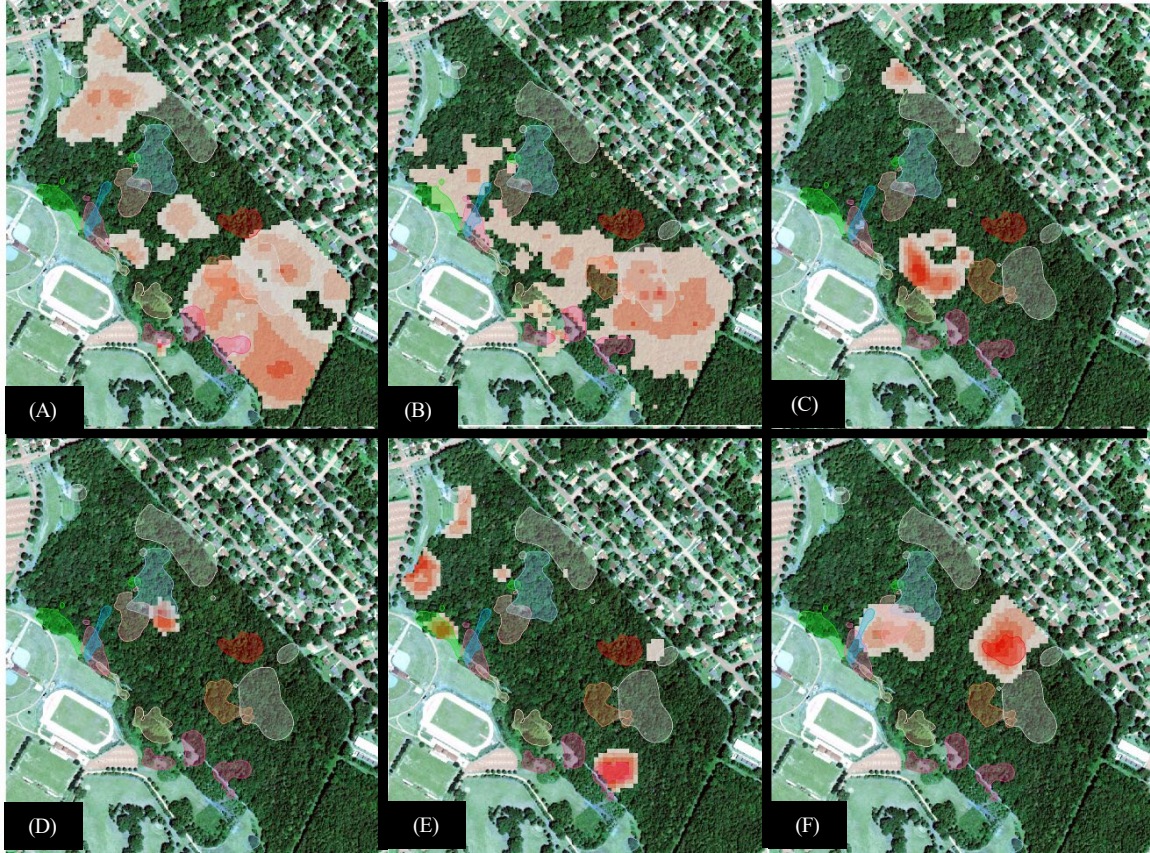


Figure 4. Core home range (estimated as 50% isopleth based on dynamic Brownian Bridge Movement Models) of female eastern box turtles overlain on interpolated distribution densities of nonnative plant. The home ranges are indicated in colored polygons. For plant densities, the color gradient of pink to red depicts the increase in density (see Figure 3 for the density gradient).

(A) *Elaeagnus umbellate* (autumn olive), (B) *Ligustrum sinense* (Chinese privet), (C) *Microstegium vimineum* (Japanese stiltgrass), (D) *Phyllostachys auera* (golden bamboo), (E) *Vinca major* (bigleaf periwinkle), and (F) *Wisteria sinensis* (Chinese wisteria).

