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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Invasive plant species alters consumer behavior by providing refuge from predation

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Abstract Understanding the effects of invasive plants on native consumers is important because consumer-mediated indirect effects have the potential to alter the dynamics of coexistence in native communities. Invasive plants may promote changes in consumer pressure due to changes in protective cover (i.e., the architectural complexity of the invaded habitat) and in food availability (i.e., subsidies of fruits and seeds). No experimental studies have evaluated the relative interplay of these two effects. In a factorial experiment, we manipulated cover and food provided by the invasive shrub Amur honeysuckle (*Lonicera maackii*) to evaluate whether this plant alters the foraging activity of native mammals. Using tracking plates to quantify mammalian foraging activity, we found that removal of honeysuckle cover, rather than changes in the fruit resources it provides, reduced the activity of important seed consumers, mice in the genus *Peromyscus*. Two mesopredators, *Procyon lotor* and *Didelphis virginiana*, were also affected. Moreover, we found rodents used *L. maackii* for cover only on cloudless nights, indicating that the effect of honeysuckle was weather-dependent. Our work provides experimental evidence that this invasive plant species changes habitat characteristics, and in so doing alters the behavior of small- and medium-sized mammals. Changes in seed predator behavior may lead to cascading effects on the seeds that mice consume.

Keywords *Lonicera maackii* · Foraging activity · Indirect effects · *Peromyscus leucopus* · Predation risk

Introduction

Plant invasions often alter the landscape of the invaded habitat by creating a dense vegetative layer (e.g., Sheley et al. 1998; Williams et al. 2009; Forseth and Innis 2004; Levine et al. 2003, Mack et al. 2000; Mattos and Orrock 2010; Orrock et al. 2010a), thereby increasing the overall architectural complexity of the habitat (Sheley et al. 1998; Forseth and Innis 2004). In addition, this altered vegetative layer is often associated with new food sources in the form of fruits and seeds that may become available for consumers (Williams et al. 1992; Ingold and Craycraft 1983; Bartuszevige et al. 2006; Gosper et al. 2006; Richardson et al. 2000; Stansbury and Vivian-Smith 2003). Although both vegetation cover and fruit availability may affect consumer behavior (Orrock et al. 2010a), experiments that manipulate both cover and food provided by an invader have not, to the best of our knowledge, been conducted.

Food and cover can interact to determine when and how long an animal will forage, as many vertebrates are thought to perceive a tradeoff between food procurement and safety. This tradeoff is manifested as a dependence of the time allocated for foraging on perceived predation risk (Lima and Dill 1990; Brown et al. 1992; Kotler 1997; Mohr et al. 2003; Verdolin 2006). The decision can apparently be influenced by weather conditions that might change the

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conspicuousness of the prey to predators (Orrock and Danielson 2009; Mattos and Orrock 2010). Most importantly, the effects of an invasive species on perceived predation risk may foster a novel effect of biological invasion, as the effects of food and shelter on consumer behavior (Mattos and Orrock 2010) and abundance (Noonburg and Byers 2005; Borer et al. 2007) may result in differential predation pressure on seedlings (i.e., apparent competition: Orrock et al. 2010b).

We evaluated the relative role of shelter and food in affecting the foraging activity of a community of small mammal consumers in areas that have been invaded by Amur honeysuckle [*Lonicera maackii* (Rupr.) Maxim., Caprifoliaceae]. *Lonicera maackii* is a highly successful and aggressive invasive plant in forests in much of the eastern United States, known for reducing diversity (Luken and Goessling 1995; Luken and Thieret 1996; Luken et al. 1997; Hutchinson and Vankat 1997, 1999), abundance (Gould and Gorchov 2000; Collier et al. 2002; Gorchov and Trisel 2003), species composition (Hartman and McCarthy 2008), and growth (Miller and Gorchov 2004) of native species. It also alters the behavior and abundance of native fauna (Schmidt and Whelan 1999; McCusker et al. 2010; Mattos and Orrock 2010, Rodewald et al. 2010). *Lonicera maackii* provides an ideal system for experimental manipulation because its branch architecture, consisting of multi-stemmed shrubs with arching branches from several trunks, produces a thick understory (Luken et al. 1997) that has been shown to serve as a refuge (here defined as cover from predation) for mammals (Meiners 2007; Mattos and Orrock 2010) and nest sites for birds (Schmidt and Whelan 1999). The plant is also known for its massive fruit production of up to 400 million berries per ha (Ingold and Craycraft 1983), or more than 20 kg of fruits in a 25-m^2 area (H.P.D., unpublished results), with approximately 62% escaping consumption by birds and falling to the ground (Bartuszevige et al. 2006). Small rodents are known to consume *L. maackii* fruits (Williams et al. 1992) especially underneath highly invaded areas (Meiners 2007) where seed caches are relatively common (H.P.D., personal observation).

