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Invasive exotic shrub modifies a classic animal-habitat relationship and alters patterns of vertebrate seed predation

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Abstract. Recent evidence suggests that invasive exotic plants can provide novel habitats that alter animal behavior. However, it remains unclear whether classic animal-habitat associations that influence the spatial distribution of plant-animal interactions, such as small mammal use of downed woody debris, persist in invaded habitats. We removed an invasive exotic shrub (buckthorn, *Rhamnus cathartica*) from 7 of 15 plots in Wisconsin. In each plot, we deployed 200 tagged *Quercus rubra* seeds in November 2014. After five months, tags were recovered to track spatial patterns of small mammal seed predation. Most recovered tags were associated with consumed seeds (95%); live-trapping, ancillary camera-trapping, and previous behavioral studies suggest that white-footed mice (*Peromyscus leucopus*) were responsible for most seed predation. In habitats without *R. cathartica*, most seed predation occurred near woody debris. In habitats with *R. cathartica*, small mammals rarely consumed seeds near woody debris, and seed predation occurred farther from the plot center and was less spatially clustered. Our results illustrate that invasive exotic shrubs can disrupt an otherwise common animal-habitat relationship. Failing to account for changes in habitat use may diminish our ability to predict animal distributions and outcomes of species interactions in novel habitats created by invasive exotic plants.

Key words: buckthorn; downed woody debris; habitat use; northern red oak; Quercus rubra; Rhamnus cathartica; *small mammal; space use.*

INTRODUCTION

Habitat characteristics can exert a strong influence on animal behavior, population dynamics, and community composition (Morris and Davidson 2000, Mabry and Stamps 2008), and may also affect the nature of plant-animal interactions (Ogden et al. 1973, Chase 1998, Orrock et al. 2010*a*, Silliman et al. 2013). For example, animals often aggregate near refuge habitats (Orrock et al. 2013) in order to avoid predators (Brown and Kotler 2004, Stankowich and Blumstein 2005), which can change the spatial patterns of plant-animal interactions within a habitat (Orrock et al. 2010*a*). Because habitat characteristics can have such strong effects on animal behavior and ecological interactions, identifying habitat features that are consistently used by animals is a major focus in ecology, particularly in systems where rapid ecological change can cause significant shifts in habitat preference (Battin 2004).

Invasive exotic shrubs can have particularly rapid and pronounced effects on habitat structure (Orrock et al. 2010*b*, Vilà et al. 2011), leading to changes in the behavior and abundance of diverse taxa, including passerines (Watling and Orrock 2010), bees (McKinney and Goodell 2010), mosquitos (Conley et al. 2011), amphibians (Watling et al. 2011), and mammals (Allan et al. 2010, Mattos and Orrock 2010, Dutra et al. 2011, Shields et al. 2014). Given these strong effects, it is possible that invasive exotic plants can modify or entirely eliminate classic relationships between animals and their habitats. For example, downed woody debris is a critical habitat component that affects small mammal foraging (McCay 2000, Zollner and Crane 2003), population dynamics (Fauteux et al. 2012), and community composition (Sullivan et al. 2012). Small mammal use of downed woody debris as habitat is also geographically widespread: it has been documented in multiple forest biomes on several continents (Loeb 1999, Takahashi et al. 2006, van Ginkel et al. 2013). Although invasive exotic shrubs can increase the magnitude of small mammal foraging (Dutra et al. 2011, Orrock et al. 2015) and its spatial distribution (Orrock et al. 2008, Malo et al. 2013), it is unknown whether the

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refuge provided by an invasive exotic plant can be sufficient to decrease the use of woody debris by small mammals. Importantly, studies that demonstrate a strong link between woody debris and small mammals are typically not conducted in forests with invasive exotic shrubs. This gap in our knowledge may obscure important effects of invasive exotic shrubs, because both woody debris and invasive exotic shrubs affect small mammal behavior primarily by providing a refuge from predation (Loeb 1999, McCay 2000, Mattos and Orrock 2010, Dutra et al. 2011, Malo et al. 2013, Steele et al. 2015). Understanding how invasive exotic shrubs alter refuge use could provide insight into plant-animal interactions, since the distribution of important habitat features can influence which plants are consumed (Orrock et al. 2010*b*).

