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Invasive shrub alters native forest amphibian communities

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ABSTRACT

Although invasive plants can have transformative effects on native plant communities, studies of the consequences of plant invasion for native fauna are generally restricted to primary consumers. Here we investigate whether an invasive shrub, *Lonicera maackii*, impacts native amphibians and evaluate evidence for the role of invasive plant-induced alteration of forest understory microclimate as a mechanism driving amphibian responses to *L. maackii* invasion. We sampled amphibian communities in forest plots with high or low density of *L. maackii*, and monitored microclimate (temperature and humidity at ground level) in the same forest plots. Amphibian species richness and evenness were lower in invaded plots. Invasion also resulted in shifts in amphibian species composition. Mean daily maximum temperature and mean daily temperature were lower in invaded plots, and counts of the Green frog *Lithobates clamitans* were marginally negatively related to mean daily temperature. Our work illustrates how an invasive ecosystem engineer may affect native organisms with which it shares no trophic connection, and suggests that changes in microclimate may be one mechanism by which alien plants affect communities where they invade.

1. Introduction

Invasive species can have far-reaching impacts on ecosystems (Brooks et al., 2004; Levine et al., 2004; Kimbro et al., 2009). Although some invasive species interact with native taxa primarily through one or few biotic or abiotic pathways (e.g., competition, allelopathy; Levine et al., 2003), habitat-forming invasive species may act as ecosystem engineers (Jones et al., 1997) with the potential to affect many organisms through multiple different pathways (Crooks, 2002). Although the impacts of invasive species are often framed in terms of trophic interactions between organisms (e.g., species that interact as competitors or as predators and prey), an emerging perspective emphasizes the ability of invasive plants to change habitat structure or quality, i.e., to act as ecosystem engineers (Jones et al., 1997; Crooks, 2002). Invasive ecosystem engineers may have widespread effects on native species that do not directly consume or compete with the invader (e.g., Maerz et al., 2005; Brown et al., 2006; Canhoto and Laranjeira, 2007). Identifying these non-trophic effects is important because they may be pervasive, yet cryptic consequences of invasion, especially given the extensive realized and potential distribution of many species in invaded landscapes (Rouget et al., 2004; Bradley, 2009).

We examined whether the invasive Amur Honeysuckle (*Lonicera maackii*) alters the structure and composition of native amphibian communities in deciduous forests of the central United States. In the oak–hickory forests of the eastern and midwestern United States, *L. maackii* is an ecosystem engineer that provides a dense shrub layer absent in uninvaded forest (Collier et al., 2002). The presence of a novel layer of dense vegetation in the understory of otherwise relatively open forest may alter the amount of light at ground level (McKinney and Goodell, 2010), reducing temperature at the soil surface (Herrera, 1997) while also increasing humidity (Chen et al., 1999). Because amphibians are relatively susceptible to desiccation (Rothermel and Luhring, 2005), abiotic conditions that reduce desiccation risk (e.g., low temperatures, high humidity) may act as an environmental filter that alters species composition in invaded sites relative to uninvaded forest (e.g., the species-sorting hypothesis, Leibold et al. (2004), see Civitello et al. (2008) for analogous exotic plant-induced shifts in tick communities associated with changes in microclimate). Therefore, we also evaluated whether microclimate differs in forest with high or low density of *L. maackii*, and test for relationships between microclimate and amphibian richness and abundance. We ask three specific questions about invasive plant–amphibian interactions in forest habitat: (1) Do amphibian communities or species counts differ in forest with high or low

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density of *L. maackii*? (2) Do amphibian species counts vary with forest understory microclimate (temperature and relative humidity on the forest floor)? (3) Does microclimate vary between high and low *L. maackii* density plots?

2. Materials and methods

Field sampling was conducted at the August A. Busch Memorial Conservation Area (38°42N, 90°44W) in St Charles county, Missouri, USA between 8 March and 17 July 2009. Amphibians were sampled using pitfall traps with drift fences (Corn, 1994); each array consisted of three separate 12 m plastic drift fences buried in the ground in a 'Y' shape, with a 19 L plastic bucket sunk in the ground at the far end of each fence and the middle of the array ($N = 4$ buckets per array). A total of 12 arrays (plots) were installed, six in forest heavily invaded by *L. maackii* (shrubs/m^2 ± 1 SE = 0.93 ± 0.09, $N = 12$ samples/plot) and six in forest with no or few *L. maackii* shrubs (shrubs/m^2 ± 1 SE = 0.02 ± 0.01, $N = 12$ samples/plot). Density of *L. maackii* was estimated in 12.1 m radius circular plots (samples) located every 10 m along three parallel transects centered on each pitfall array. Hereafter we refer to plots as invaded or uninvaded based on the density of *L. maackii*. We are not aware of systematic differences in management history at invaded or uninvaded plots (L. Bollmann and J. Vogel, personal communication), and at least some immature shrubs were present throughout the study area. We therefore conclude that *L. maackii* was largely absent from uninvaded sites because of dispersal limitation rather than land use history that may confound the effects of *L. maackii* density we describe here. Canopy tree species composition was broadly similar across plots, and dominated by *Quercus* spp. and Shagbark hickory, *Carya ovata*. All trap arrays were placed within 100 m of breeding ponds known to be used by amphibians during the study period. Plots were separated by a minimum distance of approximately 500 m, and marked individuals were never recaptured at arrays other than the one where they were originally caught. Traps were checked every 1–3 days while active; although traps were not open continuously during the study period, traps were open at all sites simultaneously when running. Individual amphibians were identified to species, weighed, measured for snout-to-vent length (anurans) or total length (salamanders), and marked with a unique toe clip for future identification.