We focused on the foraging activity of the most common vertebrate consumers in oak–hickory forests. Specifically, we targeted mesopredators (raccoons, *Procyon lotor*, and opossums, *Didelphis virginiana*) because they play a key role in regulating the abundance and diversity of both fauna and flora communities (Prugh et al. 2009), and seed predators (mice *Peromyscus* spp., and squirrels, *Sciurus* spp.). The latter are known for their negative effects on tree seedling recruitment (Ostfeld et al. 1997; Manson et al. 1998, 1999; Vander Wall 2001). *Peromyscus* spp. may also increase disease risk (Jones et al. 1998; Allan et al. 2003) and limit biological invasions (Elkinton et al. 1996; Jones et al. 1998).

We combined a factorial manipulation of *L. maackii* structure and fruit to experimentally examine how shelter and food, respectively, affect the activity of native mammals. Because consumer foraging and activity may vary with weather (e.g., Orrock and Danielson 2009; Mattos and Orrock 2010), we conducted our study over 14 months, which allowed us to evaluate the potential interaction of *L. maackii* with climatic factors. This factorial manipulation of *L. maackii* provides the first experimental evaluation of the relative impact of food versus cover provided by an invasive plant on consumer activity.

Materials and methods

Study area

This study was conducted at Busch Wildlife Conservation Area (38.70°N, 90.71°W), a 6,987-ha park in Saint Charles County, Missouri. The park is open to the public for hunting and has about 1,215 ha of oak–hickory forest, with a shrub layer dominated by *L. maackii* and *Rosa multiflora* (multiflora rose). Other common understory woody plants include *Lindera benzoin* (spice bush), *Rhus aromatica* (aromatic sumac), *Cornus* spp. (dogwood) and *Symphoricarpus orbiculatus* (coral berry).

Experimental design

Three experimental blocks were established in the fall of 2006. Each block consisted of four treatment plots (30 × 30 m each). Plots were 50 m apart and blocks were at least 3 km from each other. Plots within each block were randomly assigned to one of four experimental treatments: (1) fruits and honeysuckle cover present, (2) fruits present and honeysuckle cover removed, (3) fruit removed and honeysuckle cover present, (4) both fruits and honeysuckle cover removed. Honeysuckle individuals were physically removed from treatment plots 2 and 4 by cutting the stem at the base in the fall of 2006. Pruning of resprouts continued from late fall 2006 until the end of the study. During the fall months of 2006, 2007 and 2008, we removed all fruits by hand from treatment plots 3 and 4. In 2006, fruits in treatment plots 2 were removed from the plant and left on the ground prior to plant removal. In 2007 and 2008, fruits removed from plots of treatment 3 were added to plots of treatment 2. In order to guarantee that fruit supplementation treatments mimicked the natural availability of fruit on the ground, we started the removal at the end of the fruiting season when fruits are fully grown and ripe. Fruits were gradually added to the supplemental plots throughout our harvest. Fruit addition was done by throwing fruits on the ground in a random fashion simulating an even distribution across the entire plot. Often, we found fruit caches on the ground, amidst mouse feces, indicating that mice were consuming the fruits.

