Ecology, 96(4), 2015, pp. 1052–1061

Apparent competition and native consumers exacerbate the strong competitive effect of an exotic plant species

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Abstract. Direct and indirect effects can play a key role in invasions, but experiments evaluating both are rare. We examined the roles of direct competition and apparent competition by exotic Amur honeysuckle (*Lonicera maackii*) by manipulating (1) *L. maackii* vegetation, (2) presence of *L. maackii* fruits, and (3) access to plants by small mammals and deer. Direct competition with *L. maackii* reduced the abundance and richness of native and exotic species, and native consumers significantly reduced the abundance and richness of native species. Although effects of direct competition and consumption were more pervasive, richness of native plants was also reduced through apparent competition, as small-mammal consumers reduced richness only when *L. maackii* fruits were present. Our experiment reveals the multiple, interactive pathways that affect the success and impact of an invasive exotic plant: exotic plants may directly benefit from reduced attack by native consumers, may directly exert strong competitive effects on native plants, and may also benefit from apparent competition.

Key words: Amur honeysuckle; apparent competition; Busch Wildlife Conservation Area, Missouri, USA; direct effects; indirect effects; invasive plants; Lonicera maackii; *plant recruitment.*

INTRODUCTION

Invasive species can have transformative effects on the habitats they invade, altering the diversity of native plants and animals (Mack et al. 2000, Vila et al. 2011), affecting the dynamics of disease (Allan et al. 2010, Mack and Smith 2011), and potentially altering ecosystem function (Vila et al. 2011). Mounting evidence suggests that many invasive plants can have strong effects on native taxa via both direct effects (i.e., interactions between two species) and indirect effects (White et al. 2006), i.e., effects of exotic species on native species that are mediated through a third species. For example, invasive plants may have direct effects on native plant communities via competition for resources, such as light (Levine et al. 2003). They may also affect native plants indirectly by intensifying consumer pressure (i.e., apparent competition; Holt 1977) by increasing the abundance of consumers (Noonburg and Byers 2005) or by altering consumer foraging behavior (Orrock et al. 2010*a*). Despite evidence that both direct effects of competitors and consumers can affect the success of exotic organisms (Levine et al. 2004, Parker et al. 2006) and evidence that indirect effects like apparent competition can be important in the context of invasions (White et al. 2006, Orrock et al. 2008, Enge et al. 2013), the relative importance of both competition and apparent competition is seldom studied because it would require simultaneous manipulation of both direct competitive interactions and consumer access to competitors (Chaneton and Bonsall 2000, Orrock et al. 2010*b*).

Understanding the relative importance of direct competition and the indirect effect of apparent competition is critical because the likelihood of an invasion and the effects of an invasion on native taxa depend upon the ecological forces that promote exotic organism success. For example, if invasion is largely caused by apparent competition, then manipulation of consumer pressure may be sufficient to alter the course of the invasion (Orrock et al. 2010*b*). If exotic plants are superior competitors but also create greater consumer pressure on native plants (i.e., both direct competition and apparent competition), then theory suggests that invasions are expected to be more likely and may be more difficult to reverse (Orrock et al. 2010*b*).

One difficulty in examining the interplay of competition and apparent competition is that both can arise via multiple mechanisms; as such, determining whether either (or both) is important requires evaluating the multiple mechanisms that may be involved. For example, plant establishment and abundance may be limited by direct competition for light, competition for

Manuscript received 16 April 2014; revised 12 August 2014; accepted 15 August 2014; final version received 9 September 2014. Corresponding Editor: T. J. Valone.

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TABLE 1. Mechanistic hypotheses for how *Lonicera maackii* affects the abundance and richness of native plant species.

Mechanism	Experimental test of mechanism	Predicted outcome if mechanism is supported
a) Direct competition		
Exotic plant outcompetes native plants via shading	removal of aboveground vegetation of *L. maackii*	positive effect of *L. maackii* vegetation removal on native abundance and richness
Exotic plant outcompetes native plants via local seed production	removal of fruits of *L. maackii*	positive effect of *L. maackii* fruit removal on native abundance and richness
b) Apparent competition		
Exotic plant provides a refuge that increases consumer pressure on native seeds and seedlings	couple experimental manipulation of cover (vegetation of *L. maackii*) with treatments that restrict consumer access	consumers have greatest negative effect on native abundance and richness when vegetation of *L. maackii* is intact
Exotic plant provides food that increases the local activity of seed and seedling consumers	couple experimental manipulation of food (fruits of *L. maackii*) with treatments that restrict consumer access	consumers have greatest negative effect on native abundance and richness when fruits of *L. maackii* are intact

Notes: Each mechanism can be examined by using a specific experimental test or series of tests. Although the hypotheses are from the perspective of native species, complementary hypotheses exist for *L. maackii* and for other exotic species (e.g., if apparent competition is important for *L. maackii*, individuals of *L. maackii* should perform best when native plants perform worst).

