

Seed bank survival of an invasive species, but not of two native species, declines with invasion

John L. Orrock · Cory C. Christopher ·
Humberto P. Dutra

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Abstract Soil-borne seed pathogens may play an important role in either hindering or facilitating the spread of invasive exotic plants. We examined whether the invasive shrub *Lonicera maackii* (Caprifoliaceae) affected fungi-mediated mortality of conspecific and native shrub seeds in a deciduous forest in eastern Missouri. Using a combination of *L. maackii* removal and fungicide treatments, we found no effect of *L. maackii* invasion on seed viability of the native *Symphoricarpos orbiculatus* (Caprifoliaceae) or *Cornus drummondii* (Cornaceae). In contrast, fungi were significant agents of *L. maackii* seed mortality in invaded habitats. Losses of *L. maackii* to soil fungi were also significant in invaded habitats where *L. maackii* had been removed, although the magnitude of the effect of fungi was lower, suggesting that changes in soil chemistry or microhabitat caused by *L. maackii* were responsible for affecting fungal seed pathogens. Our work suggests that apparent competition via soil pathogens is not an important factor contributing to impacts of *L. maackii* on native shrubs. Rather, we found that fungal seed pathogens have density-dependent effects on *L. maackii* seed survival. Therefore, while fungal pathogens may

provide little biotic resistance to early invasion by *L. maackii*, our study illustrates that more work is needed to understand how changes in fungal pathogens during the course of an invasion contribute to the potential for restoration of invaded systems. More generally, our study suggests that increased rates of fungal pathogen attack may be realized by invasive plants, such as *L. maackii*, that change the chemical or physical environment of the habitats they invade.

Keywords Apparent competition · Biotic resistance · Fungi · Invasive plants · *Lonicera maackii*

Introduction

Invasive exotic plants can have transformative effects on native communities, including the alteration of the diversity and composition of plant communities (Mack et al. 2000; McKinney 2004; Wilcove et al. 1998). In addition to the direct interactions between native and invasive plants, e.g., competition (Levine et al. 2003), there is mounting evidence that exotic plants can also have important indirect effects that may have a variety of unappreciated consequences within invaded communities (reviewed in Vila et al. 2011; White et al. 2006). One such indirect effect is apparent competition, whereby exotics increase the susceptibility of native species to consumers or pathogens (Holt 1977; Noonburg and Byers 2005; Orrock et al. 2010). Although empirical studies suggest that apparent competition may play an important role in shaping the effect of invasive plants on the survival and growth of native seeds, seedlings and plants (Borer et al. 2007; Mangla et al. 2008; Meiners 2007; Orrock and Witter 2010; Orrock et al. 2008; Seabloom et al. 2009), few studies have examined how

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J. L. Orrock (✉)
Department of Zoology, University of Wisconsin,
Madison, WI 53706, USA
e-mail: jorrock@wisc.edu

C. C. Christopher
Education Department, Cincinnati Zoo and Botanical Garden,
Cincinnati, OH 45220, USA

H. P. Dutra
Department of Natural Sciences, Life University,
Marietta, GA 30060, USA

apparent competition between native and exotic plants affects seed survival in the seed bank of systems that vary in the degree of invasion (Dostál 2010; Orrock and Hoisington-López 2009).

Understanding how exotic plants alter seed survival is important because the distribution and abundance of many plant species may be limited by seed survival (Clark et al. 2007; Turnbull et al. 2000). Many invasive plants are known to impact the structure and function of soil microbial communities (Kourtev et al. 2003; Madritch and Lindroth 2009; Mangla et al. 2008; Vogelsang and Bever 2009), and microbial soil pathogens can have large effects on the mortality of both native and exotic seeds (Blaney and Kotanen 2001; Blaney and Kotanen 2002; Chambers and MacMahon 1994; Dostál 2010; Kirkpatrick and Bazzaz 1979; Kotanen 2007; O'Hanlon-Manners and Kotanen 2006; Orrock and Hoisington-López 2009; Schafer and Kotanen 2003; Wagner and Mitschunas 2008). However, it is unclear whether invasive plants indirectly impact native seed survival by altering the effect of seed pathogens on native plants (i.e., apparent competition) or whether changes in soil pathogens following invasion lead to greater impacts on invasive plants (i.e., density-dependent biotic resistance).