Tracking plates were used to quantify mammal foraging behavior. Connors et al. (2005) suggest that track plates may represent a more accurate picture of small mammals space use than trapping, as track plates do not impede animal movement. However, because one organism can visit multiple plates, this technique potentially confounds activity with density. For simplicity, we refer to track plate data as foraging activity. Track plates consisted of 14 × 22 cm acetate sheets covered in a graphite alcohol oil mixture, fastened to aluminum flashing, and nailed to the ground surface. Plates were distributed on 20 × 20 m grid positioned at the centre of the large 30 × 30 m treatment plot. The grid consisted of 16 track plates distributed in a 4 × 4 array with approximately 5 m spacing between plates. Censuses were conducted monthly from September 2007 to December 2008. Heavy rains and snow prevented data collection for November 2007 and January 2008. For each census, track plates were left in the field for three consecutive nights and then brought to the laboratory for track identification and quantification. We used Elbrock (2003) as reference for identifying the paw prints. One disadvantage of using track plates instead of more traditional methods such as sand boxes is that prints are marked on a flat surface, thus one may not be able to see the depth of the print, as opposed to a three-dimensional print left in sand. While large animals (e.g., raccoons and opossums) leave a clear print, very small mammals such as mice *Peromyscus* spp. and short-tailed shrews (*Blarina brevicauda*) do not (Wiewel et al. 2007). As such, we assigned all small-mammal tracks of this type to be *Peromyscus* spp. because live-trapping conducted in the study sites found that *Peromyscus* spp. comprised 588 of 600 or 98% of all captures, with *B. brevicauda* comprising the remaining 12 (H.P.D., unpublished data).

Cloud cover and average temperature for each night were collected from the Spirit of St. Louis airport weather station located in St. Charles, MO [quality control data, station name and ban number (SUS, 03966), http://cdo.ncdc.noaa.gov/qclcd/QCLCD SUS station, National Oceanic and Atmospheric Administration, NOAA], approximately 10 km from our field site. Hourly values for these variables were averaged over the course of each night, a 13-h period. An hour was considered cloudy if sky cover was between 0.6 and 1 (corresponding to categories broken and overcast, according to NOAA) or if weather was classified as light rain, rainy, thunderstorm, snowy and/or foggy. These data were tallied over the course of each night to give the relative amount of time that the sky was cloudy (e.g., if 3 out of 13 h had cloudy skies then cloud cover for that night was 0.23). The fraction of the moon illuminated for each night, also used as a covariate, was obtained from published tables available from the U.S. Naval Observatory (http://www.nws.noaa.gov/climate/index.php).

To determine if invasion by *L. maackii* modified the vegetation density of the understory vegetation, we measured vegetation density along a 20-m transect by counting the number of times that any plant material touched a polyester line held 2 m above the ground for the entire extension of each transect. Vegetation density measurements were taken from transects in 18 distinct areas with different natural densities of *L. maackii*. A transect was placed in each of these areas. These areas consisted of 12 plots that were not part of the study and 6 experimental plots with cover present. In each of these areas, we also recorded the number of *L. maackii* individuals within 2 m of the line. To verify if our treatment manipulations were effective in reducing the vegetation density, we also compared vegetation density between plots with honeysuckle cover present with plots from which honeysuckle had been removed. Using the same technique, we measured the vegetation density for one transect established in the middle of each 30 × 30 m plot. The ends of each transect were 5 m from the edge of the plot.

Statistical analysis

For the 18 transects in natural vegetation, we regressed number of touches on the polyester line to the number of *L. maackii* individuals that were at least 1 m tall within 2 m of the line. For manipulated plots, we calculated a *t* test for the effect of honeysuckle removal on number of touches per 20 m compared to intact plots. Regression and *t* tests were done using R (R Development Core Team 2010). Data are presented as means and standard errors.

Monthly proportion of track plates per plot with mammal paw prints (arc-sin square root transformed) was used as our response variable. Analyses were performed separately for mice, raccoons, opossums and squirrels. Although we found prints from canids, skunks, deer and chipmunks on our plates, we did not perform any analysis for these species due to their low incidence (<2% of all tracks recorded). *Peromyscus* spp. analyses consisted of mixed model using SAS Proc Glimmix (SAS Institute 2000) using a Gaussian distribution. We ran two analyses; one that used time as a factor and another one that used weather covariates (cloud cover, fraction of the moon illuminated and temperature). This approach was chosen because models did not converge when both time and covariates were incorporated in the same model due to insufficient degrees of freedom. For the first analysis, we treated time, cover and fruit as fixed effects. Our model considered all 3-way interactions between time (monthly sampling) and experimental manipulations (cover and fruit). We treated plot as the subject, and months as a repeated-measures factor. Blocks were used as random effects. We called this model the "temporal model". For the second analysis, we maintained the same error structure determined by the random effects in the temporal model (repeated measures), but instead of modeling time itself we used weather covariates that are associated with this temporal variation (temperature, fraction of moon illuminated and cloud cover). We called this the "weather-model". Analyses started with a full model including all 5-way interactions between the two treatments (fruit and cover) and 3 covariates. Model simplification was done by removing non-significant interactions unless they were marginally significant, i.e., $P < 0.15$ (Littell et al. 2006). After model simplification, we used least squares means estimated for specific values of cloud cover to compare the effects of treatments at different levels of the covariates (0.25, 0.5 and 0.75 percentile).