limited microsites among seeds, or other resource axes (Goldberg and Barton 1992). Apparent competition may arise when plants provide food resources that affect animal abundance or diet choice (Holt 1977, Holt and Kotler 1987), when plants provide safety for foraging consumers (Orrock et al. 2010*b*), or both. The importance of these habitat- vs. food-mediated mechanisms of apparent competition (also called nontrophic and trophic mechanisms, respectively; Caccia et al. 2006), while potentially important, are rarely evaluated (but see Caccia et al. 2006, Chaneton et al. 2010). Moreover, the nature of apparent competition may depend upon which consumer guilds have access to focal plants (Orrock and Witter 2010). Mechanisms that create direct competition and apparent competition may also not be mutually exclusive. For example, rapid growth may be a mechanism for directly competing for light resources with other plants, but rapid growth can also alter habitat architecture in a way that provides a refuge for foraging animals (Orrock et al. 2010*b*). High rates of seed production may increase competitive ability for suitable microsites, but may also foster apparent competition if seeds provide novel food resources that affect animal abundance or behavior (Holt 1977, Holt and Kotler 1987).

Lonicera maackii is a widespread invasive shrub in much of the eastern and midwestern United States (Luken and Thieret 1996). Aboveground stems of *L. maackii* have deleterious effects on native understory plants (Collier et al. 2002). Direct competition is likely to occur via two routes: via the shading of seedlings of putative competitors by mature *L. maackii* (Gould and Gorchov 2000, Gorchov and Trisel 2003, Miller and Gorchov 2004, Christopher et al. 2014) and by competition for limited recruitment microsites among seeds of native plants and seeds of *L. maackii* due to high levels of seed input by *L. maackii*, as such seed limitation is important for many plant species (Clark et al. 2007). *Lonicera maackii* produces large quantities of locally dispersed fruits (Luken and Thieret 1996; see Plate 1), with approximately 62% of the fruits falling on the ground without being dispersed by birds (Bartuszevige and Gorchov 2005). There is also the potential for indirect effects of *L. maackii*, as the thick understory structure created by the *L. maackii* provides refuge habitat that may affect the foraging and abundance of native animals (Cipollini et al. 2009, Allan et al. 2010, Mattos and Orrock 2010, Dutra et al. 2011), potentially generating apparent competition (Meiners 2007, but see Mattos et al. 2013) or facilitating native plant persistence via associational resistance (Gorchov and Trisel 2003, Cipollini et al. 2009). Because *L. maackii* fruits are eaten by consumers (Williams et al. 1992, Rose et al. 2014), *L. maackii* could also generate short-term apparent competition (Holt and Kotler 1987) or density-mediated apparent competition (Holt 1977) if the resource subsidy provided by fruits and seeds leads to local increases in the abundance and density of consumers.

We use an experimental approach to determine the relative importance of direct competition and apparent competition in determining how mature *Lonicera maackii* affects the plant community. Our experiment specifically manipulates several different factors that can generate direct competition and apparent competition (Table 1). Specifically, we evaluate direct competition by aboveground stems and leaves of *L. maackii*, direct competition with *L. maackii* seeds for available microsites, apparent competition created by refuge provided by *L. maackii* stems (Mattos and Orrock 2010, Orrock et al. 2010*b*), and apparent competition (Holt 1977, Holt and Kotler 1987) created by food subsidies provided by *L. maackii* fruits and seeds. Each of these mechanisms of competition and apparent competition creates a unique and testable prediction (described and summarized in Table 1). We are primarily interested in understanding how invasive *L. maackii* affects the abundance and richness of native plants, the abundance of *L. maackii* itself, as well as whether invasive *L. maackii* promotes the abundance and richness of other exotic plant species, i.e., invasional meltdown (Simberloff 2006).

METHODS

This study was conducted at Busch Wildlife Conservation Area (38.70° N, 90.71° W), a 6987-ha reserve in Saint Charles County, Missouri, USA. The area has approximately 1215 ha of oak–hickory forests with shrub layers often dominated by *L. maackii* (Dutra et al. 2011, Orrock et al. 2012). Density of *L. maackii* in invaded areas within the study area was 0.34–0.93 individuals/m^2 (Watling et al. 2011), densities consistent with other studies (e.g., 0.3–1.0 individuals/m^2; Gorchov and Trisel 2003, Christopher et al. 2014).