In this study, we examined the effects of the invasive deciduous shrub *Lonicera maackii* (Caprifoliaceae) on the viability of experimentally buried conspecific seeds and seeds of two native shrubs. *Lonicera maackii* is native to Asia and first introduced to North America in 1897 (Luken and Thieret 1996). The invasion of *L. maackii* across the eastern and midwestern US is associated with reduced cover (Hutchinson and Vankat 1997), richness, and abundance (Collier et al. 2002) of native understory vegetation, as well as important changes in the abundance and behavior of native organisms (Allan et al. 2010; Conley et al. 2011; Dutra et al. 2011; Mattos and Orrock 2010; McKinney and Goodell 2010; Watling et al. 2011a). *Lonicera maackii* invasion may be promoted by the widespread dispersal of its seeds by frugivorous birds (Bartuszevige and Gorchov 2005; Watling and Orrock 2010) and its success in direct competition with understory species (Gorchov and Trisel 2003). However, some of the success of *L. maackii* in competition with native plants could also be caused, at least in part, by changes in the survival of native seeds in the seed bank due to invasion-mediated changes in the chemical environment or microclimate of the soil. For instance, *L. maackii* produces biologically active secondary compounds (Cipollini et al. 2008; Dorning and Cipollini 2006), and invasion by *Lonicera* spp. can cause changes in soil respiration (Madritch and Lindroth 2009).

We coupled the experimental removal of *L. maackii* with soil fungicide application to evaluate the potential role

of apparent competition between *L. maackii* and two native shrub species: a confamilial native species, *Symphoricarpos orbiculatus* (Caprifoliaceae) and another common native species, *Cornus drummondii* (Cornaceae). Our design allows us to explicitly examine whether *L. maackii* invasion disproportionately decreases the survival of native seeds (i.e., apparent competition) or whether *L. maackii* experiences greater mortality due to fungal seed pathogens compared to native species (i.e., biotic resistance). Moreover, our use of experimental *L. maackii* removals also allows us to examine the degree to which any effects of *L. maackii* on seed survival persist once *L. maackii* is removed.

Materials and methods

Study site and experimental design

Our study was conducted at the Busch conservation area (BCA) in St. Charles, Missouri, USA. BCA contains 1,200 ha of oak–hickory forests with relatively open shrub layers containing *C. drummondii*, *S. orbiculatus*, *Lindera benzoin*, and *Rhus aromatica*. Much of the understory has been heavily invaded by *L. maackii*.

We established six experimental plots in each of three habitat types that differed in the degree of habitat invasion: (1) stands invaded by *L. maackii* (0.84 ± 0.12 SE shrubs/m²), hereafter referred to as “invaded stands”, (2) stands uninvaded by *L. maackii* (0.01 ± 0.01 SE shrubs/m²; “uninvaded stands” hereafter), and (3) previously invaded stands that have been kept clear of *L. maackii* by clipping all *L. maackii* shrubs since fall 2006, hereafter referred to as “invader removal stands”. Because *L. maackii* is widespread in the study region, uninvaded sites were not completely free of *L. maackii*, but had significantly reduced densities of *L. maackii*. Thus, we believe that our uninvaded plots are suitable for the establishment of *L. maackii*, and are otherwise similar to invaded plots. All plots were at least 200 m apart.

To determine differences in seed survival due to fungal infection, we buried fungicide-treated and untreated seed bags in each of the three habitat types. We constructed mesh seed bags (approx. 3 × 4 cm) from fiberglass window screening (Orrock and Damschen 2005). Each mesh bag was then placed into a 3 × 4 cm aluminum screen sleeve for added protection from non-fungal seed predators (Orrock and Hoisington-López 2009); the mesh of both fiberglass and aluminum screens was approximately 1 mm². We placed ten seeds of *Cornus drummondii*, *Symphoricarpos orbiculatus*, or *Lonicera maackii* into a separate bag (i.e., one species per bag) and sealed the bags with standard staples. To ensure that differences in fungal

infection were due to experimental treatments and not to pre-experimental contamination during seed collection, all seeds were surface-sterilized by placing them in a 10% bleach solution (0.62% hypochlorite) for 10 min prior to being placed into seed bags. This surface sterilization technique had no effect on seed viability of the study species (generalized linear model with binomial response distribution, all $P > 0.8$).