In both models, temporal and weather, we used the Kenward–Rogers method to generate the appropriate denominator degrees of freedom due to the repeated measures nature of the data (Littell et al. 2006). Residual covariance model structure was chosen based on AICc and the treatment structure of the data following Littell et al.'s (2006) recommendations. Compound symmetry (CS) and autoregressive [AR(1)] yielded the lowest AICc for the temporal model and weather model, respectively.

Due to the low density of raccoons, opossum and squirrels, our datasets did not meet the analysis assumptions (zero inflated data), so we tallied their activity over the course of all 14 months and used mean proportion of tracks per plot as a response variable. We used Proc Mixed procedure (SAS Institute 2000) with treatments as fixed effects and block as a random factor to verify the role of food and cover in the overall foraging activity of each of these mammals.

Results

Vegetation sampling

Vegetation density was four times higher ($t = 3.27$, $P < 0.01$) on plots with honeysuckle cover present (22.7 ± 11.3 touches per 20 m) relative to plots from which honeysuckle had been removed (5.0 ± 6.9 touches). The number of honeysuckle individuals explained approximately 49% of the variation in vegetation density ($r^2 = 0.487$, $P < 0.001$; Fig. 1), supporting our hypothesis that honeysuckle increases the vegetation density of the understory.

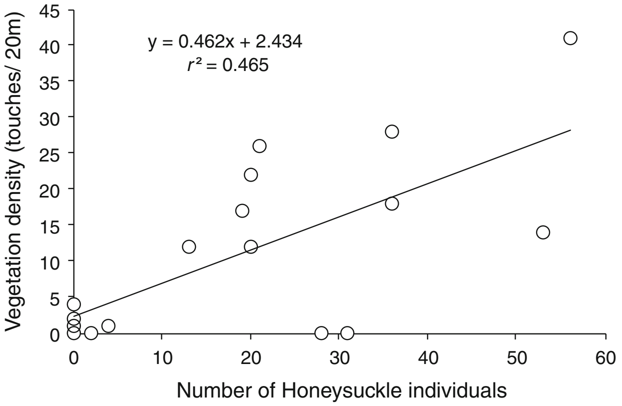

Fig. 1 Regression between number of Amur honeysuckle (*Lonicera maackii*) plants and vegetation density showing a positive relationship between these two variables ($n = 18$ plots)

Overall mammal activity

Our 14 censuses summed to 2,688 track plate nights. Overall, 48.8% (1,310 plates) of these plates had signs of vertebrate activity. Mouse paw prints were found on 56.8% of the plates showing any activity, followed by raccoons, squirrels and opossums with 15.4, 14.6 and 6.9%, respectively. Birds represented only 4.7% of the prints found. Approximately 15% of prints could not be identified because the organisms scratched and smudged the graphite suspension.

Mouse activity: temporal model

Mouse activity significantly increased throughout the duration of the study ($F_{13,26} = 5.35$, $P = 0.0001$; Fig. 2). In the beginning of the experiment, mouse prints were found on approximately 20% of the track plates, increasing to approximately 35% in the summer of 2008, and going back to about 25% in the fall until a peak of 60% in December 2008 (Fig. 2). Mouse activity was always lower on plots that had the honeysuckle removed, with the exception of September 2009 when mouse activity rose to more than 40% instead of the usual percentage in the mid-teens (Fig. 2). Our temporal model analysis showed that honeysuckle cover (foliage and branches) positively affected mouse foraging activity ($F_{1,6} = 15.63$, $P = 0.007$). On average, 33% (±4%) of plates in plots with honeysuckle present had mouse paw prints as opposed to 22% (±3%) in plots that had honeysuckle removed. Although in some months of the fruiting season (September through December) there were peaks of activity in plots with fruits (Fig. 2), the effect of fruit was not statistically significant ($F_{1,6} = 0.37$, $P = 0.564$). Interactions between fruit, cover and time were not significant (Table 1).