We conducted a completely randomized factorial experiment in the autumn of 2006. Our split-plot design manipulated *L. maackii* fruit and vegetation cover to two levels each (present and removed) in three blocks. Each block consisted of four treatment plots (30 × 30 m each) at a minimum distance of 50 m from each other. For plots that received the *L. maackii* aboveground vegetation removal treatment, *L. maackii* individuals were physically removed from treatment plots by cutting the stem with a pruner or machete. Pruning of sprouting honeysuckle individuals continued from late fall 2006 until the end of the study in 2008. Posttreatment surveys of *L. maackii* in a central 2 × 20-m strip traversing the plot (Dutra et al. 2011) confirmed that the *L. maackii* removal was very successful at reducing *L. maackii* ($t_5 = 4.18$, $P < 0.01$): vegetation-removal plots averaged 0 *L. maackii* plants/m^2, whereas vegetation-intact plots averaged 0.34 ± 0.08 plants/m^2 (mean ± SE).

For plots that received the *L. maackii* fruit removal treatment, we removed all fruits by hand during the autumn months of 2006, 2007, and 2008. For the treatment plot in each block that received the aboveground vegetation removal treatment and the nonmanipulated fruit treatment, all fruits were removed in 2006 and left on the ground prior to removal of aboveground vegetation. To mimic fruit input in subsequent years (necessary because all aboveground vegetation of *L. maackii* was removed), fruits from one of the fruit-removal plots in the same block were added to these treatment plots in 2007 and 2008. Based on the mass of fruits collected from one of our plots (9 kg) and an average fruit mass of 0.18 g (Williams et al. 1992), our fruit manipulations added approximately 50 000 fruits containing 190 000 seeds (55 fruits/m^2 and 211 seeds/m^2); these values are within the range (340 ± 84 seeds/m^2) found in other studies of forest-growing *L. maackii* (Luken and Mattimiro 1991)

Within the center portion of each of the 12 treatment plots, we constructed exclosures to manipulate consumer access (forming the small plot of our split-plot design). To allow us to focus on recruitment of *L. maackii* from seed, exclosures were placed so as not to contain cut *L. maackii* stems. Exclosures were cylindrical cages made of hardware cloth (20 cm radius, 40 cm high) with closed tops. There were three types of exclosure treatment: a complete exclosure that used a mesh size of 0.6 × 0.6 cm to exclude all mammalian consumers, a partial exclosure that used a mesh size of 3 × 5 cm to exclude large mammals (i.e., white-tailed deer, rabbits, and squirrels) but allow access by small mammals, such as mice and chipmunks, and an unfenced control treatment that allowed access of all consumers. Hereafter, we refer to these treatments as consumers excluded, open to rodents only, and open to consumers, respectively. In December 2007, we established two replicates of each exclosure type within each experimental plot. Exclosures were buried to a depth of 5 cm to prevent access by burrowing rodents. No signs of exclosure breaching were observed during the experiment. During exclosure installation, we controlled for disturbance associated with the creation of our exclosure treatments by removing existing vegetation and lightly raking the top layer of soil.

In September 2008, we recorded the number and identity of all plants within each exclosure. Our sampling occurred near the end of the growing season and was intended to quantify plants that had established and grown to appreciable size, helping ensure that we avoid transient community dynamics by measuring plants early in the growing season when seedling mortality is likely high. However, an important caveat is that our approach was not likely to fully capture the dynamics of plant species that bloom and senesce early in the growing season. Plants that could not be identified in the field were pressed and identified in the lab; if necessary, plants were transplanted to pots and were grown in the greenhouse until they reached reproductive maturity or were otherwise identifiable. Most plants were identifiable to species (see *Results* and the Appendix); if it was not possible to identify plants to species level with 100% confidence, we treated the genus as being the relevant taxonomic unit in order to err on the side of a conservative estimate of taxonomic richness.

We analyzed the effects of our experimental treatments on overall abundance and species richness by using linear mixed models that treated block as a random effect, vegetation cover, fruits, and exclosure treatment as fixed effects. Specifically, we examined five response variables: the richness and abundance of native plants, the abundance of *L. maackii* plants, and the richness and abundance of all other exotic species (excluding *L. maackii*). Because we were not interested in estimating variance among exclosure replicates within a plot, our analyses pool variation among replicates to within a plot using two approaches depending upon the type of response variable. For abundance-based re-