On 17 and 18 November 2008, we dug two ($10 \times 5 \times 5$ cm) holes in three randomly chosen locations in each of the 18 experimental sites. We placed one seed bag per species into each hole and randomly assigned each hole to either fungicide application or no-fungicide control. The mesh bag design allowed soil to freely enter the bags, but also kept seeds of the target species that might be present in the in situ seed bank from entering the bag. We used Captan fungicide (50% wettable powder, Hi-Yield brand; Arysta LifeScience North America, Cary, NC, USA), a fungicide that is effective against a variety of fungal soil pathogens and commonly used for examination of fungi-mediated seed mortality (e.g., Blaney and Kotanen 2001, 2002; Dostál 2010; Kotanen 2007; Mitschunas et al. 2009; O'Hanlon-Manners and Kotanen 2006; Orrock and Damschen 2005; Schafer and Kotanen 2003). Fungicide was liberally applied both to the soil and the seed bags in the hole assigned to the fungicide treatment. The holes containing fungicide and those containing control bags were approximately 2 m apart. This design yielded a total of 108 seed bags per species (18 sites \times 3 seed bag locations per site \times 2 holes per location \times 1 bag per hole).

On 13 March 2009, all seed bags were excavated, gently rinsed, and surface sterilized (using the methods described above) to reduce fungal contamination during germination trials. The duration of this seed burial mimicked the time over which seeds would naturally be exposed to fungi after dispersal and prior to germination. We follow the approach of other studies (e.g., Kotanen 2007; O'Hanlon-Manners and Kotanen 2006) in that we employ laboratory-based germination trials to gain a maximum estimate of germination for each species under consistent environmental conditions (i.e., without the potentially confounding effects of field-based trials). Upon removal from the field, seeds from each bag were placed on moistened filter paper in a Petri dish. Dishes were randomly arranged in a Conviron TC80 growth chamber set to a 14 h/25°C light:10 h/20°C dark cycle, conditions intended to maximize germination by mimicking early growing season environment at our experimental sites. Each day, dishes were randomly rearranged, checked for germinated seeds, and any germinated seeds were discarded.

On 9 April 2009, seeds that had not germinated were removed from the growth chamber and examined for fungal infection. Blackened seeds with liquefied endosperm

were considered non-viable. Remaining seeds were tested for viability with triphenyl tetrazolium chloride reduction assays (TZ; Peters 2000). We considered seeds to be viable when their embryo and endosperm stained entirely bright pink or red (Peters 2000). Total seed survival was quantified for each seed bag by summing the number of seeds that germinated with the number of ungerminated seeds that were classified as viable based on TZ assays.

Statistical analyses

For each species in the study, we used a generalized linear model with a binomial response distribution (Littell et al. 2006) to determine whether invasion or fungicide treatment affected seed viability of *L. maackii*, *C. drummondii*, and *S. orbiculatus*. The response variable in each of these analyses was the proportion of seeds in each seed bag that was viable. Our analyses incorporated the split-plot nature of our experiments, which yielded two levels of experimental unit. Invasion treatment (invaded, uninvaded, or invader removed) was the largest experimental unit. Fungal pathogen manipulation (addition of fungicide or no fungicide) was the next experimental unit, and was applied to three groups of three seed packets at each site. These two treatments (invasion treatment, fungicide addition) were examined as fixed effects. Because of the split-plot nature of our design, multiple levels of variation in our analyses, and slight unbalancing of our data due to loss of 6 of our 324 samples during deployment, we used the Kenward–Roger correction for standard errors, tests of significance, and for estimation of degrees of freedom (Littell et al. 2006). All analyses were conducted in SAS (Littell et al. 2006); all means presented are ± 1 standard error.