Temperature and humidity were recorded at hourly intervals using a single Hygrochron iButton™ data logger placed within approximately 5 m of each trap array ($N = 12$ data loggers) from 7 April to 30 June 2009. Data loggers were placed on the ground to monitor conditions relevant for terrestrial amphibians. We calculated mean daily temperature and humidity in addition to mean daily maximum temperature and mean daily minimum humidity because amphibians generally prefer relatively cool and moist environments and may show responses to undesirable microclimate extremes.

We analyzed three amphibian community response metrics (species richness, evenness and species composition). We used a two-sample *t*-test adjusted for unequal variance to determine whether species richness varied between plots invaded or uninvaded by *L. maackii*. We also constructed species accumulation curves based on 1000 randomizations of the observed species counts per treatment in program EcoSim version 7.72 (Gotelli and Entsminger, 2009). We compared overlap of 95% confidence intervals for species richness between treatments (forest invaded or not by *L. maackii*). We calculated the evenness of species abundance distributions in each plot using EcoSim, and tested for differences in evenness between treatments using a *t*-test. Following analyses of species richness and evenness, we used additional *t*-tests to determine whether counts of individual species varied between treatments; these analyses were limited to species represented by 20 or more individuals in the total data set ($N = 5$ species). To test the hypothesis that species composition varied between invaded and uninvaded plots we used an analysis of similarity (ANOSIM) based on the Bray–Curtis dissimilarity metric with invasion status as the predictor variable; significance of the ANOSIM was tested based on 200 permutations of the dissimilarity matrix. We calculated the contribution of each species to the average dissimilarity between invaded and uninvaded plots using the similarity percentage (SIMPER) routine in program Primer (Clarke and Warwick, 2001). We categorized each individual as juvenile or adult based on observed body size using a field guide (Conant and Collins, 1998) and used a *t*-test on arcsin-root transformed proportions to determine whether the proportion of juvenile individuals varied between invaded and uninvaded plots. We used linear regression to associate microclimate variables with amphibian responses (species richness and individual species counts) and tested for differences in temperature and humidity between treatments using *t*-tests. All *t*-tests and linear regressions were calculated in program R (R Development Core Team, 2005). Means are presented ±1 standard deviation.

3. Results

We encountered a total of 1597 individual amphibians representing 10 species over the 1188 trap nights of sampling (Table S1). Two species (the Plains leopard frog, *Lithobates blairi* and the Long-tailed salamander, *Eurycea longicauda*) were represented by a single individual in the total sample. To verify that these two rare species did not alter the results of statistical comparisons, tests of community responses (species richness, evenness and composition) were conducted with and without the two rare species. Results of all tests were qualitatively similar with and without the two rarest species, so we report analyses for all 10 species throughout the paper.

Significantly more species were encountered in uninvaded forest ($\bar{x}$ richness = 6.0 ± 1.1) than in invaded forest ($\bar{x}$ richness = 4.3 ± 1.2; $t = -2.5$, df = 9.90, $P = 0.032$), and 95% confidence intervals were non-overlapping after approximately 400 individuals had been sampled in each forest type (Fig. 1). Species evenness per plot was greater in uninvaded forest ($\bar{x}$ evenness = 0.68 ± 0.07) than invaded forest ($\bar{x}$ evenness = 0.52 ± 0.14; $t = -2.45$, df = 7.37, $P = 0.042$; Table S1), indicating a trend towards dominance of a few species in plots invaded by *L. maackii*. Counts of the Green frog, *Lithobates clamitans* were twice as great in invaded plots ($\bar{x}$ individuals = 48.83 ± 28.07) than uninvaded plots ($\bar{x}$ individuals = 24.00 ± 10.60), and this difference was marginally non-significant ($t = 2.03$, df = 6.40, $P = 0.086$; Fig. 2A), whereas Pickerel frog (*Lithobates palustris*) counts were much lower in invaded plots ($\bar{x}$ individuals = 0.50 ± 0.55) than unin-

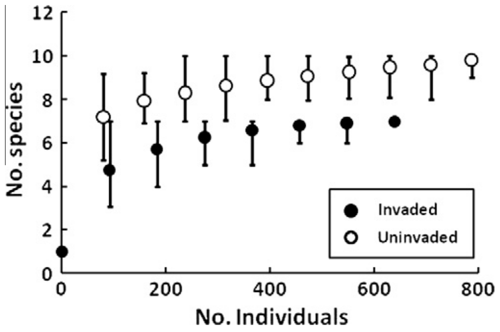

Fig. 1. Species accumulation curve (±95% confidence intervals) for amphibians in forest invaded or not by Amur Honeysuckle, *Lonicera maackii*. Data are from 12 plots (six invaded by *L. maackii*, six uninvaded by *L. maackii*) sampled from March–July 2009.