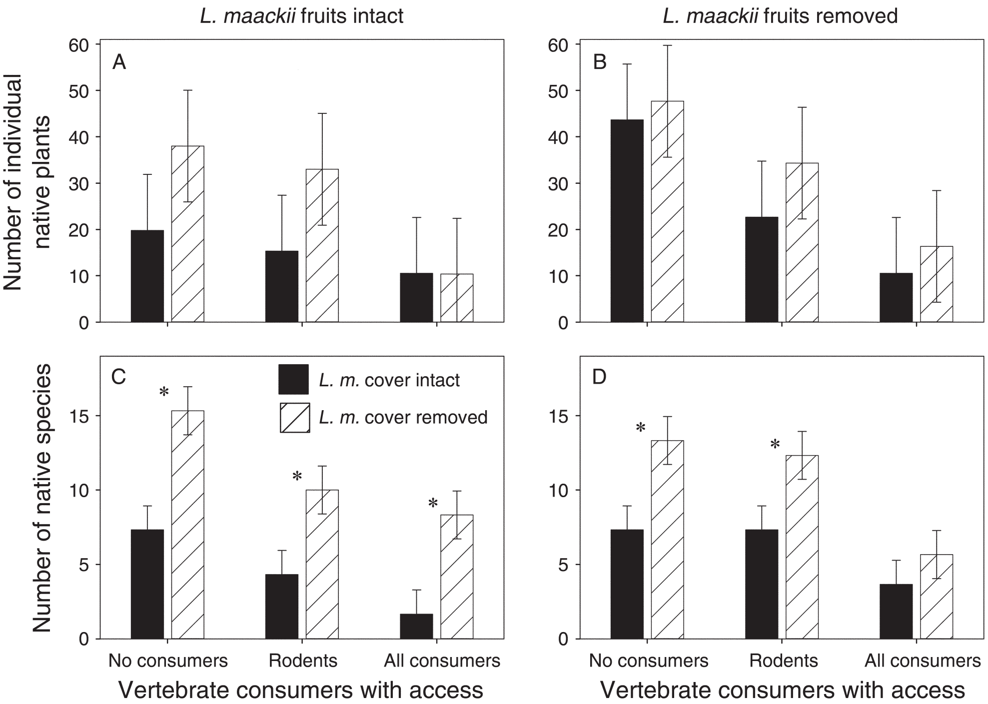

FIG. 1. The effect of experimental manipulation of Amur honeysuckle (*Lonicera maackii*) aboveground vegetation cover, *L. maackii* fruit manipulation, and consumer exclosure on the number of native plants that establish and the number of species of native plants that establish; means are presented ±SE. Numbers of native plants are shown when *L. maackii* fruits are (A) intact and (B) removed; numbers of native species are shown when *L. maackii* fruits are (C) intact and (D) removed. An asterisk positioned between a pair of bars in a particular consumer treatment indicates that there was a significant effect of *L. maackii* vegetation removal ($P < 0.05$) for that particular consumer exclosure and fruit manipulation treatment. Means are presented ±SE.

sponse variables (i.e., the number of native plants, number of *L. maackii* plants, and number of other exotic plants), we use the number of plants in each replicate plot and use appropriate random effects to correctly specify model structure and avoid pseudoreplication. For richness-based response variables (i.e., the number of native species and the number of exotic species), we pooled among replicates by summing the number of unique species between both replicates. We chose this approach to maximize the area sampled for species within each site and to avoid losing species-level information by averaging among replicates. Importantly, we note that our decision to pool across replicates does not affect our conclusions, which are qualitatively identical if alternative approaches are used (i.e., a pooled model for abundance-based response variables and a plot-based model for richness-based response variables). Following general guidelines (Bolker et al. 2009), we evaluated the relative fit of generalized linear mixed models (i.e., Poisson or negative binomial) with nontransformed dependent variables and general (i.e., Gaussian) linear mixed models with square-root- or cube-root-transformed dependent variables. In all cases, we opted to use general linear mixed models with transformed dependent variables because evaluation of residual plots indicated that these models produced the best fit to the data, with residuals exhibiting homogeneous variance and an approximately Gaussian distribution (Littell et al. 2006). Analyses were conducted in SAS v. 9.1 (SAS Institute 2009).

RESULTS

We recorded 2361 individual plants in our experimental plots. These plants were classified into 87 unique groups: 72 unique species (including 13 morphospecies that could not be identified) and 12 unique genera; see the Appendix for complete information regarding the abundance and identity of the plants in this study. A total of 2086 plants (>88%) could be classified as native or introduced: 1815 were native species (87%) and 271 were introduced species (13%). Five native taxa represented over half of the total number of individual plants (relative abundance in parentheses): *Carex* spp. (0.18), *Geum* spp. (0.11), *Ageratina altissima* (0.10), *Sanicula* spp. (0.07), and *Cardamine pensylvanica* (0.05).

Direct effects of the removal of aboveground *L. maackii* cover had a strong effect on the abundance of native plants (Fig. 1, Table 2): averaged across all other treatments, the mean number of native plants was over 46% higher in sites where *L. maackii* vegetative cover was removed (Fig. 1). We found no support for local seed production by *L. maackii* as a means of direct competition, as there was no significant effect of *L. maackii* fruit removal on the abundance of native plants

TABLE 2. Summary of analyses to evaluate the effects of *L. maackii* vegetation treatment (cover left intact or removed), *L. maackii* fruit treatment (fruits left intact or removed), and consumer exclosure on five focal variables.