Results

There were significant differences in overall viability among species (generalized linear model comparing species using only non-fungicide seeds; $F_{2,15} = 61.41$, $P < 0.001$), with exotic *L. maackii* exhibiting a greater proportion of viable seeds (0.92 ± 0.02) than the average proportion of viable native *C. drummondii* (0.77 ± 0.03) and *S. orbiculatus* (0.28 ± 0.03). Species differed in the degree to which viable seeds germinated during germination trials or whether or not viable seeds were detected using TZ assays ungerminated seeds (i.e., dormant seeds). Nearly all of the viable seeds of *L. maackii* germinated (proportion germinating 0.96 ± 0.01), the majority of viable *C. drummondii* seeds germinated (0.82 ± 0.02), and none of the viable seeds of *S. orbiculatus* germinated (i.e., all viable *S. orbiculatus* seeds were dormant).

Habitat invasion status and fungicide treatment effects

The effects of fungicide on viability of the three seed species were not equal across invasion treatments (Table 1; Fig. 1). Fungal pathogens were significant causes of mortality for exotic *L. maackii*, but effect size depended upon habitat invasion status (Table 1; Fig. 1). There was no significant effect of habitat invasion on *L. maackii* seed viability (Table 1), but there was a significant effect of fungicide application (Table 1; $F_{1,99} = 12.29$, $P < 0.001$), and a significant interaction between habitat invasion and fungicide application ($F_{2,99} = 3.78$, $P < 0.03$). In invaded stands and invader removal stands, fungicide treatment increased the viability of *L. maackii* seeds (Fig. 1; Table 1). Fungicide addition increased the proportion of viable *L. maackii* seeds by 0.125 ± 0.04 in invaded stands and by 0.06 ± 0.02 in invader removal stands (Fig. 1). There was no difference in *L. maackii* viability of treated and untreated seeds in uninvaded stands (Table 1; Fig. 1).

For seeds of native *C. drummondii* and *S. orbiculatus*, there was no significant main effect of habitat invasion status or fungicide application in affecting the proportion of viable seeds (Table 1). The interaction of habitat invasion and fungicide was also not significant for *C. drummondii* or *S. orbiculatus* (Table 1). Despite the lack of significant effects at $\alpha = 0.05$ for native species, we note that the effect of fungicide application on viability of native species was qualitatively most important in *L. maackii* invaded habitats (Fig. 1), such that viability of fungicide-treated *C. drummondii* seeds in *L. maackii*-invaded stands was significantly higher than viability of untreated seeds (Table 1; Fig. 1).

Discussion

Invasive plants can have important indirect effects on native plants by altering the composition and function of

soil microbial communities (Lankau 2011; Madritch and Lindroth 2009; Mangla et al. 2008; Vogelsang and Bever 2009). By conducting a factorial fungicide experiment in invaded habitats, uninvaded habitats, and invaded habitats where *L. maackii* was experimentally removed, we provide evidence that invasion by *L. maackii* leads to changes in the activity of fungal seed pathogens, and that increases in pathogen attack primarily affect the invasive *L. maackii*. Our results illustrate several important points that we discuss below: (1) because the increased loss of seeds to pathogenic fungi is largely experienced by exotic *L. maackii* rather than the two native species we studied, it seems unlikely that fungi-mediated apparent competition is important in fostering invasion; (2) density-dependent increases in pathogen attack on *L. maackii* (i.e., Janzen–Connell effects) can occur in habitats following *L. maackii* invasion; and (3) seeds of woody understory species in temperate deciduous forests have significant differences in seed bank persistence.

Lonicera maackii has widespread effects on native plants (e.g., Collier et al. 2002) and animals (e.g., Dutra et al. 2011; Mattos and Orrock 2010; McKinney and Goodell 2010). Our results show that *L. maackii* invasion does not extend to altered rates of seed bank mortality of the two investigated native shrub species (Fig. 1a). Other research illustrates that the effects of *L. maackii* on native plants may arise via indirect effects, as *L. maackii* may affect reproduction of native plants by altering pollinator services (McKinney and Goodell 2010) or by increasing predation by post-dispersal seed predators in some situations (Meiners 2007) but not in others (Mattos et al., in review). Our work suggests that the significant impact of *L. maackii* that is often observed for native plant species (Collier et al. 2002) is likely to arise via direct competition between *L. maackii* and natives species for key resources (e.g., light availability; Gorchov and Trisel 2003), rather than via indirect effects (e.g., apparent competition) mediated by fungal seed pathogens.

