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ABSTRACT. Seasonal variation in animal activity influences fitness and the intensity of ecological interactions (e.g., competition, predation), yet aspects of global change in the Anthropocene may catalyze shifts in seasonal activity. Invasive plants are components of global change and can modify animal daily activity, but their influence on animal seasonal activity is less understood. We examined how invasive woody shrubs (Autumn olive [*Elaeagnus umbellata*] and Amur honeysuckle [*Lonicera maackii*]) affect seasonal activity of three common small-mammal species by coupling experimental shrub removal with autumnal camera trapping for two consecutive years at six paired forest sites (12 total plots). Eastern chipmunks (*Tamias striatus*) foraged more, and foraging was observed at least 20 days longer, in shrub-invaded forests. White-footed mice (*Peromyscus leucopus*) foraged more in invaded than cleared plots in one study year, but *P. leucopus* autumn activity timing did not differ between shrub-removal treatments. Fox squirrel (*Sciurus niger*) activity displayed year-specific responses to shrub removal suggesting intraannual cues (e.g., temperature) structure *S. niger* autumnal activity. Our work highlights how plant invasions can have species-specific effects on seasonal animal activity, may modify the timing of physiological processes (e.g., torpor), and could generate variation in animal-mediated interactions such as seed dispersal or granivory.

INTRODUCTION

The seasonal timing of animal activity is strongly associated with individual fitness (e.g., hibernation during stressful seasons, Armitage 2017), population dynamics (e.g., reproduction timing; McLean and Guralnick 2021), and community interactions (e.g., herbivory during seasonal migrations; Bauer and Hoye 2014). Seasonal activity is structured by environmental factors, yet global change in the Anthropocene is altering environments with consequences for animal activity (Gilbert et. al. 2023). Shifting temperature regimes, for example, can modify mammal hibernation (Ozgul et. al. 2010; Lane et. al. 2012), accelerate insect activity (Renner and Zohner 2018), and correlate with bird migration timing (Van Buskirk et. al. 2009). With the potential for global change to affect animal seasonal activity, and the established role of seasonal activity in affecting individuals, populations, and communities, exploring how different aspects of global change affect seasonal animal activity is a high priority (Gilbert et. al. 2023).

Invasive, non-native plants are agents of global change that modify habitats and native populations (Mack et. al. 2000; Richardson and Rejmánek 2011). Transformation of habitats by invasive plants can alter animal behavior (Stewart et. al. 2021); for example, invasive shrubs in United States (U.S.) forests produce seasonal pulses of food (i.e., fruits, seeds) and exhibit extended leaf phenology, altering seasonal habitat structure (Schuster et. al. 2021) and buffering climate extremes (Maynard-Bean and Kaye 2021) in ways that modify the animal behavior. Invasive shrubs can shift small mammal diel activity patterns (Guiden and Orrock 2019), predator-avoidance behavior (Dutra et. al. 2011), and habitat use (Guiden and Orrock 2017). These shifts in activity patterns alter plant-animal interactions (Bartowitz and Orrock 2016) and predator-prey dynamics (Mattos and Orrock 2010). Yet, despite evidence that invasive shrubs modify diel activity for some small mammals (e.g., *Peromyscus leucopus*; Guiden and Orrock 2019), it is unclear whether these shrubs modify seasonal patterns of behavior for multiple species or whether they affect some species but not others. This knowledge gap is important to address because differences in life history and ecology among small-mammal species are likely to lead to different seasonal responses to invasive shrubs.

In autumn, small mammals adopt various strategies to survive winter (Ruf and Geiser 2015). Some small mammals minimize metabolic demands by entering hibernation, and the timing of this life stage transition may depend on the abiotic environment and resource availability (Ozgul et al. 2010; McLean and Guralnick 2021) or the minimization of predation risk (Turbill and Stojanovski 2018). Because invasive shrubs may modify all three of these variables in forests, invasive shrubs could drive important alterations in small mammal autumnal activity, thereby shifting spatial trends in animal fitness and abundance and altering the ecological interactions moderate by these small mammals.