		Native abundance		Native richness		*L. m.* abundance		Exotic abundance		Exotic richness	
Variables	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Vegetation treatment	1, 6	10.03	0.019	16.92	0.006	5.17	0.063	10.42	0.018	19.06	0.005
Fruit treatment	1, 6	3.59	0.107	0.13	0.729	2.82	0.144	<0.01	0.950	0.10	0.758
Vegetation × fruit	1, 6	0.35	0.577	1.08	0.339	0.90	0.381	0.02	0.900	1.05	0.346
Consumer exclosure	2, 16	15.15	<0.001	67.41	<0.001	0.68	0.519	0.51	0.610	0.75	0.489
Vegetation × consumer exclosure	1, 16	0.17	0.845	0.13	0.877	0.10	0.909	0.59	0.567	0.36	0.705
Fruit × consumer exclosure	1, 16	0.21	0.813	4.92	0.022	0.15	0.858	1.41	0.272	0.22	0.808
Vegetation × fruit × consumer exclosure	1, 16	0.30	0.743	2.63	0.103	0.87	0.437	1.59	0.234	0.06	0.941

Note: The five focal variables are the abundance and richness of native plants, the abundance of *L .maackii*, the abundance of other exotic species, and the richness of exotic species (excluding *L. maackii*; although, we note that results that include *L. maackii* produce the same patterns of significant effects).

(Table 2). There was a significant direct effect of vertebrate consumers on native plant abundance (Table 2): plots that allowed only rodent access had over twice as many plants (26.33 ± 9.8; mean ± SE) compared to plots that allowed access by all consumers (11.92 ± 9.8), and plots that excluded all vertebrate consumers (37.29 ± 9.8) had over three times as many plants compared to plots that allowed access by all consumers (Fig. 1). However, there was no indication of either mechanism of apparent competition (Table 1), as the presence of either vegetation or fruits of *L. maackii* did not lead to a change in the effect of consumers on native plant abundance (Table 2).

Species richness of native plants was also affected by *L. maackii* vegetation removal and consumer exclosure (Table 2). On average, removal of *L. maackii* doubled the number of native plant species (10.83 ± 1.05; mean ± SE) compared to plots with *L. maackii* intact (5.27 ± 1.05). Averaged across all other treatments, excluding all consumers led to the greatest richness of native plants (10.83 ± 1.05), with a slight reduction in richness in rodent-access treatments (8.50 ± 1.05) and a greater reduction in richness in the all-consumer treatment (4.83 ± 1.05). There was no support for direct competition for microsites being important (Table 1), as local seed production by *L. maackii* alone did not significantly affect native richness (Table 2). There was no indication of refuge-mediated apparent competition (Table 1), as the presence of *L. maackii* stems did not alter consumer pressure (Table 2). The richness of native plants was affected by a significant interaction between the fruit treatment and consumer exclosure ($P = 0.022$; Table 2): compared to plants with no consumer access, there was a significant decrease in richness in rodent-access plots with *L. maackii* fruits intact ($t_{16} = 5.01$, $P < 0.001$; Fig. 2), but no change in richness in rodent-access plots where *L. maackii* fruit was removed ($t_{16} = 0.69$, $P = 0.501$; Fig. 2). The interactive effects of *L. maackii* fruit production and consumer access were more evident when the abundance and richness of rare native species is examined (i.e., the 50 of 57 native taxa with less than 0.02 relative frequency). These analyses revealed a significant interaction between fruit removal and exclosure on both the abundance ($F_{1,16} = 5.85$, $P = 0.012$; Table A1 in the Appendix) and the richness ($F_{1,16} = 6.74$, $P = 0.008$) of rare native plant species (see also Fig. A1 in the Appendix). This effect was specifically mediated by rodent consumers in all cases, as there was no effect of *L. maackii* on native plants in treatments where all consumers (e.g., rodents, squirrels, rabbits, and deer) had access to plots (Fig. 2; Appendix: Fig. A1).

The number of *L. maackii* plants was greater when *L. maackii* cover was removed (Fig. 3), but there was no significant effect of consumer exclosure, fruit removal, or any of their associated interactions (Table 2). Because vegetation was removed upon the installation of our exclosures, exclosures were not placed near cut *L. maackii*, and resprouting of *L. maackii* was not observed within our exclosures, these *L. maackii* recruits were most likely from seeds that germinated after *L. maackii* removal. The abundance of plants of other exotic species

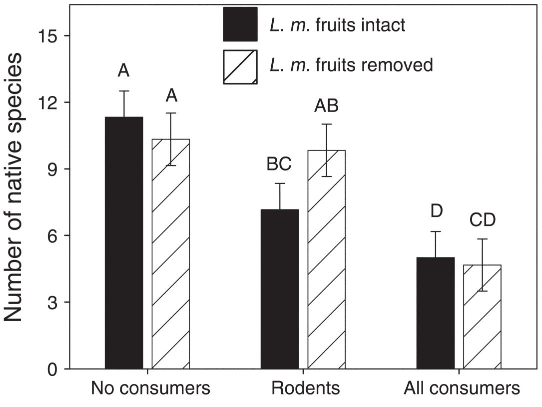

FIG. 2. The effect of experimental manipulation of *L. maackii* fruit and consumer exclosure on the number of species of native plants that establish (mean ± SE, averaged across the vegetation manipulation treatment). Bars that do not share a letter are significantly different ($P < 0.05$).