We used an experimental approach to test the hypothesis that an invasive exotic shrub (*Rhamnus cathartica*) decreases small mammal use of downed woody debris, a classic refuge, therefore altering spatial patterns of seed predation. Like other invasive exotic shrubs (Dutra et al. 2011, Malo et al. 2013), *R. cathartica* can alter habitats in ways that increase small mammal activity (Bartowitz and Orrock 2016). Reduced predation risk is likely the primary mechanism responsible for behavioral changes in invaded habitats (Mattos and Orrock 2010). In habitats with low predation risk, small mammals should increase space use (Anderson 1986) and reduce aggregation near refugia (Sih et al. 1988), e.g. woody debris. We tested three predictions that would arise if the novel refuge provided by *R. cathartica* might reduce the reliance of small mammals on downed woody debris: (1) small mammals would consume fewer seeds near woody debris in invaded habitats compared to uninvaded habitats, resulting in (2) greater movement between the seed source and the point of seed consumption in invaded habitats and (3) less spatial clustering of seed predation in invaded habitats.

METHODS

This study was conducted at the University of Wisconsin-Madison Arboretum in Madison, Wisconsin. Plots were located in a 50 ha forest dominated by *Quercus rubra*, with associated *Carya ovata* and *Pinus strobus*. In June 2014, fifteen 20 × 20 m plots were delineated, and seven plots were randomly selected to have all invasive shrubs removed (Bartowitz and Orrock 2016). Removing *R. cathartica* increased light penetration and decreased stem density, but did not alter the percent cover of downed woody debris (Appendix S1).

We obtained *Q. rubra* seeds from central New York (Sheffield's Seeds, Locke, New York, USA), which we tagged with 14.1 mm nails (Moore et al. 2007, Lichti et al. 2014). On 16 November 2014, 200 seeds were placed in a 0.5 × 0.5 m hardware-cloth box at the center of each plot. Boxes had two 7 × 7 cm holes that allowed small mammals to access seeds, but excluded other consumers (e.g., *Odocoileus virginianus*). Seeds were deployed in November because the late dehiscence of *R. cathartica* leaves (Knight et al. 2007) likely decreases predation risk relative to uninvaded habitats in autumn. Between 30 March and 28 April 2015, we recovered tags with a metal detector (Bounty Hunter Platinum, First Texas Products, El Paso, Texas, USA). At each site, we comprehensively searched for tags within a 25 m radius of the box. Tags recovered within a box ($n = 9$ total tags) were assigned a distance of 0 m, as they were not removed. Blind recovery trials show that tag detection rate did not differ between treatments (Appendix S2). We assume that most unrecovered seeds were located in arboreal hoards (Tamura and Shibasaki 1996), where they are very unlikely to contribute to plant recruitment. When a tag was recovered, we recorded whether the tag was <0.5 m from downed woody debris, the distance and compass bearing of each recovered tag from the seed source, and whether the seed had been consumed. In a follow-up study to identify which species were responsible for seed removal, we placed motion-activated digital cameras in front of boxes, and observed small mammal activity for three nights (Appendix S3).

For analysis, we only considered tags associated with consumed seeds that were found within the radius of our *R. cathartica* removal treatment (≤10 m from the seed source), which represented 58% of recovered tags (see *Results*). Including all recovered tags did not change our conclusions (Appendix S2). To examine how *R. cathartica* invasion changed small mammal use of woody debris, we constructed a binomial generalized linear model estimating the proportion of seeds consumed near woody debris in plots with and without *R. cathartica*. We also assessed whether *R. cathartica* invasion changed the spatial distribution of small mammal foraging. We compared the median distance seeds were moved before being consumed (Moore et al. 2007, hereafter, "seed predation distance") between *R. cathartica* removal treatments using a *t*-test. To verify that seed predation distances reflected small mammal activity, we used linear regression to examine seed predation distance as a function of the number of *Peromyscus leucopus* live-captures in the summer of 2014. The number of live-captures provides a measure of activity (Orrock and Danielson 2005), which we broadly define as time spent outside of refuge (e.g., Brown and Kotler 2004). Because the number of tags recovered at each plot was highly variable (range: 3–28), analyses using seed predation distance as a response variable were weighted by the number of recovered tags at a plot. We evaluated the two-dimensional spatial clustering of seed predation (i.e., seed-predation intensity) by creating pooled spatial point patterns for each treatment (Appendix S4). Using the distance and compass bearing data, we determined the coordinate of each recovered tag (Puerta-Piñero et al. 2010). Seed predation intensity was estimated at the same scale at which we measured the distance of tags to woody debris (0.5 m) but additional analyses showed that our results were consistent across a range of spatial scales (Appendix S4). We also investigated the effect of *R. cathartica* on the distance that unconsumed seeds were moved (Appendix S5), but we