Table 1 Summary of ANOVA on effects of habitat type (invaded by *L. maackii*, invaded habitats with *L. maackii* removed, and habitats uninvaded by *L. maackii*) and fungicide treatment on seed viability of *Cornus drummondii*, *Lonicera maackii*, and *Symphoricarpos orbiculatus*

| Effect | <i>C. drummondii</i> | | | <i>L. maackii</i> | | | <i>S. orbiculatus</i> | | |
|---------------------------------|----------------------|-----------|----------|-------------------|-----------|----------|-----------------------|-----------|----------|
| | <i>F</i> | <i>df</i> | <i>P</i> | <i>F</i> | <i>df</i> | <i>p</i> | <i>F</i> | <i>df</i> | <i>p</i> |
| Habitat type | 0.47 | 2,15 | 0.63 | 1.02 | 2,16 | 0.38 | 1.58 | 2,50 | 0.22 |
| Fungicide | 2.50 | 1,100 | 0.12 | 12.29 | 1,99 | <0.01 | 2.40 | 1,101 | 0.12 |
| Habitat type \times fungicide | 1.95 | 2,100 | 0.15 | 3.78 | 2,99 | <0.03 | 0.30 | 2,101 | 0.74 |
| Fungicide in invaded | 5.78 | 1,100 | 0.02 | 17.16 | 1,99 | <0.01 | 2.25 | 1,101 | 0.14 |
| Fungicide in removed | 0.02 | 1,100 | 0.90 | 8.90 | 1,99 | <0.01 | 0.29 | 1,101 | 0.59 |
| Fungicide in uninvaded | 0.12 | 1,100 | 0.74 | 0.07 | 1,99 | 0.79 | 0.37 | 1,101 | 0.53 |

Interaction terms are dissected into linear contrasts focusing on the effect of fungicide at each level of habitat type (invaded, invader removed, and uninvaded)