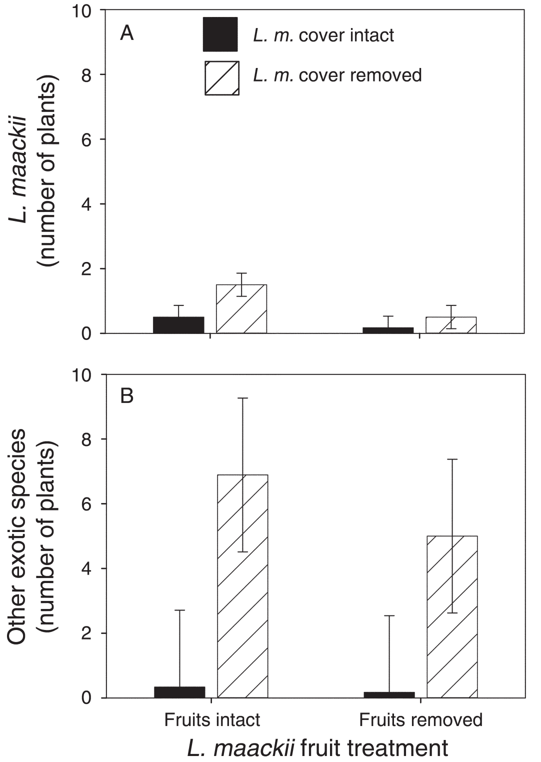

FIG. 3. The effect of experimental manipulation of *L. maackii* aboveground vegetation cover and *L. maackii* fruit manipulation on the recruitment (number of plants, mean ± SE) of (A) *L. maackii* and (B) other exotic plant species, not including *L. maackii.*

was only affected by *L. maackii* cover (Table 2): plants of the other exotic species were over 23 times more abundant when *L. maackii* cover was removed (Fig. 3). The richness of other exotic species was also affected only by *L. maackii* removal (Table 2) and was over 6.6 times greater when *L. maackii* was removed (Fig. 4).

DISCUSSION

Our experimental study demonstrates that the deleterious effects of a widespread invasive species on native plant communities occur via two complementary mechanisms. Direct competition with established *L. maackii* individuals led to a large reduction in the abundance of native plants (as well as exotic plants; Fig. 1), while both direct competition and apparent competition via food subsidies reduced the richness of native plants (Fig. 2). We found no evidence that local seed production by *L. maackii* altered direct competition for microsites or that refuge-mediated apparent competition was important in determining the effect of *L. maackii.* In addition to illustrating the complimentary and detrimental effects of direct competition and apparent competition that exotic plants can have on native plants, our work also demonstrates that *L. maackii* may inhibit its own recruitment via competition. Our study also informs the nature of competition between *L. maackii* and the recruitment of other exotic species. Finally, although the effect of consumers was sometimes modified by *L. maackii* fruits, our work demonstrates a clear direct role for native consumers in determining the abundance and richness of native plants in this system, but not in determining the abundance or richness of exotic plants. We will discuss each of these key points.

The relative roles of direct competition and apparent competition

Our results experimentally show that competition with already established *L. maackii* individuals, instead of competition with plants resulting from locally dispersed *L. maackii* seeds, is the primary means by which direct competition occurs. Indeed, the effect of aboveground portions of established *L. maackii* had clear, significant effects on all groups of taxa we studied (Table 1), with substantial effect sizes (Figs. 1, 3, 4). Because our removal of aboveground *L. maackii* did not preclude continued resource acquisition by *L. maackii* roots (established *L. maackii* can resprout following removal of aboveground stems), it is most likely that our treatments manipulated direct competition for light rather than direct competition for soil resources (although we cannot exclude this possibility). Previous work has shown that competition for light with *L. maackii* can lead to reduced growth and fecundity of understory plants (Gorchov and Trisel 2003) and that removal of *L. maackii* leads to increased abundance of understory plants (Gould and Gorchov 2000, Christopher et al. 2014); our results provide experimental evidence that competition with established *L. maackii* for light has community-level consequences, reducing the overall abundance of native plants and the number of native plant species.

A key aspect of our study is that it allows us to evaluate the relative contribution of different forms of apparent competition in the context of biological

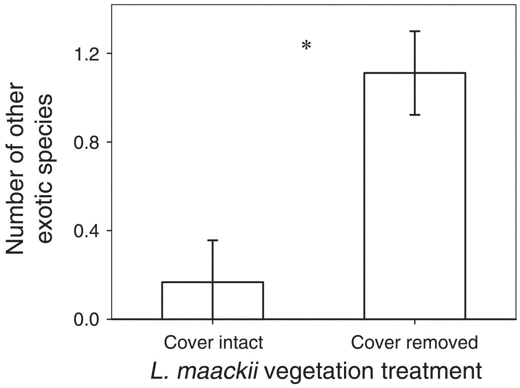

FIG. 4. The effect of experimental manipulation of *L. maackii* aboveground vegetation on the richness (mean ± SE) of all exotic plant species (excluding *L. maackii*). The asterisk indicates the significant difference in richness due to the *L. maackii* vegetation treatment ($P < 0.001$).