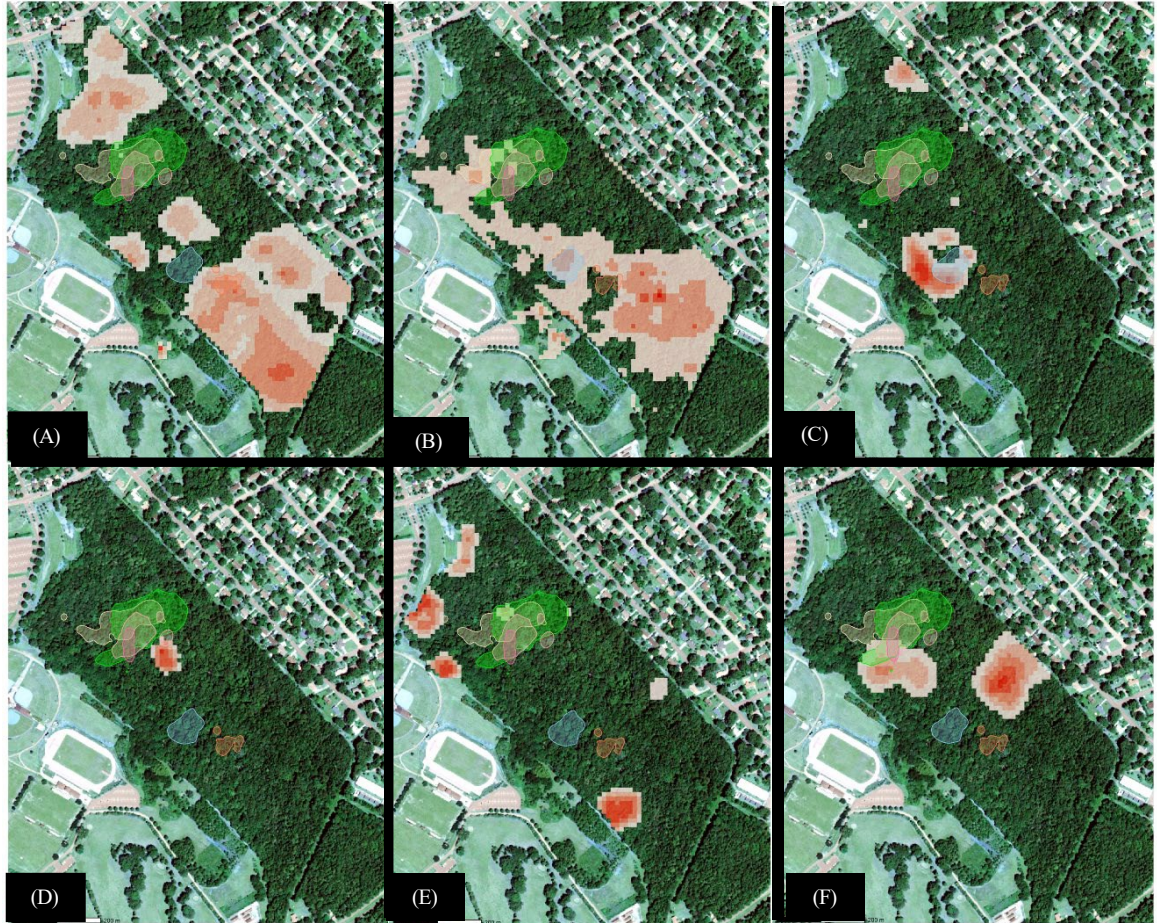


Figure 5. Core home range (estimated as 50% isopleth based on dynamic Brownian Bridge Movement Models) of male eastern box turtles overlain on interpolated distribution densities of nonnative plant. The home ranges are indicated in colored polygons. For plant densities, the color gradient of pink to red depicts the increase in density (see Figure 3 for the density gradient).

(A) *Elaeagnus umbellate* (autumn olive), (B) *Ligustrum sinense* (Chinese privet), (C) *Microstegium vimineum* (Japanese stiltgrass), (D) *Phyllostachys auera* (golden bamboo), (E) *Vinca major* (bignone periwinkle), and (F) *Wisteria sinensis* (Chinese wisteria).