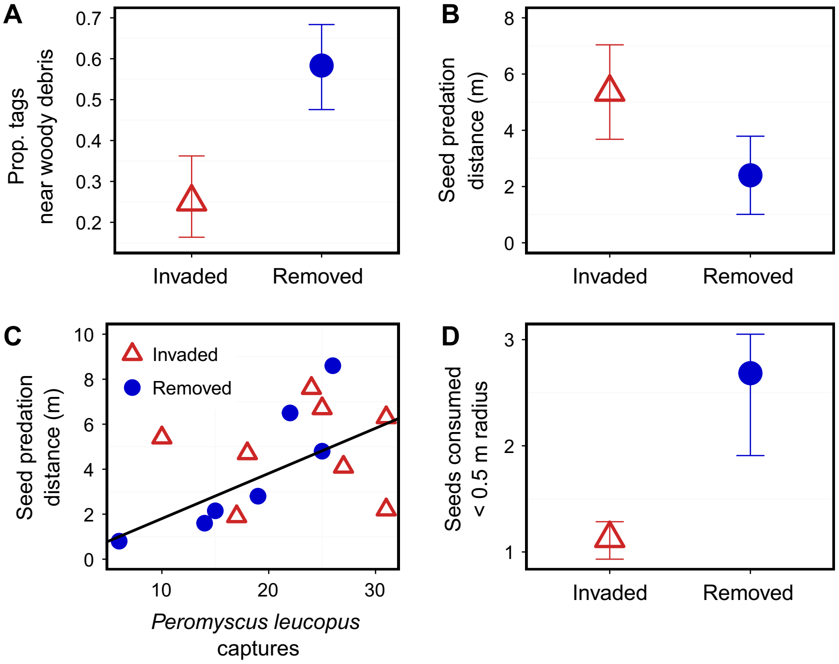

Fig. 1. (A) Proportion of seeds consumed adjacent to downed woody debris in plots invaded by *R. cathartica*, and plots with *R. cathartica* removed ($P < 0.05$). Error bars represent one standard error. (B) Median seed predation distance in plots invaded by *R. cathartica*, and plots with *R. cathartica* removed ($P = 0.01$). Error bars represent one standard error. (C) Relationship between seed predation distance and *Peromyscus leucopus* live-captures ($P < 0.01$) in two summer live-trapping sessions. Trapping was conducted in plots invaded by *R. cathartica* (triangles), and plots with *R. cathartica* removed (circles). (D) Spatial intensity of seed predation in plots invaded by *R. cathartica* and plots with *R. cathartica* removed, estimated at 0.5 m. Higher values indicate more clustered seed predation. Error bars represent 95% confidence intervals.

focus on patterns of seed predation due to the small number of intact seeds recovered. Analyses were conducted in R v. 3.2.2 (R Core Team 2015).

Results

We recovered 8.9% ($n = 165$) of the tags deployed, a recovery rate consistent with other studies (6–17%, Moore et al. 2007, Lichti et al. 2014). Most recovered tags (95%, $n = 156$) were found without the seed, indicating seed predation. The number of recovered tags did not differ between treatments ($t_{14} = 1.9$, $P = 0.19$). Ancillary observations with camera traps suggest that *Sciurus carolinensis* and *P. leucopus* were likely responsible for seed removal (Appendix S3). A greater proportion of consumed seeds was found near woody debris in plots with *R. cathartica* removed (0.58 ± 0.14, mean ± SE) compared to plots with *R. cathartica* intact (0.25 ± 0.07; $F_{1,13} = 4.7$, $P = 0.05$, Fig. 1A). Seed predation distance was also 25% greater in plots invaded by *R. cathartica* (4.9 ± 2.1 m) compared to plots with *R. cathartica* removed (3.9 ± 2.9 m, $t_{14} = 8.6$, $P = 0.01$, Fig. 1B). Seed predation distance was positively related to the number of *P. leucopus* live-captures at each plot in the summer ($F_{1,13} = 11.8$, $P < 0.01$, Fig. 1C), but no capture data was available for *S. carolinensis* (Appendix S3). Seed predation was more clustered in habitats with *R. cathartica* removed (2.9 ± 0.8, intensity ± 95% confidence interval) compared to habitats invaded by *R. cathartica* (1.2 ± 0.2, Fig. 1D).