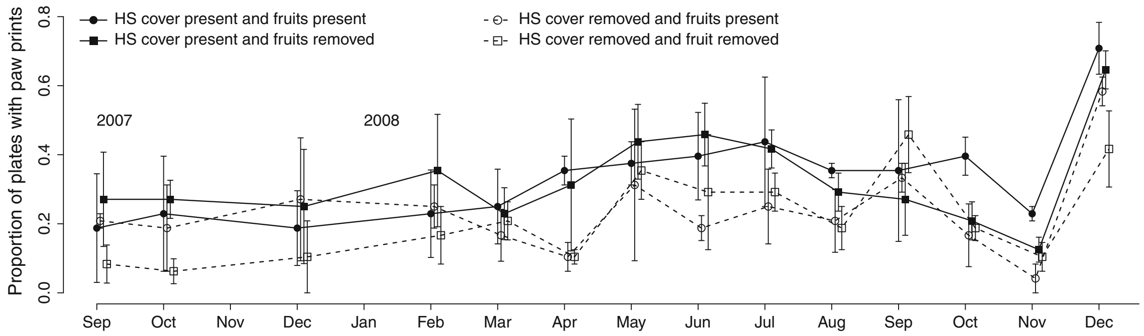

Fig. 2 Effects of honeysuckle (*HS*) vegetation cover and fruit production on mouse foraging behavior over time (see Table 1 and text for details). Means ± 1SE are shown (data points were slightly jittered along the *x*-axis to prevent overlapping of error bars)

Table 1 *Temporal model* and *weather model* for mouse foraging activity in experimental plots that had Amur honeysuckle (*Lonicera maackii*) (*HS*) cover and fruits manipulated to two levels each (present or removed)

Effect	*df*	*F*	*P*
Temporal model			
HS cover	1,6	15.63	0.007
HS fruit	1,6	0.37	0.564
HS cover × HS fruit	1,6	0.13	0.735
Time	13,26	5.35	0.0001
Time × HS cover	13,78	0.98	0.477
Time × HS fruit	13,78	0.35	0.98
HS cover × HS fruit × time	13,78	0.79	0.66
Weather model			
HS cover	1,88.51	11.51	0.001
HS fruit	1,27.72	0.40	0.531
Cloud	1,34.93	0.24	0.631
Moon	1,35.82	0.84	0.367
Temp	1,39.57	2.12	0.153
Moon × HS cover	1,120.1	1.72	0.192
Cloud × HS cover	1,118.8	8.67	0.004

Fixed effects were honeysuckle cover, honeysuckle fruit, and time for temporal model. The weather model used cloud cover, fraction of the moon illuminated and temperature as covariates (only interactions with $P < 0.20$ are shown). Error structure for both models was a randomized block, with experimental plot identity as the repeated factor. See text for details

Mouse activity: weather model

After the removal of non-significant interactions, our final weather model was reduced to the singular effects of treatments (honeysuckle cover and fruit), covariates (temperature, cloud cover and fraction of the moon illuminated), and two 2-way interactions of honeysuckle cover × cloud cover and honeysuckle cover × temperature (Table 1). Our weather model analyses also show a significant effect of vegetation on mouse foraging activity ($F_{1,88.51} = 11.51$, $P < 0.001$). There was no effect of fruit, cloud cover, fraction of the moon illuminated or temperature (Table 1), but there was a significant interaction of honeysuckle cover and cloud cover ($F_{1,118.8} = 8.67$, $P = 0.004$). Least square means estimates of mouse foraging activity holding constant the cloud cover covariate at 0.1, 0.26 and 0.58 (1st, 2nd and 3rd quartile, respectively) show that differences on mouse activity between honeysuckle cover present and honeysuckle removal plots were only significant when cloud cover was low (cloud cover = 0.1, $t = 4.88$, $df = 67.06$, $P < 0.0001$; cloud cover = 0.26, $t = 4.51$, $df = 31.09$, $P < 0.0001$), but as cloud cover intensified, honeysuckle cover did not affect mouse behavior (cloud cover = 0.58, $t = 0.35$, $df = 74.28$, $P = 0.724$; Fig. 3).