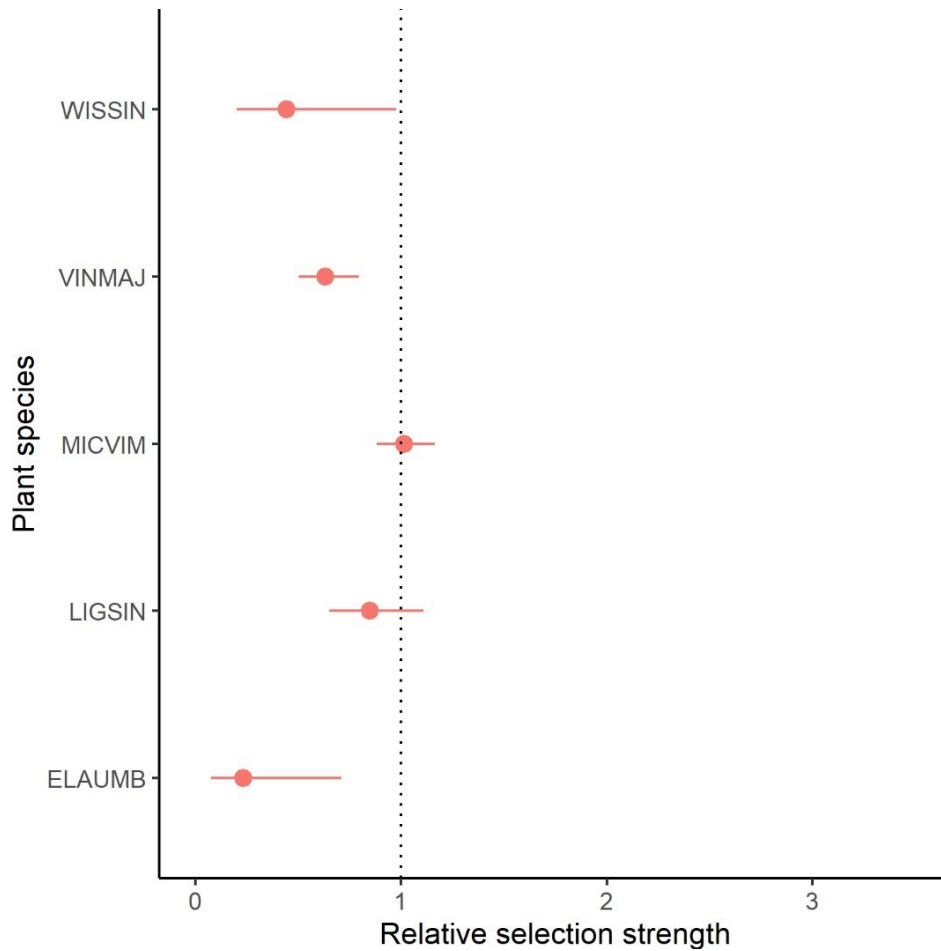


Figure 6. Relative selection strength for the second-order selection by female eastern box turtles estimated with generalized linear mixed effects models with five nonnative plant species: WISSIN (Chinese wisteria), *Wisteria sinensis*; VINMAJ (bigleaf periwinkle), *Vinca major*; MICVIM (Japanese stiltgrass), *Microstegium vimineum*; LIGSIN (Chinese privet), *Ligustrum sinense*; ELAUMB (autumn olive), *Elaeagnus umbellate*. Selection for a species is inferred when $RSS > 1$ and avoidance when $RSS < 1$. Circles and error bars represent a mean and a 95% confidence interval.

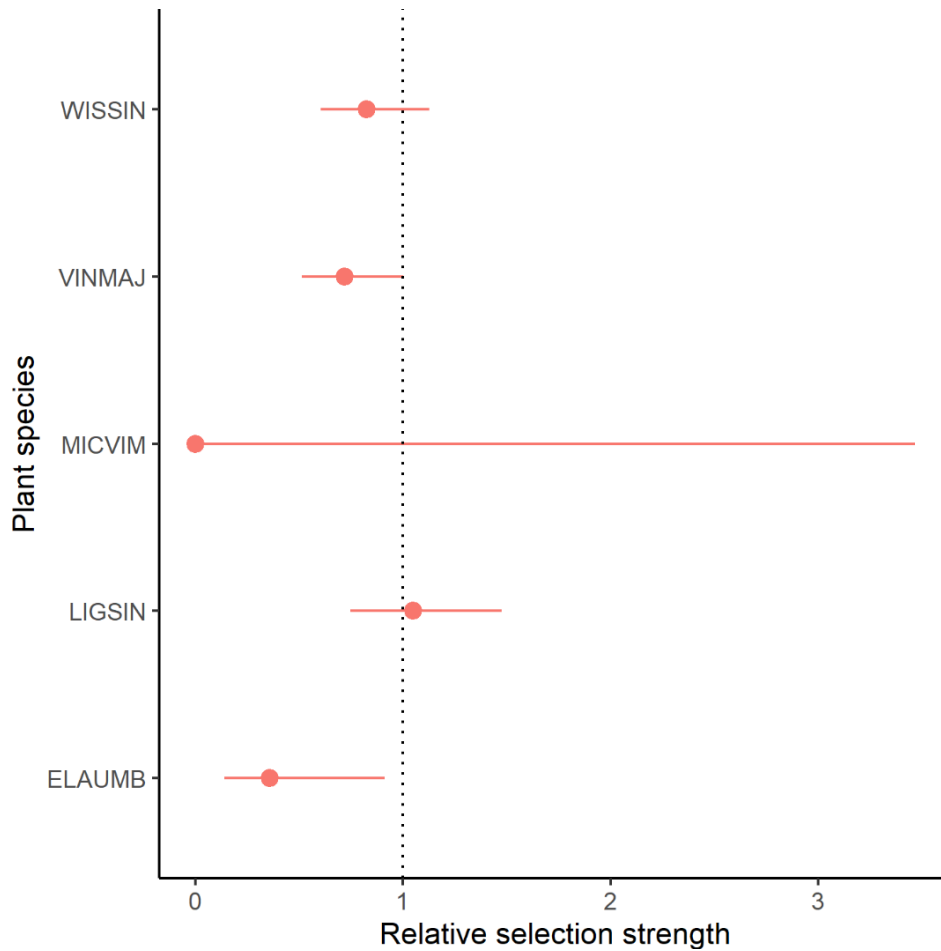


Figure 7. Relative selection strength for the second-order selection by male eastern box turtles estimated with generalized linear mixed effects models with five nonnative plant species: WISSIN (Chinese wisteria), *Wisteria sinensis*; VINMAJ (bigleaf periwinkle), *Vinca major*; MICVIM (Japanese stiltgrass), *Microstegium vimineum*; LIGSIN (Chinese privet), *Ligustrum sinense*; ELAUMB (autumn olive), *Elaeagnus umbellata*. Selection for a species is inferred when $RSS > 1$ and avoidance when $RSS < 1$. Circles and error bars represent a mean and a 95% confidence interval.