We tested whether autumnal small-mammal activity in a temperate U.S. forest was modified by the presence of two co-occurring invasive shrubs, *Lonicera maackii* and *Elaeagnus umbellata*. We examine daily small-mammal activity collected over two autumns (2019, 2020) using the experimental removal of invasive shrubs on half of our study sites, an effective approach for exploring how invasive shrubs modify animal activity (e.g., Guiden and Orrock 2017, 2019). We focused our study on three common small-mammal species: the eastern chipmunk (*Tamias striatus*), the white-footed mouse (*Peromyscus leucopus*), and the fox squirrel (*Sciurus niger*). These species serve important roles as prey, granivores, and seed dispersers in these forests (e.g., Synder 1982, Lackey et. al. 1985). Importantly, these species differ in their overwintering strategies, and environmental shifts mediated by invasive shrubs may generate predictable changes in the autumnal activity unique to each species. *Tamias striatus* initiate hibernation during autumn in response to harsh environmental conditions and low resource availability (Ruf and Geiser 2015), suggesting invasion by shrubs could prolong *T. striatus* autumn activity. In contrast, *P. leucopus* and *S. niger* largely remain active over winter (Ruf and Geiser 2015, Wassmer and Refinetti 2019), suggesting the autumnal activity timing for these two species may be less affected by shrub invasion. By coupling experimental removal of invasive shrubs with activity data collected over two autumns, we aim to estimate how invasive shrubs modify activity in autumn. Specifically, we examined two *a priori* research questions: 1) does invasive shrub removal influence the probability of observing animal activity? And 2) does invasive shrub removal influence the seasonal duration of animal activity as autumn progresses?

METHODS:

Field site locations and invasive shrub removal

To evaluate the activity patterns of small mammals in shrub-invaded and shrub-removed habitats, we conducted replicated manipulations of invasive shrub presence in a central Michigan mixed hardwood forest. Experiments took place at Fish Lake Environmental Education Center (GPS coordinates: 43.11356 N, -83.24362 W), a 240-acre forest managed by Eastern Michigan University. Twelve 20 m × 20 m plots were delineated along an east to west gradient, paired spatially to generate six blocked pairs of plots. The minimum distance between all plot edges was 50 m, greater than the estimated home range size for *T. striatus* and *P. leucopus* (Synder 1982; Lackey et. al. 1985). Prior to removal, *L.maackii* and *E. umbellata* comprised the invasive shrub sub-canopy in this forest, averaging 1.4 stems/m^2 and 5.8 stems/m^2 per plot, respectively (Appendix S1: Section 1). One plot within each blocked pair was randomly assigned to either have invasive shrubs mechanically removed with a handsaw 3-4 cm above the soil surface ("shrub-removed") or invasive shrubs left intact ("shrub-present") in June 2018. Stumps of invasive shrubs were treated with glyphosate via daubers and shrub removal treatments were maintained bi-annually (Connolly et. al. 2024; Appendix S1: Section S1).

Quantifying animal activity

We quantified animal activity during autumn 2019 and 2020 using camera traps. Dates and durations of camera deployment differed slightly by plot and study year, but all cameras in each year were sampling for a minimum of 34 days from October to November to capture at least one full lunar cycle (Appendix S1: Table S1). Single cameras (Bushnell Trophy Trail Cameras 20MP) were secured to a mature tree rooted within the southern half of each plot. Cameras were positioned ~0.4 m above the soil surface and each camera was oriented north towards the plot's center to standardize the field of vision, minimize potential effects of direct radiation on the camera, and best estimate the effects of shrub-removal treatments on activity (Zimmerman et. al. 2016). Because greater stem densities may affect animal detection (Hofmeester et. al. 2017), we selected camera locations to have few stems in the 3m area in camera's visual field, regardless of plot-level treatment. Three meters encompasses an effective detection distance for small animals in dense forest understories (Appendix S1: Section S2).

Data processing and analysis

We imposed a minimum 10-minute duration between observations of the same species at each plot to increase independence between observations and avoid inflating observations with periods of intense activity by single individuals (Meek et. al. 2014). We used this observation data to then summarize photo presence ("1") or absence ("0") per species per day at each plot. Using R (R Core Team 2022), we constructed separate generalized linear mixed models for each small mammal species evaluating year, invasive shrub removal, and day of year (DOY) as main fixed effects including all higher order interactions ("glmmTMB"; Brooks et. al. 2017). We used a binomial error distribution and included a first-order autoregressive term in each model to account for non-independence between likelihoods of a detection on consecutive days. We also included a random effect in our model accounting for plots nested within pairs. Because interannual differences in the environment may contribute to year-specific patterns of activity (e.g., Landry-Cuerrier et. al. 2008), we also compared the effect of shrub removal on the likelihood of observing species as DOY progressed within each year (Appendix S1: Table S2).