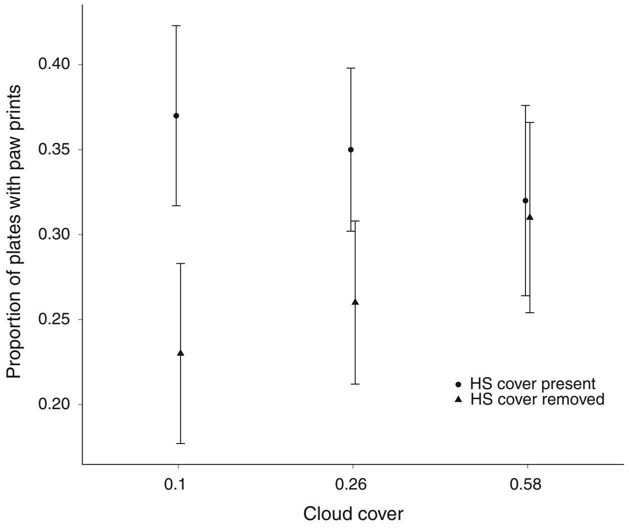

Fig. 3 Effects of cloud cover and honeysuckle (*HS*) cover on mouse foraging behavior. Results are based on our weather model that used mixed model analysis of covariance (see Table 1 and text for details). Means ± 1SE are shown (data points were slightly jittered along the *x*-axis to prevent overlapping of error bars)

Raccoon, squirrel and opossum

Honeysuckle cover had a significant positive effect on the activity of raccoons ($F_{1,6} = 17.6$, $P = 0.006$; Fig. 4) and a

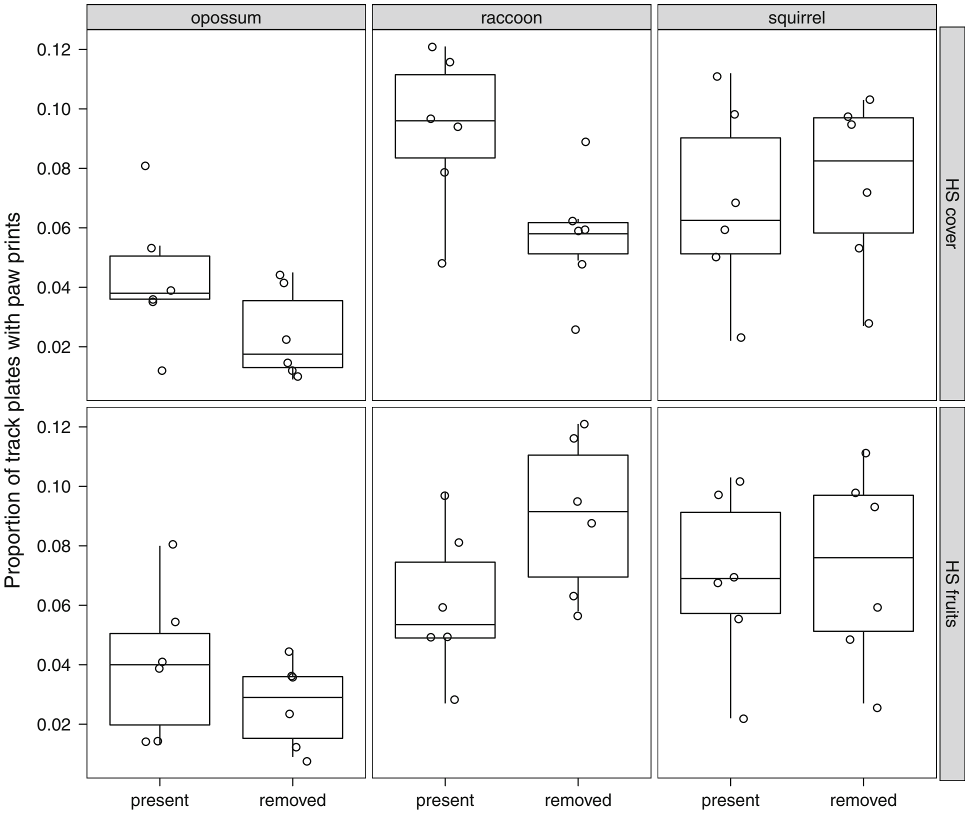

Fig. 4 Box-plot showing the effects of honeysuckle (*HS*) vegetation cover and fruit production on raccoon, squirrel and opossum foraging behavior over time. Results are based on mixed model analysis of variance (see text for details). *Circles* represent the average of paw prints in each plot. Horizontal lines represent quartiles (25, 50, and 75%). Vertical lines represent 1.5 times interquartile range