PLATE 1. Mature *Lonicera maackii* shrub with ripe fruits; *L. maackii* produces prodigious quantities of fruits and also alters habitat structure. Both of these features may lead to changes in the effect of consumers on native and exotic plants, which we investigate here. Photo credit: R. J. Marquis.

invasions; this is important because recent work has shown how refuge habitats and food subsidies can be drivers of indirect effects among native plants (Chaneton et al. 2010). In the context of exotic species, evidence for refuge-mediated apparent competition has been found in several recent studies (Orrock et al. 2008, Orrock et al. 2010*b*, Enge et al. 2013). Despite evidence that it may be important in some systems, the generality of refuge-mediated apparent competition in invasion remains unknown because few studies have explicitly tested for it. Our study provides an explicit experimental test of the refuge-mediated hypothesis, predicting a significant interaction between *L. maackii* vegetation removal and consumer exclusion (Table 1). We did not find a significant interaction between *L. maackii* vegetation removal and consumer exclosure on the number of native plants (Table 2). The lack of substantial refuge-mediated apparent competition in this system is interesting in light of strong evidence that *L. maackii* cover increases the local activity of deer (Allan et al. 2010) and small mammals (Dutra et al. 2011), as well as the abundance of small mammals (Dutra 2011). Although it is possible that the lack of refuge-mediated apparent competition is because consumers are using the landscape at larger scales than the scale of the experimental area, the differences in deer and rodent activity observed in these previous studies suggest that the scale of the experimental manipulations was sufficient to uncover refuge-mediated apparent competition, if it existed. An additional, untested explanation is that deer herbivory is so severe that plants were locally extirpated, such that the lack of apparent competition via deer in our study may reflect the ghost of herbivory past (Howe and Brown 2001). We also did not find evidence that aboveground structure of *L. maackii* generates a positive indirect effect mediated by consumers. While previous studies have shown that *L. maackii* may reduce the effect of large consumers (i.e., deer) on native plants (Gorchov and Trisel 2003, Cipollini et al. 2009), presumably because herbivores are less able to access plants within the dense habitat often formed by mature *L. maackii*, we did not observe this outcome in our study (Table 2, Fig. 1).

Instead, our data suggest that apparent competition is mediated by the production of food resources in the form of *L. maackii* fruits (Fig. 2; Appendix: Fig. A1) and that rodents, not deer, are the primary consumer guild driving this indirect effect. Although intact fruits of *L. maackii* may not be preferred by native rodents (Rose et al. 2014), seeds of *L. maackii* are readily consumed by rodents (Williams et al. 1992, Mattos et al. 2013) and may increase local consumer pressure by producing feeding aggregations of mice, as has been found with rodents in other systems (Malo et al. 2013). Evidence from our study system suggests that fruits do not alter total activity patterns of mice (Dutra et al. 2011), but does suggest that food subsidies can change rodent abundance because fruit removal results in lower numbers of individual mice (Dutra 2011). Because seed removal by mice has been found to be strongly correlated with rodent abundance in this study system (Mattos et al. 2013), the presence of more rodents could create increased granivory or seedling herbivory.

In finding a significant role of apparent competition in reducing the richness of native plants, our results support the suggestion of Meiners (2007) that changes in plant diversity as a result of indirect effects may be a common phenomenon. Our findings also support recent experimental evidence that the nature of indirect effects may depend upon the associated consumer guild (Orrock and Witter 2010). Additional analyses using the less-abundant members of the native community (i.e., 50 of 57 native morphospecies) further reveals that this mechanism of apparent competition can affect abundance of plants as well as richness (Appendix: Fig. A1, Table A1). Recent work illustrates the potential for food subsidies to generate important beneficial indirect effects in plant communities (Chaneton et al. 2010); our analyses suggest that the role of indirect effects in this system is to constrain the dynamics of establishment and persistence of less-abundant species rather than the dynamics of the most abundant members of the native community.