RESULTS

Our sampling effort yielded a total of 1,732 photos of focal animals. Of this total, 24.9% were *T. striatus* photos (2019: 154 photos, 2020: 277 photos) and 21.5% were *S. niger* photos (2019: 164 photos, 2020: 209 photos). *Peromyscus leucopus* was the most observed small mammal (53.6% of total; 2019: 597 photos, 2020: 349 photos).

In both study years we found greater probability of observing *T. striatus* on shrub-present plots than shrub removed plots; the magnitude of this effect differed by study year and as DOY progressed (Fig. 1; Table 1). We observed a significant year × shrub interaction (Table 1), such that the probability of observing *T. striatus* did not differ between study years in shrub-present plots ($z = -0.95$, $p = 0.343$), but we observed significantly fewer *T. striatus* on shrub-removed plots in 2020 than in 2019 ($z = 2.63$, $p = 0.009$). We also observed a significant DOY × shrub interaction: averaged across years, the probability of observing *T. striatus* declined more steeply as DOY progressed in shrub-cleared plots (slope [SE]: -4.06 [0.96]) than in shrub-present plots (slope [SE]: -0.82 [0.31]; $z = -3.48$, $p < 0.001$). Year-specific contrasts report the probability of observing *T. striatus* declined more steeply in shrub-removed plots than shrub-present plots as DOY progresses in both study years (Appendix S1: Table S3).

The effect of shrub removal on the probability of observing *P. leucopus* differed by study year and as DOY progressed (Fig. 1; Table 1). We observed a significant year × shrub interaction (Table 1), such that the probability of observing *P. leucopus* was greater in shrub-present versus shrub-removed plots in 2020 (z = -4.47, $p < 0.001$), but did not differ between plot types in 2019 (z = 0.01, p = 0.993). We also observed a significant DOY × shrub interaction: averaged across years, the probability of observing *P. leucopus* declined more rapidly in shrub-cleared plots (slope [SE]: -0.66 [0.49]) than in shrub-present plots (slope [SE]: -0.25 [0.48]), but the difference between slopes was only marginally significant (z = -1.69, $p = 0.090$). Year-specific contrasts reveal a greater decline in *P. leucopus* observation over time in shrub-removed than shrub-present plots in 2019, but no difference in observation likelihood over time between invasive shrub treatment plots in 2020 (Appendix S1: Table S3).

The effect of shrub removal on the probability of observing *S. niger* differed by study year (Fig. 1; Table 1). We observed a significant year × shrub interaction (Table 1): the probability of observing *S. niger* was significantly greater on shrub-removed plots than shrub-cleared plots in 2019 (z = 3.44, $p < 0.001$), but *S. niger* were observed more on shrub-cleared plots than shrub-present plots in 2020 (z = -2.03, $p = 0.042$). Year-specific contrasts reveal no difference in *S. niger* observation likelihood as DOY progressed between plot types in either study year (Appendix S1: Table S3).

DISCUSSION

Invasive shrubs are prevalent in North American deciduous forests (Richardson and Rejmánek 2011), with pervasive effects on native plant communities (Miller and Gorchov 2004) and animal behavior (Guiden and Orrock 2017, 2019). We demonstrate that invasive shrubs also affect seasonal animal activity in patterns that are inherently spatial and species-specific: extended seasonal activity is observed in shrub-invaded areas, may be found only in particular years, and does not affect all species (Fig. 1). In demonstrating that invasive plants alter patterns of seasonal activity for some small-mammal species but not others, our results provide a mechanism that may contribute to spatiotemporal disparities in small-mammal populations, community structure, and the ecological interactions where small mammals are key participants.

Potential drivers of extended seasonal small mammal activity in shrub-invaded habitats

Multiple factors could contribute to the shifts in seasonal activity we observed. Temperature affects animal daily activity (Guiden and Orrock 2020) and signals the cessation of autumnal above ground activity for some small mammals. Although variable within and between study years, shrub removal did affect air temperatures in 2019 (Appendix S1: Section S4). Maximum daytime air temperatures in 2019 were greater in shrub-present than shrub-removed plots in early autumn, but colder in shrub-present plots in late autumn (Appendix S1: Figure S5). Greater *T. striatus* activity on shrub-present plots in 2019 may be driven partially by warmer temperatures in mid-autumn on this plot type (Fig. 1). However, the greater thermal costs of foraging as temperatures decline should result in less activity for seasonally torpid animals in shrub-present plots, and we did not find strong support for this pattern.