Discussion

Habitat characteristics affect animal behavior, survival, and dispersal (Brown and Kotler 2004, Mabry and Stamps 2008, Orrock et al. 2013), and can ultimately change plant-consumer interactions (e.g., Orrock et al. 2010*b*). By coupling an experimental invasive exotic shrub removal with fine-scaled animal space use data, we show that invasive exotic plants weaken a common animal-habitat association, creating distinct spatial patterns of seed predation that do not occur in habitats with the invasive plant removed. Our results have several implications, which we discuss below. First, because downed woody debris is used to model small-mammal distributions (Bowman et al. 2000, Orrock et al. 2000), invasive exotic plants may complicate efforts to predict large-scale changes in small mammal communities. Second, by changing the spatial distribution of seed predation, *R. cathartica* could increase consumer pressure on native plant populations (Orrock et al. 2008, 2015, Schauber et al. 2009), altering patterns of plant survival. Our findings suggest that changes in animal habitat use can provide an underappreciated mechanism by which invasive exotic plants might modify species interactions.

Rhamnus cathartica *reduces small mammal use of coarse woody debris*

Structurally complex habitat features can provide important habitat for animals, but few studies have investigated how shifts in habitat structure caused by invasive exotic plants might alter the use of specific, commonly used habitat components (Schmidt and Whelan 1999) like downed woody debris. Previous work demonstrates that small mammals use woody debris as a refuge when consuming seeds (Huggard and Arsenault 2009), but we find conclusive evidence that invasive plants override this dynamic, as small mammals were unlikely to consume seeds near downed woody debris in habitats invaded by an exotic shrub (Fig. 1A). This pattern was likely observed because the predation refuge provided by invasive exotic plants is superior to the refuge provided by woody debris, as previous work with *P. leucopus* finds a strong link between risk-averse behavior and invasive exotic shrubs (Mattos and Orrock 2010). Native shrubs can provide a more effective predation refuge than woody debris, even when woody debris volume is high (Hinkelman et al. 2012). A logical extension of this is that invasive exotic shrubs provide an even more effective refuge than native shrubs: invasive exotic shrubs can increase stem densities and light interception by an order of magnitude compared to uninvaded forests (Appendix S1).

These findings have important management implications, as woody debris is often salvaged after timber harvest, and many studies show that removing woody debris reduces small mammal abundance and seed predation (e.g. Loeb 1999, Huggard and Arsenault 2009). Our experiment suggests that the presence of invasive exotic shrubs after timber harvest could sustain high levels of small mammal seed predation, even in the absence of woody debris. Moreover, several studies show that invasive exotic plants alter the foraging behavior of multiple small-mammal species (e.g., *P. leucopus*, *P. maniculatus*, *Tamias striatus*) over relatively short time scales (Mattos and Orrock 2010, Radtke and Wilson 2015, Bartowitz and Orrock 2016). However, in this study, small mammal behavioral changes persisted over a relatively long time scale (i.e., several months, Dutra et al. 2011, Malo et al. 2013). Given the long duration of these effects, and the importance of downed woody debris for predicting the presence and abundance of small mammals at larger scales (Bowman et al. 2000, Orrock et al. 2000), invasive exotic shrubs may decrease the predictive power of small mammal species distribution models. Thus, a mechanistic understanding of consumer behavior in novel invaded habitats is needed to model future species distributions (Conley et al. 2011, Gustafson 2013), including efforts to understand climate-induced shifts in small mammal distributions (Myers et al. 2009) and to forecast the risk of diseases for which small mammals are important hosts (Ostfeld et al. 2006).