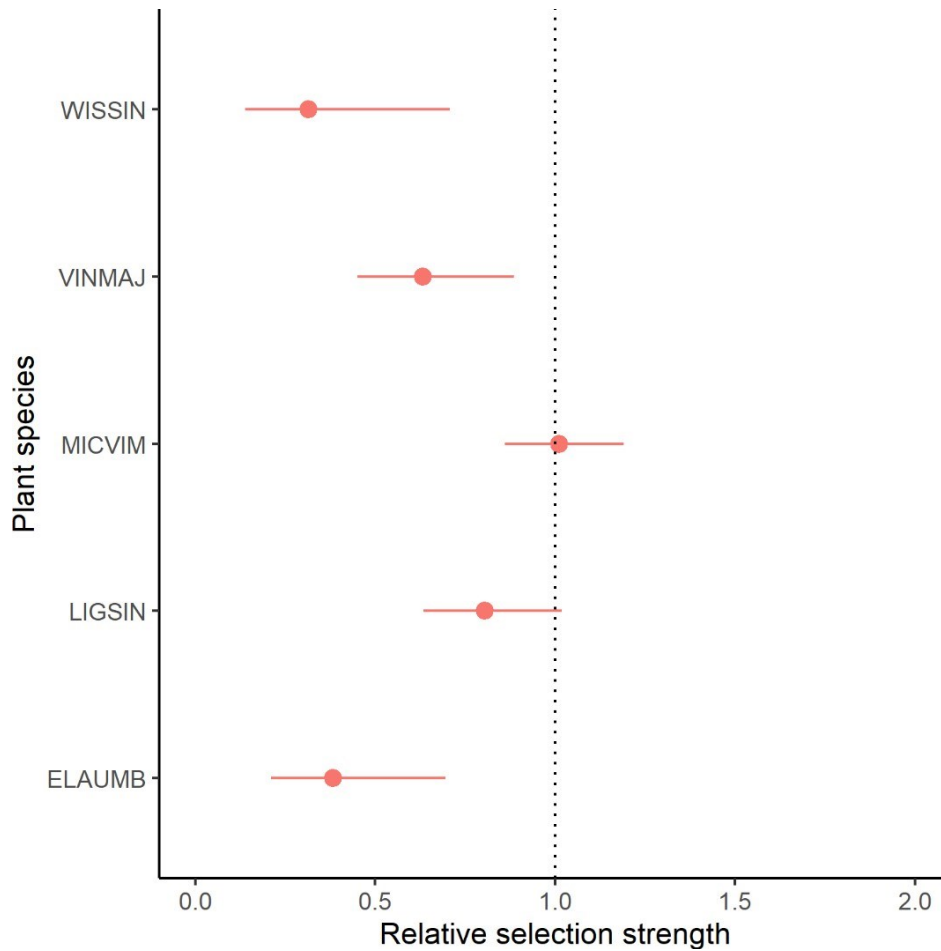


Figure 8. Relative selection strength for the third-order selection by female eastern box turtles estimated with generalized linear mixed effects models with five nonnative plant species: WISSIN (Chinese wisteria), *Wisteria sinensis*; VINMAJ (bigleaf periwinkle), *Vinca major*; MICVIM (Japanese stiltgrass), *Microstegium vimineum*; LIGSIN (Chinese privet), *Ligustrum sinense*; ELAUMB (autumn olive), *Elaeagnus umbellata*. Selection for a species is inferred when $RSS > 1$ and avoidance when $RSS < 1$. Circles and error bars represent a mean and a 95% confidence interval.