Shifts in predation risk could also contribute to changes in seasonal activity (e.g., Turbill and Stojanovski 2018). As perceived predation risk is less in shrub-invaded forests (Mattos and Orrock 2010), seasonal reductions in predation risk could promote prolonged autumnal foraging in shrub-invaded forests. Evidence for this hypothesis is inconclusive: Dutra et. al. (2011) demonstrate more mesopredator *Procyon lotor* activity in *L. maackii* invaded forests, but their estimates were aggregated across seasons. *Procyon lotor* was the most prevalent mesopredator at our sites, but *P. lotor* activity during our study did not differ between shrub treatment plots during autumn (Appendix S1: Section S5), implying that cessation of rodent activity was unlikely to be driven by *P. lotor* activity. Rodents, however, are attacked by multiple predators whose hunting is influenced by habitat structure (e.g., raptors; Preston 1990), suggesting autumn rodent activity in shrub-invaded forests could be a function of risk posed by other predators.

Changes in seasonal activity could also arise if invasive shrubs provide food for small mammals (e.g., Engle 1962), increasing autumnal activity when the fruits and seeds of invasive shrubs are abundant and other resources are scarce (Dutra et. al. 2011). Invasive shrubs are prolific fruit and seed producers. Individual *L. maackii* shrubs growing in forest interiors can produce >700 seeds annually (Lieurance and Landsbergen 2016), and *L. maackii* fruits can comprise over 50% of the total autumn fleshy fruit crop in eastern North America landscapes with some animals depending on this resource (e.g., Gleditsch and Carlo 2011). Small mammal populations may similarly be support by this autumn resource. Dutra (2011) demonstrate an increase in *P. leucopus* abundance on plots where *L. maackii* fruits were present compared to plots where the fruits had been experimentally removed, supporting conclusions that this autumn resource may support more foraging and greater rodent populations in shrub-invaded forests.

Implications of shrub-mediated shifts in animal seasonal behavior

Invasive shrubs modified the activity patterns for some small-mammal species (Fig. 1) and this effect was greatest for the species in our study that relies more heavily upon torpor to cope with environmental stress (Ruf and Geiser 2015). *Tamias striatus* enter torpor earlier when resources are scarce (Landry-Cuerrier et. al. 2008), yet this species was active in our study at least 20 days longer in sites with invasive shrubs present in both study years. Shifts in *T. striatus* seasonal activity, regardless of the mechanism, prolong opportunities for foraging that could increase overwinter survival (e.g., Ozgul et. al. 2010; Lane et. al. 2012) and sustain larger populations during the growing seasons when small mammal populations are typically measured (e.g., Bartowitz and Orrock 2016). Although low *T. striatus* activity in shrub-removed plots may have resulted from animal movement off shrub-removed plots, this possibility seems less likely. Most *T. striatus* activity occurs within 15 m of burrow systems (Yahner 1978; Elliott 1978), suggesting our observations of *T. striatus* occurred near burrow entrances and an absence of *T. striatus* observations after certain autumn dates most likely signals the onset of hibernation. Importantly, the proposed timing of hibernation observed in our study is consistent with *T. striatus* hibernation timing observed in other northern temperate forests (Synder 1982).

Prolonged and intensified autumn activity could modify ecological interactions associated with small mammals. More rodent activity within shrub-invaded forests could modify plant community diversity (Orrock et. al. 2015), via increases in granivory (Mattos and Orrock 2010, Connolly et. al. 2024). Among studies addressing seasonal granivory in shrub-invaded forest, Bartowitz and Orrock (2016) demonstrate less removal of *Acer* spp. and *Rhamnus cathartica* seed in forests cleared of invasive shrubs, but only during September and November and not mid-summer. *Tamias striatus* were also captured more in shrub-invaded forest plots during summer trapping sessions (Bartowitz and Orrock 2016), suggesting the prolonged *T. striatus* activity we observed in shrub-invaded plots may lead to greater local abundance and contribute to the greater woody plant seed removal observed in shrub-invaded U.S. forests.

Future directions

Given the prevalence of invasive shrubs in habitats globally (Richardson and Rejmanek 2011), our results highlight how pervasive but underappreciated shifts in habitat structure may drive changes in small mammal phenology. Future studies exploring the effect of invasive plants in different seasons will help strengthen the linkages between altered habitat structure, animal seasonal activity, and animal demography and their interactions in their communities. Studies exploring how invasive shrubs alter spring animal activity and how these responses change across landscape context (e.g., rural versus urban forests) will be essential for understanding the scale of invasive shrubs effect on animal ecology across different forest systems.