Rhamnus cathartica *alters the spatial distribution of small mammal seed predation*

While *R. cathartica* invasion decreased small mammal use of woody debris, it also changed the spatial distribution of small mammal seed predation in two ways. First, seeds were consumed farther from the seed source in habitats invaded by *R. cathartica* (Fig. 1B), which is most likely due to increased *P. leucopus* activity in invaded habitats. This conclusion is based on our own findings of a significant relationship between seed predation distance and *P. leucopus* captures (Fig. 1C), as well as previous studies demonstrating that *Peromyscus* spp. increase activity under invasive exotic shrub cover (Dutra et al. 2011) and increase space use in low-risk habitats (Anderson 1986). The response of *S. carolinensis* to invasive exotic shrubs is less clear: *S. carolinensis* foraging behavior is sensitive to predation risk (Lima et al. 1985), but an experimental removal of invasive exotic shrub cover had no effect on *S. carolinensis* activity (Dutra et al. 2011). Moreover, direct observations show that on average, *S. carolinensis* move >18 m before caching *Q. rubra* seeds (Steele et al. 2014). Because our seed predation data were collected in a 10 m radius around the seed source (but see Appendix S2), it is more likely that *P. leucopus* (mean foraging range = 4 m, Anderson 1986), was responsible for the observed patterns of seed predation. Therefore, it is likely that *S. carolinensis* did not substantially contribute to differences in spatial patterns of seed predation between removal treatments.

Additionally, the aggregation of seed predation was lower in habitats with *R. cathartica* intact (Fig. 1D). This is likely linked to the decreased use of downed woody debris by *P. leucopus* in invaded habitats. Small mammals typically consume large food items near refugia to reduce predation risk (Lima et al. 1985, Vander Wall 2010), but prey are unlikely to aggregate near refugia when predation risk is low (Sih et al. 1988). Therefore, we interpret the decreased aggregation of seed predation in invaded habitats as the result of small mammals using novel refuge provided by invasive exotic shrubs instead of classic refuge like woody debris.

Changes in refuge availability, and the resulting changes in the spatial distribution of small mammals in invaded habitats could have important consequences for plant-consumer interactions (Orrock et al. 2008). The increased availability of refuge in invaded habitats likely increases the distance small mammals travel while foraging (Anderson 1986), meaning that seeds may need to disperse farther to escape zones of intense seed predation near conspecifics (Janzen 1970). Additionally, by reducing the clustering of small mammal foraging, invasive exotic shrubs could increase encounters between seed predators and native seeds. This could be particularly important in systems where seed density has a nonlinear effect on seedling establishment (Dalling et al. 2002). When small mammal space use is restricted to classic refugia, such as downed woody debris, many seeds will be consumed at the few microsites adjacent to woody debris, but seeds farther from woody debris will likely remain at sufficient densities to promote recruitment. However, when invasive exotic shrubs also provide effective refuge, a few seeds will be consumed in many microsites, leading to a greater negative effect on seedling establishment throughout the habitat. Furthermore, small mammals can be important seed dispersal vectors (Vander Wall 2010), and predation risk is known influence the spatial distribution of seed caching (Steele et al. 2015). Therefore, it is possible that invasive exotic shrubs could alter the quality of small mammal seed dispersal (Appendix S5).

Conclusion

Novel habitats produced by invasive exotic plants can have a strong, yet unappreciated effect on animal habitat use, which may consequently change the nature of species interactions (Pearson 2009). Our results show how the habitat provided by an invasive exotic shrub can decrease the importance of classic refuge habitat (woody debris), altering the spatial distribution of seed predation. By changing patterns of small mammal habitat use, invasive exotic plants might have other unconsidered indirect effects on important species interactions, prompting several fruitful avenues for future research. For example, invasive exotic shrubs can increase the abundance of both vectors and hosts of tick-borne illnesses (Allan et al. 2010, Williams and Ward 2010). By increasing the extent of small mammal space use, invasive exotic shrubs might increase the likelihood that parasites will encounter hosts, ultimately facilitating disease transmission (Brunner and Ostfeld 2008). Additionally, because seed predation can limit plant range expansions (Brown and Vellend 2014), our findings suggest that invasive exotic plants might impair our ability to predict shifts in plant species distributions resulting from climate change. Developing a comprehensive understanding of which species-habitat relationships do (or do not) persist in the presence of invasive exotic species will be critical to understanding species interactions in these novel habitats.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1678/suppinfo