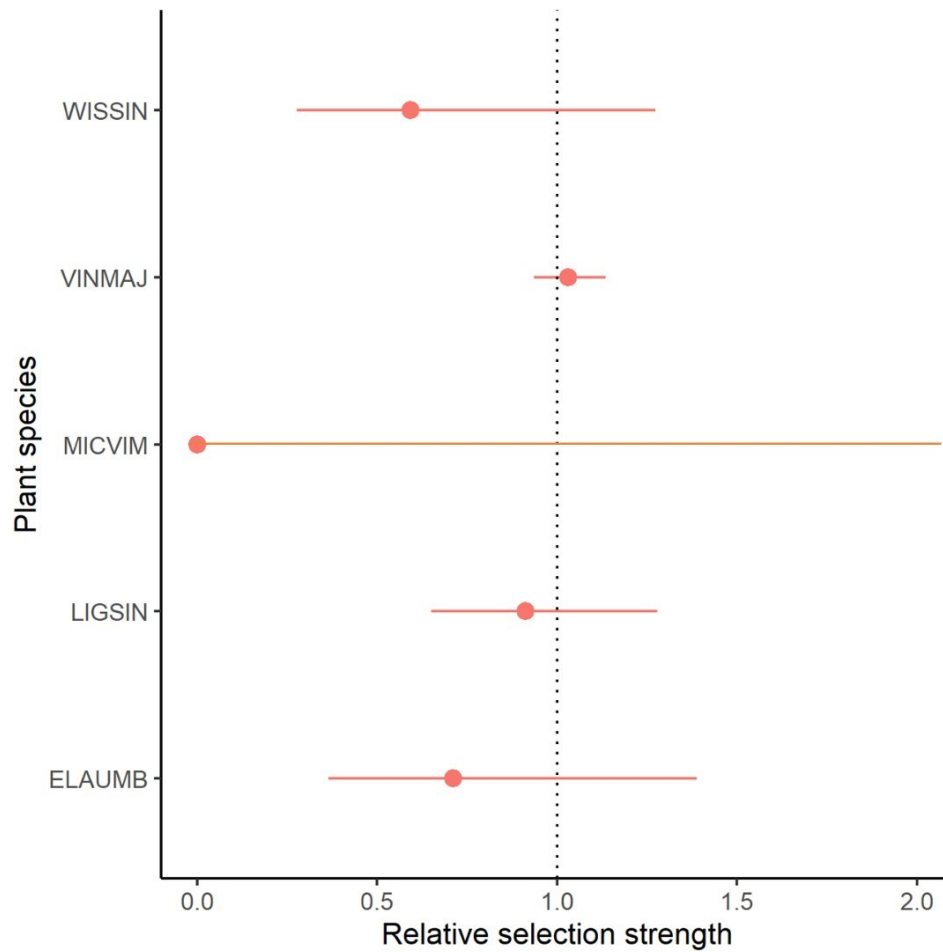


Figure 9. Relative selection strength for the third-order selection by male eastern box turtles estimated with generalized linear mixed effects models with four nonnative plant species WISSIN (Chinese wisteria), *Wisteria sinensis*; VINMAJ (bignone leaf periwinkle), *Vinca major*; MICVIM (Japanese stiltgrass), *Microstegium vimineum*; LIGSIN (Chinese privet), *Ligustrum sinense*; ELAUMB (autumn olive), *Elaeagnus umbellata*. Selection for a species is inferred when $RSS > 1$ and avoidance when $RSS < 1$. Circles and error bars represent a mean and a 95% confidence interval.

LITERATURE CITED

- Agha M, Todd D, Augustine B, Lhotka M, Fleckenstein J, Lewis M, Price J. 2018. Effects of gap-based silviculture on thermal biology of a terrestrial reptile. *Wildl Res.* 45(1):72-81.
- Angoh SYJ, Freeland J, Paterson J, Rupasinghe PA, Davy CM. 2021. Effects of invasive wetland macrophytes on habitat selection and movement by freshwater turtles. *Biol Invasions.* 23:2271–2288.
- Armstrong M, Boufassa A. 1988. Comparing the robustness of ordinary kriging and lognormal kriging: Outlier resistance. *Math Geol.* 20:447–57.
- Attum O, Lowry J, Kingsbury B, Carter E. 2016. The distribution of Amur honeysuckle and box turtle habitat use in an urban forest. *Urban Nat.* 12:1–9.
- Bellard C, Cassey P, Blackburn TM. 2016. Alien species as a driver of recent extinctions. *Biol Lett.* 12(2):1-4.
- Bellard C, Genovesi P, Jeschke JM. 2016. Global patterns in threats to vertebrates by biological invasions. *Proc Biol Sci.* 283(1823):1-9.
- Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behav Ecol.* 22(2):236–9.
- Bilcke J, Downes S, Büscher I. 2006. Combined effect of incubation and ambient temperature on the feeding performance of a small ectotherm. *Austral Ecol.* 31(8):937–947.
- Brooks J. 1976. Woodland Management Plan. (Filing Cabinet, Folder: W.C. Farms). Winthrop University Louise Pettus Archives, Rock Hill, SC, USA.
- Bossard, CC, Randall, JM, Hoshovsky M C. 2000. Invasive plants of California's wildlands. Univ of California Press.
- Burke RL. 2011. Nesting ecology and hatching success of the eastern box turtle, *Terrapene carolina*, on Long Island, New York. *The Amer. Mid. Natur.* 165:137–142.
- Calenge C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model.* 197(3–4):516–519.
- Campanello PI, Gatti MG, Ares A, Montti L, Goldstein G. 2007. Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *For Ecol and Manag.* 252(1–3):108–117.
- Carrier MA, Rollinson N, Suley AN, Brooks RJ. 2008. Thermoregulation when the growing season is short: sex-biased basking patterns in a northern population of painted turtles (*Chrysemys picta*). *J Herpetol.* 42(1):206–209.
- Carter ET, Eads BC, Ravesi MJ, Kingsbury BA. 2015. Exotic invasive plants alter thermal regimes: implications for management using a case study of a native ectotherm. *Funct Ecol.* 29(5):683–693.
- Cash JS, Anderson CJ, Gulsby WD. 2020. The ecological effects of Chinese privet (*Ligustrum sinense*) invasion: a synthesis. *Invasive Plant Sci. Manag.* 13(1):3–13.
- Ceradini JP, Chalfoun AD. 2017. When perception reflects reality: Non-native grass invasion alters small mammal risk landscapes and survival. *Ecol Evol.* 7(6):1823–1835.
- Chandler HC, Stegenga BS, Stevenson DJ. 2020. Thermal ecology of Spotted Turtles (*Clemmys guttata*) in two southern populations. *Copeia.* 108(4):737–745.
- Chen TH, Lue KY. 2008. Thermal preference of the yellow-margined box turtle (*Cuora flavomarginata*) (Testudines: Geoemydidae) inhabiting a mesic lowland forest, northern Taiwan. *Amphibia-Reptilia.* 29(4):513–522.
- Collier H, Vankat L, Hughes R. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *Americ Midland Natur.* 147:60–71.
- Congello K. 1978. Nesting and egg laying behavior in *Terrapene carolina*. 1978. *Proc. Pa. Acad. Sci.* 52:51–56.

- Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*. 97:153–166.
- Crystal-Ornelas R, Lockwood JL. 2020. The ‘known unknowns’ of invasive species impact measurement. *Biol Invasions*. 22(4):1513–1525.
- Daniels K, Larson R. 2020. Effects of forest windstorm disturbance on invasive plants in protected areas of southern Illinois, USA. *J Ecol*. 108(1):199–211.
- Department of Biology - Recreational & Research Complex. c2023. Winthrop University; [accessed 2023 Apr 20]. <https://www.winthrop.edu/cas/biology/recreational-and-research-complex.aspx>.
- Dodd CK. 2001. North American Box Turtles: A Natural History. University of Oklahoma Press.
- Downes S, Hoefer M. 2007. An experimental study of the effects of weed invasion on lizard phenotypes. *Oecologia*. 153:775–785.
- Enloe F, O’Sullivan E, Loewenstein J, Brantley E, Lauer K. 2018. The influence of treatment timing and shrub size on Chinese privet (*Ligustrum sinense*) control with cut stump herbicide treatments in the southeastern United States. *Invasv Pla Sci Manag*. 11(1):49–55.
- Fairbrothers E, Gray R. 1972. *Microstegium vimineum* (Trin.) A. Camus (Gramineae) in the United States. *Bulletin of the Torrey Botanical Club*. p. 97–100.
- Figueras MP, Green TM, Burke RL. 2021. Consumption patterns of a generalist omnivore: eastern box turtle diets in the Long Island pine barrens. *Diversity*. 13(8):345–357.
- Fletcher RA, Brooks RK, Lakoba VT, Sharma G, Heminger AR, Dickinson CC, Barney JN. 2019. Invasive plants negatively impact native, but not exotic, animals. *Glob Chan Biol*. 25(11):3694–3705.
- Flitz A, Mullin J. 2006. Nest site selection in the eastern box turtle, *Terrapene carolina carolina*, in Illinois. *Chelonian Conserv. Biol*. 5(2):309–312.
- Fredericksen T. S. 2014. Thermal regulation and habitat use of the eastern box turtle in southwestern Virginia. *Northeast Natu*. 21(4):554–564.
- Garcia RA, Clusella-Trullas S. 2019. Thermal landscape change as a driver of ectotherm responses to plant invasions. *Proc Biol Sci*. 286(1905):1–9.
- Gardner IC. 1958. Nitrogen fixation in *Elaeagnus* root nodules. *Nature*. 181:717–718.
- Graham A, Nguyen J, Sasaki K. 2022. Woodland Box Turtle (*Terrapene carolina carolina*) abundance declines with increasing urban land use in the Piedmont. *Ichthyol. Herpetol*. 110(4):705–13.
- Greenspan S, Condon EP, Smith LL. 2015. Home range and habitat selection in the eastern box turtle (*Terrapene carolina carolina*) in a longleaf pine (*Pinus palustris*) reserve. *Herpetol Conserv Biol*. 10:99–111.
- Greggor AL, Berger-Tal O, Blumstein DT, Angeloni L, Bessa-Gomes C, Blackwell BF, St Clair CC, Crooks K, de Silva S, Fernández-Juricic E, Goldenberg SZ. 2016. Research priorities from animal behaviour for maximising conservation progress. *Trends Ecol Evol*. 31(12):953–64.
- Habeck CW, Figueras MP, Deo JE, Burke RL. 2019. A surfeit of studies: what have we learned from all the box turtle (*Terrapene carolina* and *T. ornata*) home range studies? *Diversity*. 28:11(5):68.
- Hacking J, Abom R, Schwarzkopf L. 2014. Why do lizards avoid weeds? *Biol Invasions*. 16:935–947.
- Hale R, Blumstein DT, Mac Nally R, Swearer SE. 2020. Harnessing knowledge of animal behavior to improve habitat restoration outcomes. *Ecosphere*. 11(4):e03104.
- Harris A, Clark D, Elmore R, Harper C. 2020. Spatial ecology and resource selection of eastern box turtles. *J Wildl Manage*. 84(8):1590–1600.
- Hawthorne TL, Elmore V, Strong A, Bennett-Martin P, Finnie J, Parkman J, Reed J. 2015. Mapping non-native invasive species and accessibility in an urban forest: A case study of participatory mapping and citizen science in Atlanta, Georgia. *App Geo*. 56:187–198.
- Hayes SJ, Holzmüller EJ. 2012. Relationship between invasive plant species and forest fauna in eastern North America. *Forests*. 3(3):840–852.
- Hejda M, Pyšek P, Jarosik V. 2009. Impact of invasive plants on the species richness, composition, and composition of invaded communities. *J. Ecol*. 97:393–403.
- Hiemstra P, Hiemstra MP. 2013. Package ‘automap’. *Compare*. 105:10.
- Iannone BV, Oswalt CM, Liebhold AM, Guo Q, Potter KM, Nunez-Mir G. C, Fei S. 2015. Region-specific patterns and drivers of macroscale forest plant invasions. *Divers Distrib*. 21(10):1181–1192.