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Table 1. Results from generalized linear mixed model analysis testing the effects of invasive shrub removal, day of year, and study year on the likelihood of observing three small mammal species in a midwestern U.S. forest. Bolded factors are significant at a Type I error = 0.05 and italicized factors are marginally significant at a Type I error = 0.10.

	χ2	df	p value
Eastern Chipmunk (Tamias striatus)			
Intercept	27.80	1	**<0.001**
Shrub Removal	15.03	1	**<0.001**
Day of year (scaled)	12.82	1	**<0.001**
Year	6.90	1	**0.009**
Shrub removal:Day of year	6.27	1	**0.012**
Shrub removal:Year	8.21	1	**0.004**
Day of year:Year	1.31	1	0.252
Shrub removal:Day of year:Year	1.89	1	0.169
White-footed Mouse (Peromyscus leucopus)			
Intercept	1.12	1	0.290
Shrub Removal	0.00	1	0.993
Day of year (scaled)	1.23	1	0.267
Year	2.57	1	0.109
Shrub removal:Day of year	5.17	1	**0.023**
Shrub removal:Year	23.91	1	**<0.001**
Day of year:Year	0.00	1	0.994
Shrub removal:Day of year:Year	0.82	1	0.367
Fox Squirrel (Sciurus niger)			

Intercept	3.20	1	*0.074*
Shrub Removal	11.84	1	**<0.001**
Day of year (scaled)	0.53	1	0.466
Year	1.98	1	0.160
Shrub removal:Day of year	0.00	1	0.960
Shrub removal:Year	21.85	1	**<0.001**
Day of year:Year	1.07	1	0.302
Shrub removal:Day of year:Year	0.52	1	0.472

Figure Captions

Figure 1. Summary of the presence or absence of *Tamias striatus, Peromyscus leucopus*, and *Sciurus niger* photos from Day of Year 285 through 340 (11-Oct through 6-Dec) for two consecutive sampling years 2019 and 2020. Lines represent estimated probability of observing one of the focal species; shaded gray regions represent +/- 1 SE. Estimates obtained using a binomial generalized linear mixed model with a smoothing function. Appendix S1: Table S3 reports results of contrasts testing Day of Year trends between each plot types (invasive shrubs removed versus invasive shrubs present) for each species within each year.

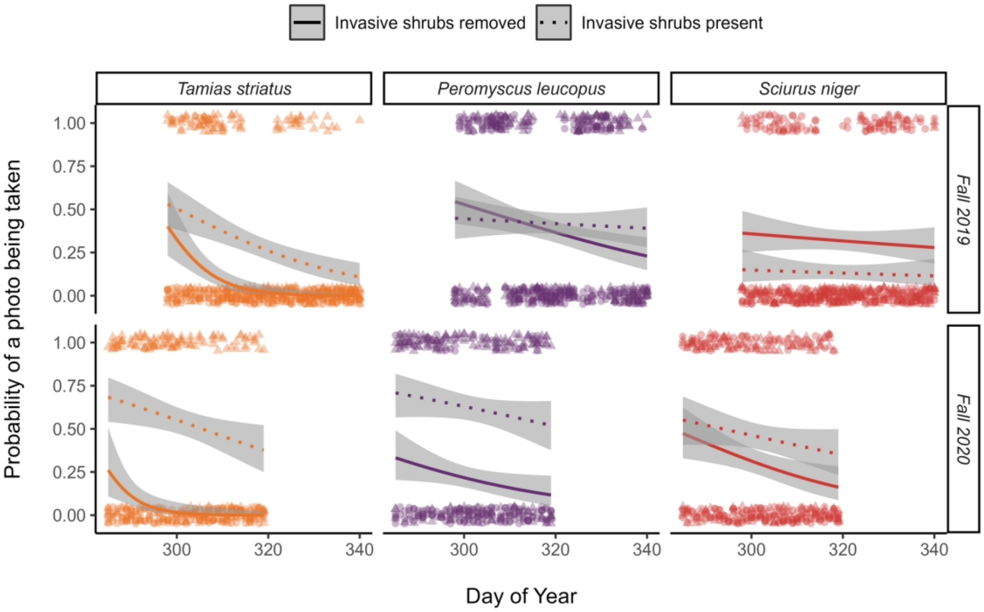

Figure 1

179x119mm (300 x 300 DPI)