marginally significant effect on opossums ($F_{1,6} = 4.46$, $P = 0.079$; Fig. 4). Mean proportion of plates in control plots with raccoon and opossum paw prints was greater (60 and 100%, respectively) than the mean for honeysuckle removal plots. Honeysuckle cover removal did not affect squirrels ($F_{1,6} = 0.40$, $P = 0.552$; Fig. 4). Fruits did not affect opossums ($F_{1,6} = 1.61$, $P = 0.252$) or squirrels ($F_{1,6} = 0.09$, $P = 0.773$; Fig. 4), but had a significant negative effect on raccoon foraging activity ($F_{1,6} = 17.60$, $P = 0.006$, Fig. 4). We did not find a significant interaction between honeysuckle cover and fruits for raccoons ($F_{1,6} = 0.03$, $P = 0.863$), opossums ($F_{1,6} = 2.63$, $P = 0.156$), or squirrels ($F_{1,6} = 0.65$, $P = 0.450$).

Discussion

Traditionally, studies of the impacts of invasive plants in terrestrial ecosystems have focused on native plant species. The results of our experiment illustrate several points regarding the direct effects on native animals: invasive plants cause changes in the activity density of native consumers (Figs. 2 and 4); the primary mechanism of this effect is via the provision of a refuge, not a food source; and the impact of the refuge on activity is mitigated by abiotic conditions. As we discuss below, these findings have important implications for understanding biological invasions, for predicting the response of native consumers to invasive plants, and for interpreting field studies of plant–consumer interactions (Allan et al. 2010).

Vegetation density after honeysuckle removal was similar to density levels found in areas not infested with *L. maackii* (Allan et al. 2010). Our honeysuckle cover removal treatment indicated that the high vegetation density, as a result of the invasion by *L. maackii* (Fig. 1), is linked with greater foraging activity of three taxa of nocturnal mammals (mice, opossums and raccoons; Figs. 2 and 4). This result agrees with other studies that have shown greater foraging by mammals in areas with denser vegetation (Kotler et al. 1991; Korpimäki et al. 1996; Anderson et al. 2003, 2006).

Although other studies have shown that *L. maackii* plants alter foraging activities of mice (Meiners 2007; Edalgo et al. 2009; Mattos and Orrock 2010), ours is the first to demonstrate that the high vegetation density of this invasive is the mechanism responsible for modifying mammal behavior. This higher consumer foraging activity in areas infested with the invasive honeysuckle may lead to changes in consumer pressure, which could be critical for both plant and animal species (Orrock et al. 2010a, b). One explanation for higher mouse foraging activity underneath invaded areas is that the invasive plant species increases vegetation complexity, which is then perceived as a refuge from predation (Orrock et al. 2004; Edalgo et al. 2009;

Mattos and Orrock 2010). Dense horizontal vegetation reduces the chance that avian (e.g., hawks and owls) and terrestrial predators (e.g., foxes and coyotes) will spot a mouse foraging on the ground (Lima and Dill 1990; Kotler et al. 1991; Korpimäki et al. 1996). Increased prey availability associated with invaded habitats may also be important. *Lonicera maackii* is preferred over native plants by understory nesting birds (Schmidt and Whelan 1999; Rodewald et al. 2010), increasing the availability of both eggs and nestlings, which are common prey for mice (Bradley and Marzluff 2003). These two mechanisms, shelter and indirect food sources, are not mutually exclusive: both may have contributed to the higher mouse foraging activity seen in honeysuckle-infested plots.

The results of our weather model are in agreement with other studies that have shown that mouse activity may be conditioned by weather factors (Orrock and Danielson 2004, 2009; Mattos and Orrock 2010). Mice appear to take into consideration their conspicuousness to predators while foraging, since they are less likely to use areas without honeysuckle cover when cloud cover is low and visibility to avian predators is high. The interaction of cloud cover and vegetation structure corroborates our shelter hypothesis, and reveals flexibility in their behavior. This result also underscores the importance of long-term studies that might reveal interactions that otherwise would be undiscovered.