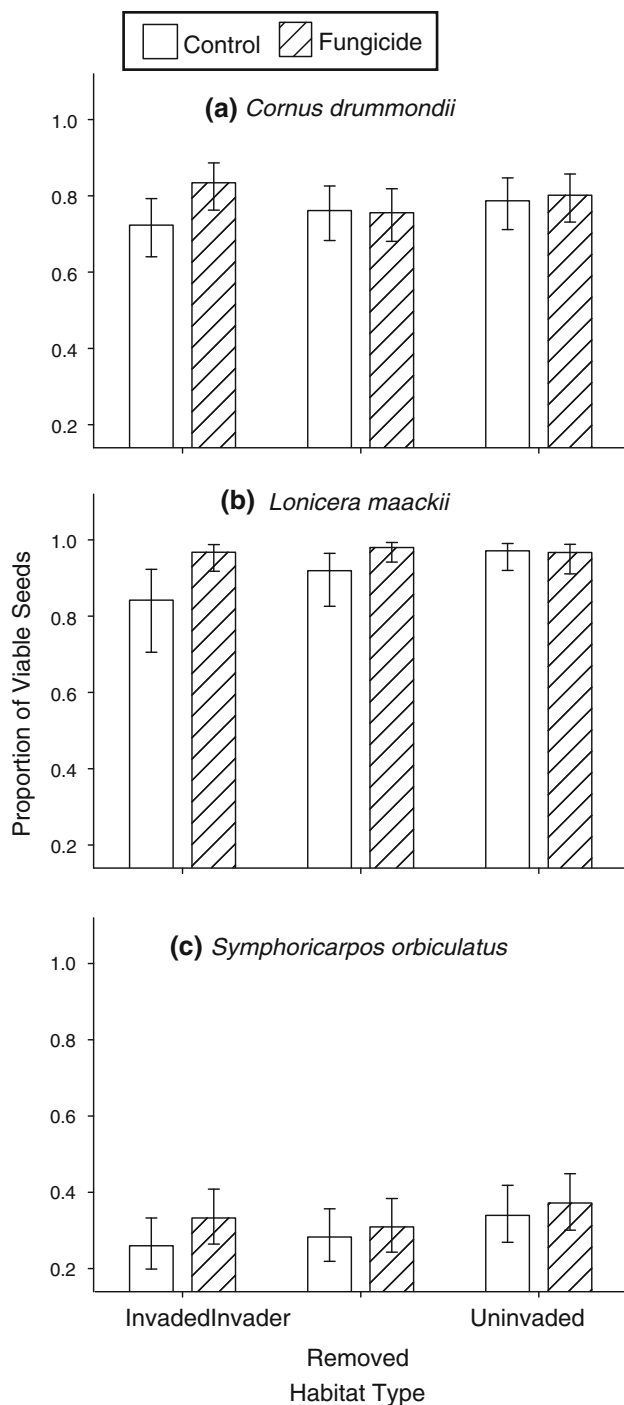


Fig. 1 Effect of fungal seed pathogens on viability of seeds of **a** native *Cornus drummondii*, **b** invasive exotic *Lonicera maackii*, and **c** native *Symphoricarpos orbiculatus* in three habitat treatment types. All data are means ± 1 SE. Significant differences among treatments are detailed in Table 1

Our results show that fungi-mediated mortality of *L. maackii* seeds is greatest in areas invaded by *L. maackii* and least in uninvaded areas (Fig. 1). As a result of the smaller effect of fungal pathogens in uninvaded habitats (Fig. 1), it is unlikely that changes in *L. maackii* seed mortality are

important for providing biotic resistance during the initial phases of an invasion when *L. maackii* is colonizing a novel location. Importantly, even under highest rates of pathogen attack, mortality of *L. maackii* is still much lower than mortality of *S. orbiculatus* and *C. drummondii* (Fig. 1). Ultimately, because of the strong competitive ability of established *L. maackii*, and evidence that competitive interactions with mature *L. maackii* limits seedling establishment of both *L. maackii* and native species (Gorchov and Trisel 2003; Luken and Goessling 1995), future studies will be required to determine whether pathogen-mediated indirect effects are important relative to the strong direct effects of *L. maackii* on native plants (e.g., via competition for light) and the degree to which pathogen- or predator-mediated seed limitation can affect *L. maackii* population dynamics. As our study is one of the first to examine fungi-mediated seed mortality of exotic and native species in forested systems, it is difficult to draw direct comparisons with other studies of variation in seed bank mortality among native and exotic plants. In grassland systems in California, overall seed bank survival of two exotic species was lower than a native species (Orrock and Hoisington-López 2009), there was no difference in fungi-mediated mortality among native and exotic species in temperate meadows (Blaney and Kotanen 2001), and fungicide application increased native seed survival but not exotic seed survival in grassland habitats in Europe (Dostál 2010).

Density-dependent attack by pathogens, a form of Janzen–Connell effect (Connell 1971; Janzen 1970), may be important for shaping widespread patterns of plant distribution and abundance (e.g., Mangan et al. 2010). Although other studies have illustrated that fungi may mediate Janzen–Connell effects for seeds of a native tree species (Kotanen 2007) and pathogens may generate Janzen–Connell effects for seedlings of native tree species (Packer and Clay 2000), our study is unique in finding that fungi mediate Janzen–Connell effects on an exotic species in temperate deciduous forests. Our findings contrast from findings in grassland systems, where persistence of exotic plants in the seed bank does not differ among invaded and uninvaded habitats (Dostál 2010; Orrock and Hoisington-López 2009). Our finding that levels of fungal attack observed when *L. maackii* is removed from invaded areas (Fig. 1) are intermediate between invaded and uninvaded habitats suggests that changes in fungal attack are a direct effect of *L. maackii* invasion. An interesting possibility is that plant characteristics associated with environmental change (e.g., changes in the chemical or physical environment) might be used to predict fungi-mediated Janzen–Connell effects.