Direct effects of L. maackii *on conspecific plants and other exotic plants*

Our results also inform the processes that limit the establishment of *L. maackii* plants and the plants of other exotic species. We found that, much as with native plants, mature *L. maackii* suppressed exotic plants via direct competition, i.e., established *L. maackii* do not promote invasional meltdown by facilitating the establishment of other exotic species (Simberloff 2006). Interestingly, we found no evidence that local recruitment of *L. maackii* can be limited by the availability of sufficient seeds or that *L. maackii* seeds preempted microsites from other exotic species: removal of *L. maackii* fruits did not significantly reduce the number of *L. maackii* plants that established (Fig. 3) or alter the abundance or richness of other exotic species (Table 2). The lack of seed limitation we observed suggests that, although other studies have found lower levels of seed-bank persistence for *L. maackii* in invaded areas (Orrock et al. 2012), sufficient seeds may have remained or arrived (Bartuszevige and Gorchov 2005) over the course of our experiment to maintain *L. maackii* recruitment. From a pragmatic perspective, our results clearly show that removal of standing mature *L. maackii* as a restoration strategy may create opportunities for the establishment of both native and exotic plants.

Direct effects of consumers were greatest on native plants

A strength of our experimental approach is that it allowed us to directly evaluate consumer effects in addition to providing insight into how exotic *L. maackii* might modify consumer effects (i.e., apparent competition). Although consumer pressure was sometimes modified by *L. maackii* fruits (e.g., for native plants; Table 2), our work demonstrates a clear direct role for native consumers in reducing the abundance and richness of native plants (main effect of consumers in Table 2, Fig. 1). Moreover, it is possible that our study underestimated the effect of consumers on native plants: if plant species most susceptible to deer herbivory were extirpated from our study area prior to our experiment, then our results illustrate the significant effect of herbivores on those remaining native plants that had not already been locally extirpated. Because our plant surveys were performed in summer, our conclusions may not necessarily apply to spring ephemeral species, although we recorded several early blooming species (e.g., *Dicentra cucullaria* and *Cardamine pensylvanica*) whose vegetation persists into summer.

In comparison, consumers did not have significant effects on the abundance of *L. maackii* plants or other exotic plants (Table 2). These results have several important implications. First, they indicate how different vertebrate consumer guilds (i.e., rodents vs. deer) can have additive effects on the abundance and richness of native plants. Although it is known that deer can affect the structure of plant communities in temperate deciduous forests (Russell et al. 2001), including forests invaded with *L. maackii* (Gorchov and Trisel 2003, Cipollini et al. 2009, Christopher et al. 2014) the importance of small rodents in governing plant recruitment in these forest systems has rarely been examined. Our work suggests that, just as in coniferous forests in North America (Tallmon et al. 2003) and Europe (Olofsson et al. 2004) and in grasslands (Howe et al. 2002, Orrock and Witter 2010, Bricker and Maron 2012), small mammal consumers can have significant deleterious effects on plant recruitment, and that these consumers can also mediate indirect effects via their activities. Second, these results indicate that exotic plants in forested systems may benefit from native consumers that prefer to consume native plants, much as Parker et al. (2006) found for several diverse plant communities. However, this finding must be tempered by the lack of a positive significant effect of consumers on overall exotic plant richness, which suggests that consumers are not strong, direct agents of invasional meltdown in the context of plant recruitment.

Conclusions and future directions

Invasive plants have the potential to affect native species via direct and indirect effects; our work shows that direct competition for light is a primary means whereby *L. maackii* reduces the abundance and diversity of native plants. While direct competition was clearly important and pervasive, we also find that indirect effects, generated by the provision of resource subsidies for small-mammal consumers, can also have a significant effect on the richness of native communities. Additional studies are needed to determine how commonly such complimentary direct and indirect effects are found in the context of biological invasions. In documenting the role of short-term apparent competition in biological invasions, our results suggest that subsidizing consumer populations is a mechanism for promoting the success invasive *L. maackii* and for generating the deleterious effects of *L. maackii* on native plants. Future studies that manipulate resource subsidies from exotic plants and consumer pressure will be needed to understand whether this form of apparent competition plays an important role in other systems. Given observations that exotic species are sometimes more fecund in their introduced range (Parker et al. 2013), that some exotic species produce prodigious seed resources relative to native plants, e.g., annual exotic grasses vs. native grasses in California grasslands (Seabloom et al. 2003), and that unanticipated subsidies linked to exotic plants may yield changes in human disease risk (Pearson and Callaway 2006, Allan et al. 2010), as well as indirect effects (Pearson and Callaway 2008), apparent competition via food subsidies may be a common, yet unappreciated, component of invasion biology.

ACKNOWLEDGMENTS

This study was possible thanks to the assistance of student volunteers from high schools in the St. Louis, Missouri area. Comments from B. Connolly and P. Hahn greatly improved the manuscript. We thank staff at Busch Wildlife Conservation Area, especially John Vogel, for facilitating this work and for critical assistance with project logistics. This project was funded by NSF DEB-0444217 to J. L. Orrock, a dissertation improvement grant to H. P. Dutra and R. J. Marquis (NSF DEB-0710341), and grants from the Webster Groves Nature Study Society and the Whitney R. Harris World Ecology Center to H. P. Dutra.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-0732.1.sm