- Jeschke JM, Bacher S, Blackburn TM, Dick JT, Essl F, Evans T, Kumschick S. 2014. Defining the impact of non-native species. *Conserv Biol.* 28(5):1188–1194.
- Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology.* 61(1):65–71.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos.* 373–386.
- Kranstauber B, Kays R, Lapoint SD, Wikelski M, Safi K. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *J Anim Ecol.* 81:738–746.
- Kranstauber B, Smolla M, Scharf K. 2018. move: visualizing and analyzing animal track data. R package version 3.1.0.
- Landsman AP, Burghardt KT, Bowman JL. 2020. Invasive grass (*Microstegium vimineum*) indirectly benefits spider community by subsidizing available prey. *Ecol and Evol.* 10(20):1133–1143.
- Landsman AP, Schmit JP, Matthews ER. 2021. Invasive plants differentially impact forest invertebrates, providing taxon-specific benefits by enhancing structural complexity. *Front Ecol. Evol.* 9:1–11.
- Lefevre K, Brooks RJ. 1995. Effects of sex and body size on basking behavior in a northern population of the painted turtle, *Chrysemys picta*. *Herpetologica.* 51(2):217–224.
- Leicht S A, Silander Jr A, Greenwood K. 2005. Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. *J. Torrey Bot. Soc.* 132(4):573–580.
- Maes J, Walton EM. 2012. An initial box turtle (*Terrepenne* spp.) population assessment at Southern Illinois University Edwardsville. *Illinois Geogr.* 54(2):1–8.
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, Brooks M. 2017. Package ‘glmmtmb’. R Package Version 0.2. 0.
- McEvoy L, Durtsche D. 2003. The effect of invasive plant species on the biodiversity of herpetofauna at the Cincinnati Nature Center. *Norse Sci.* 1:51–55.
- McKnight T. 2011. Observed plant preferences of eastern box turtles (*Terrapene carolina carolina*) in a Maryland forest. *Herpetol Notes.* 4:97–102.
- Millar CS, Graham JP, Blouin-Demers G. 2012. The effects of sex and season on patterns of thermoregulation in Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada *Chelonian Conserv Biol.* 11(1):24–32.
- Miller JH, Chambliss EB, Loewenstein NJ. 2010 (slightly revised 2012, 2013, and 2015). A field guide for the identification of invasive plants in southern forests Gen. Tech. Rep. SRS–119. Asheville, NCC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 126 p. https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs119.pdf.
- Miller KM, McGill BJ, Weed AS, Seirup CE, Comiskey JA, Matthews ER, Perles S, Schmit J. 2021. Long-term trends indicate that invasive plants are pervasive and increasing in eastern national parks. *Ecol Appl.* 31(2):1–17.
- Nazdrowicz NH, Bowman JL, Roth RR. 2008. Population ecology of the eastern box turtle in a fragmented landscape. *J Wildlife Manage.* 72(3):745–53.
- Nelson BW, Oliveira AD, Batista GT, Vidalenc, D, Silveira M. 2001. Modeling biomass of forests in the southwest Amazon by polar ordination of Landsat TM. In *Proceedings, Tenth Brazilian Remote Sensing Symposium*. INPE. Foz de Iguaçu, Paraná, Brazil. p. 1683-1690.
- Nestleroad J, Zimmerman D, Ebinger J. 1987. Autumn olive reproduction in three Illinois state parks. *Trans of the IL Sta Acad of Sci.* 80:33–39.
- Nutting WL, Graham TE. 1993. Preferred body temperatures in five Nearctic freshwater turtles: a preliminary study. *Comp Biochem Phys A.* 104(2):243–246.
- Ollier S, Bertelsmeier C. 2022. Precise knowledge of commodity trade is needed to understand invasion flows. *Front Ecol Environ.* 20(8):467–473.
- Oliphant AJ, Wynne RH, Zipper CE, Ford WM, Donovan PF, Li J. Autumn olive (*Elaeagnus umbellata*) presence and proliferation on former surface coal mines in eastern USA. *Biological Invasions* 19(1):179–195.
- Olson J. 1983. A Request for an Official Designation of the Winthrop Woods as a Teaching and Research Laboratory. John B. Olson. (Filing Cabinet, Folder: W.C. Farms). Winthrop University Louise Pettus Archives, Rock Hill, SC, USA.
- Orr JM, Ernst CH, Boucher TP. 2020. Long-term comparison of relocated and resident box turtles. *Terrapene carolina carolina*. *Herpetol Bull.* 151:6–9.
- Oswalt CM, Fei S, Guo Q, Iannone III BV, Oswalt SN, Pijanowski BC, Potter KM. 2015. A subcontinental view of forest plant invasions. *NeoBiota.* 24:49–54.