The reduced (but still significant) effect of fungal seed pathogens in habitats where *L. maackii* was removed suggest that changes in invaded habitats caused by *L. maackii*

may be important for mediating fungi effects. One mechanism by which *L. maackii* may alter the effects of fungal seed pathogens is via altering the soil chemical environment via the production of allelopathic chemicals (Cipollini et al. 2008; Dorning and Cipollini 2006; McEwan et al. 2010) or via other inputs to the soil (e.g., the production of voluminous quantities of leaf litter). Allelochemicals can stimulate the activity of pathogenic fungi in the soil (Ruan et al. 1995), and *Lonicera* leaf litter has been shown to increase soil microbial respiration rates (Madritch and Lindroth 2009). The possibility that allelochemicals may affect fungal attack highlights a novel costs of allelochemical production: whereas the traditional model holds that production of allelochemicals may be energetically costly, our work suggests that production of allelochemicals may have additional costs fostered by soil-borne pathogens, just as herbivores can alter the costs and benefits of allelopathic chemicals (Lankau 2007).

An additional mechanism whereby *L. maackii* might alter the effects of fungal pathogens includes alteration of soil microclimate. In invaded areas, *L. maackii* forms a thick understory layer, and some evidence suggests that this leads to changes in light availability and temperature (Hutchinson and Vankat 1997; Watling et al. 2011b). Changes in microclimate might be important in the context of fungal pathogens, as higher seedling mortality has been observed in shaded areas of tropical forests (Augsburger and Kelly 1984). Moisture has also been found to be important in affecting seed survival in meadow systems: Blaney and Kotanen (2001) and Schafer and Kotanen (2003) found that susceptibility to fungal pathogens may be greater in wetter soil. Thus, shade provided by *L. maackii* (Hutchinson and Vankat 1997) may increase *L. maackii* (and possibly *C. drummondii*; Fig. 1; Table 1) fungal infection rates because of increased humidity or soil moisture under the *L. maackii* canopy.

As little is known about seed bank persistence of woody plants in temperate deciduous forests (but see Kotanen 2007; O'Hanlon-Manners and Kotanen 2006), an important finding of our study was high variation in overall mortality of seeds of the three species studied. In general, *S. orbiculatus* exhibited significantly lower seed bank persistence than *C. drummondii* or *L. maackii* (Fig. 1). Seeds of *S. orbiculatus* have underdeveloped embryos that must mature before germination can begin (Hidayati et al. 2001), but do not seem to form a long-lived seed bank (Hidayati et al. 2001). This requirement for embryo maturation is consistent with the complete dormancy of *S. orbiculatus* we observed in our study; it is also possible that the low rates of viability we observed may be because *S. orbiculatus* produces few viable seeds. Although we found little effect of fungal pathogens on *S. orbiculatus*, it remains unclear whether other seed pathogens (e.g., bacteria) or seed

predators (e.g., rodents) may be important agents of *S. orbiculatus* seed mortality (Mattos et al., in review). For *L. maackii*, our work confirms previous observations that there is little seed dormancy (Hidayati et al. 2000; Luken and Goessling 1995), as most seeds germinated immediately upon initiation of the germination trial. Although multi-year studies would be required to provide definitive support, our results also provide a possible mechanism for the low levels of seed bank persistence that have been suggested for *L. maackii* (Luken and Goessling 1995): seed bank persistence may be low because seeds that do not germinate are susceptible to fungal seed pathogens (Fig. 1). Although not explicitly examined in our study, it would also be informative to perform experiments where the exposure duration of seeds varied, as this might reveal temporal signals of fungi-mediated mortality that can become obscured in longer studies because other forces of mortality become important (Wagner and Mitschunas 2008).

In finding that invasive plants can alter the effect of fungal pathogens on invaders themselves, our work illuminates several future areas of research. An important future question is whether the increased seed mortality we observed for *L. maackii* in invaded stands is sufficient to alter the population dynamics of *L. maackii*. More generally, future work is needed to understand whether particular traits of invasive species (e.g., production of novel chemicals, growth forms that alter microclimate) can be used to understand which exotic species are likely to exhibit fungi-mediated Janzen–Connell effects and which species are not. Although our work adds to the growing evidence that invasive plants may alter the environments that they invade, with potentially important indirect effects on native (Allan et al. 2010; Conley et al. 2011; Dutra et al. 2011; Vila et al. 2011) and exotic species (Madritch and Lindroth 2009), additional work is needed to fully understand the mechanisms whereby exotic plants affect native communities and to understand the extent of the direct and indirect effects produced by exotic plants.

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