In addition, we found that mouse foraging activity increased during the timespan of the study (Fig. 2). Possibly, mice may have had an initial aversion to plot areas due to the human (experimental) disturbance, followed by a slow acclimation to the altered habitat. Alternatively, a severe freeze in early April 2007 had critical effects on many communities across the Midwest of the U.S. (Gu et al. 2008). The freeze could have reduced the abundance of mammals, and the study period just happened to record the data when the population was recovering and overall proportion of paw prints was increasing.

The copious amount of fruit produced by honeysuckle, and the evidence that mice actually consume and cache these fruits, led us to believe that fruits would at least influence mouse activity if not also their abundance. Despite our expectations, we found no evidence that *L. maackii* fruits influenced mice. However, we cannot entirely rule out this hypothesis. In the first calendar year of the study (2007), early warm temperatures in the spring sped up plant activity and were followed by a killing frost (Gu et al. 2008) that destroyed a majority of the flower buds and flowers on *L. maackii*. As a result, fruit production was severely reduced in the fall of 2007. It is important to point out that, in 2006, a crew of 2–10 persons removed honeysuckle berries for approximately 8 h daily from September to late December, while in 2007, we had only 6 field trips with the same number of people to remove all the berries. Thus, the frost of 2007 may have been responsible for the lack of a fruit effect on mammal behavior in that year. One must also consider the scale of the experiment and the possibility of a spillover effect. Our plots were 900 m^2, which might be too small to affect food availability for mammals, especially considering that mice can be quite mobile. Our trapping data showed that individuals moved between plots on 24 occasions. Thus, honeysuckle fruits might not constitute an important source of food at such a scale, especially considering that the surrounding vegetation matrix is full of honeysuckle shrubs and that mammals could forage in these other areas and return to the experimental plots. In addition, birds are known to disperse *L. maackii* seeds and generate an extensive seed shadow (Bartuszevige et al. 2006). Our treatment might not have been effective in controlling food availability for mice, as birds also feed on *L. maackii* seeds.

The positive effect of honeysuckle cover on mesopredators (Fig. 4) can be critical for native species. As the invasive modifies the behavior of mesopredators, it has the potential to disrupt an entire ecosystem, as this guild can regulate both the diversity and abundance of plant and animal communities (Prugh et al. 2009). Higher activity of mesopredators could be related to the shelter provided by the invasive plant and increased food sources in the form of nestlings. For instance, some birds suffer higher nestling predation rates in honeysuckle-infested areas (Schmidt and Whelan 1999; Rodewald et al. 2010); facilitation for predators has often been suggested as the mechanism behind increased nestling predation. Studies have shown that these two factors (shelter and cover) affect mesopredator behavior (Bowman and Harris 1980; Chamberlain et al. 2003; Beasley et al. 2007). However, there are few predators of raccoons and opossums in the study area (H.P.D., personal observation). Hence, the higher abundance of birds (Schmidt and Whelan 1999) and mice (H.P.D., in preparation) in honeysuckle-infested areas could help explain the higher foraging activity of mesopredators, as they are known to prey upon these organisms (Azevedo et al. 2006; Staller et al. 2005). The effect of fruits on raccoon activity is counter-intuitive. Areas with fruits removed had greater raccoon activity than areas with fruit present (Fig. 4). One would expect omnivores like raccoons to respond positively to fruit production; however, they were consistently more active in fruit removal areas in 11 of 14 surveys. There is no evidence that raccoons consume *L. maackii* fruits, but perhaps fruits have a positive indirect effect on other raccoons' resources (i.e., birds). Resource abundance has been show to lead to more sparse distribution of raccoons (Gehrt and Fritzell 1998). Squirrels, on the other hand, did not respond to honeysuckle cover or fruits (Fig. 4), perhaps because they are mostly arboreal.

This study demonstrates an effect of an invasive plant species on the foraging behavior of native mammals. We would predict similar effects for any plant species that influences cover, including herbaceous plant species. However, densely branching shrubs and small trees should affect the greatest number of mammal species because the affected refuge habitat would be relevant for a greater range of body sizes. We were not able to demonstrate an effect of added resources in our system, but we do not reject this hypothesis based on the decrease in fruit production in 2007. Experimental demonstration of such an effect will need to take into account the size of the added resource, foraging range of the target animal species, and pre-dispersal distance of fruits and seeds. The next step in our system is to uncover the indirect effects that changes in consumers' foraging behavior have on native plant species.

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