- Oswalt CM, Oswalt SN, Clatterbuck WK. 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *For. Ecol. Manag.* 242(2–3):727–732.
- Parlin AF, Amaral JPS, Dougherty JK, Stevens MH, Schaeffer PJ. 2017. Thermoregulatory performance and habitat selection of the Eastern Box Turtle (*Terrapene carolina carolina*). *Conserv. Physiol.* 5:cox070.
- Pebesma EJ. 2004. Multivariable geostatistics in S: the gstat package. *Comput Geosci.* 30(7):683–691.
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P. 2020. Scientists' warning on invasive alien species. *Biol Rev.* 95:1511–1534.
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M. 2012. A global assessment of invasive plant impacts on resident species, communities, and ecosystems: the interaction of impact measures, invading species' traits, and environment. *Glob Change Biol.* 18(5):1725–1737.
- Qu T, Du X, Peng Y, Guo W, Zhao C, Losapio G. 2021. Invasive species allelopathy decreases plant growth and soil microbial activity. *PloS One.* 16(2):1–12.
- Randall M. and Marinelli J. 1996. *Invasive Plants: Weeds of the Global Garden*. New York, NY: Brook Bot Gard Publ.
- Refsnider JM, Carter SE, Diaz A, Hulbert AC, Kramer GR, Madden P, Streby HM. 2022. Macro- and microhabitat predictors of nest success and hatchling survival in eastern box turtles (*Terrapene carolina carolina*) and spotted turtles (*Clemmys guttata*) in Oak Savanna Landscapes. *Front. Ecol. Evol.* 24:9:967
- Rehder A. 1940. *Manual of cultivated trees and shrubs*. 2nd Edition. Macmillan Publishing, New York. p. 996.
- Roe H, Kish L, Nacy P. 2020. Variation and repeatability of home range in a forest-dwelling terrestrial turtle: implications for prescribed fire in forest management. *J Zool.* 310(1):71–82.
- Rossell R, Rossell M, Patch S. 2006. Microhabitat selection by eastern box turtles (*Terrapene c. carolina*) in a North Carolina mountain wetland. *J Herpetol.* 40(2):280–284.
- Sarkar SN, Sarkar PD, Maiti. 1996. Photothermal effects on ovarian growth and function in the soft-shelled turtle *Lissemys punctata punctata*. *J Exp Zoology.* 274:41–55.
- Schirmel J, Bundschuh M, Entling MH, Kowarik I., Buchholz S. 2016. Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. *Glob Change Biol.* 22(2):594–603.
- Seebens H, Blackburn TM., Hulme PE, van Kleunen M, Liebhold AM, Orlova-Bienkowskaja M, Pyšek, P, Schindler S, Essl F. 2021. Around the world in 500 years: Inter-regional spread of alien species over recent centuries. *Global Ecol Biogeogr.* 30:1621–1632.
- Sol D, Lapedra O, González-Lagos C. 2013. Behavioural adjustments for a life in the city. *Anim behav.* 85(5):1101–12.
- South Carolina Natural Heritage Program. Tracking South Carolina's Species of Concern. c2023. [accessed 2023 Apr 30]. <https://schtportal.dnr.sc.gov/portal/apps/sites/#/natural-heritage-program>.
- Stewart PS, Hill RA, Stephens PA, Whittingham MJ, Dawson W. 2021. Impacts of invasive plants on animal behavior. *Ecol Lett.* 24(4):891–907.
- Stickel LF. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecol Monog.* 20(4):351–378.
- Turbelin AJ, Malamud BD, Francis RA. 2017. Mapping the global state of invasive alien species: patterns of invasion and policy responses. *Global Ecol Biogeogr.* 26(1):78–92.
- U.S. Department of Agriculture, Plant Epidemiology and Risk Analysis Laboratory (PERAL). 2012. Weed Risk Assessment for *Phyllostachys aurea* Carr. Ex A. & C. Riviere (Poaceae) - Golden Bamboo. Raleigh, North Carolina. 14 p. https://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/wra/wra-guidelines.pdf
- Unknown. 1932–1937. College Farm Valuable to Winthrop Students. Unknown. (Filing Caniet, Folder: Vertical Farm). Winthrop University Louise Pettus Archives, Rock Hill, SC, USA.
- Valentine LE, Roberts B, Schwarzkopf L. 2007. Mechanisms driving avoidance of nonnative plants by lizards. *J Appl Ecol.* 44:228–237.
- van Dijk PP. 2011. Eastern box turtle. *The IUCN Red List of Threatened Species* 2011:8235:1– 14.
- van Kleunen, M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, and Antonova LA. 2015. Global exchange and accumulation of nonnative plants. *Nature.*

- 525(7567):100–103.
- Vilà M., Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities, and ecosystems. *Ecol Lett.* 14:702–708
- Wells F, and Brown L. 2000. An annotated checklist of the vascular plants in the forest at historic Mount Vernon, Virginia: a legacy from the past *Castanea*. 65(4):242–257.
- Willey L, Sievert R. 2012. Notes on the nesting ecology of eastern box turtles near the northern limit of their range. *NE Natural*. 19(3):361–372.