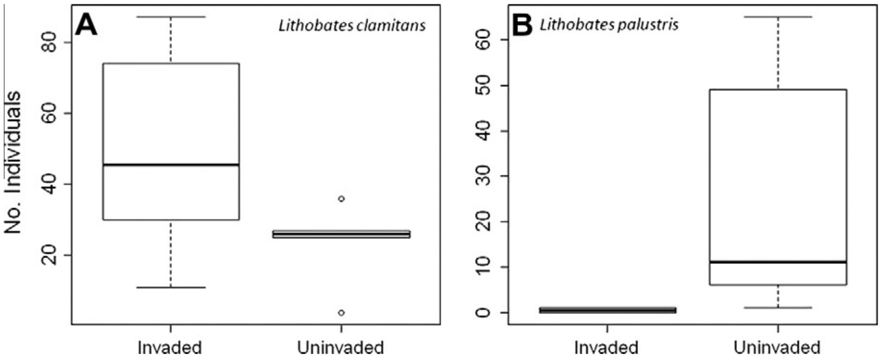

Fig. 2. (A) Increase in counts of the Green frog, *Lithobates clamitans*, in forest plots invaded by the Amur Honeysuckle, *Lonicera maackii* ($N = 6$) compared with uninvaded plots ($N = 6$) and (B) Decrease in counts of the Pickerel frog, *L. palustris* in invaded plots relative to uninvaded plots.

vaded plots ($\bar{x}$ individuals = 23.83 ± 26.57), also a marginally non-significant result ($t = -2.15$, df = 5.00, $P = 0.084$; Fig. 2B). There were no associations between *L. maackii* density and counts of the remaining three species tested ($0.298 < P < 0.813$).There was a significant difference in amphibian species composition between invaded and uninvaded plots ($R = 0.281$, $P = 0.015$). These differences were driven primarily by two species, the American toad *Anaxyrus americanus* and *L. clamitans*, that collectively contributed to 59% of the overall difference in species composition between invaded and uninvaded plots. Most individuals (77%) in the total sample were juveniles, but the proportion of juveniles did not differ between invaded plots ($\bar{x}$ proportion = 0.80 ± 0.16) and uninvaded plots ($\bar{x}$ proportion = 0.74 ± 0.14; $t = 0.89$, df = 8.85, $P = 0.395$).

The humidity sensors failed in two plots invaded by *L. maackii*, so we estimated data from those plots based on regression of humidity by temperature from the other invaded plots (because there was a significant difference in slopes of the temperature–humidity regression between invaded and uninvaded plots, $F_{1,19677} = 34.78$, P < 0.001; $R^2 = 0.21$ and 0.38 in invaded and uninvaded plots, respectively). The humidity by temperature regressions were very significant for the four plots from which we had reliable humidity data (all $P < 0.001$) and we took the average of the estimated humidity values obtained from the observed temperature data at the two plots where data loggers failed. None of the relationships between amphibian community metrics and humidity differed whether we use estimated humidity or exclude the two plots where the humidity sensors failed, so we include analyses with all 12 plots below.

Counts of *L. clamitans* were negatively associated with mean daily temperature ($F_{1,10} = 7.08$, $P = 0.024$, $R^2 = 0.41$; Fig. 3A) and *L. palustris* counts were marginally positively associated with mean daily maximum temperature ($F_{1,10} = 3.37$, $P = 0.096$, $R^2 = 0.25$; Fig. 3B. All other species-microclimate relationships were non-significant ($P > 0.213$).

Mean daily temperature was marginally lower in invaded plots ($\bar{x}$ temperature = 16.92 ± 0.30) than uninvaded plots ($\bar{x}$ temperature = 17.33 ± 0.44; $t = -1.85$, df = 8.76, $P = 0.099$; Fig. 4A), but mean daily maximum temperatures were significantly lower in invaded plots ($\bar{x}$ high temperature = 20.19 ± 1.16) than in uninvaded plots ($\bar{x}$ high temperature = 21.93 ± 1.28; $t = -2.47$, df = 9.90, $P = 0.033$; Fig. 4B). There was no relationship between either mean daily ($t = -0.29$, df = 7.17, $P = 0.776$) or mean daily minimum humidity ($t = 0.92$, df = 9.91, $P = 0.380$) and invasion status.

4. Discussion

Although it is widely appreciated that the effects of invasive plants on native communities may extend to organisms that consume and/or compete with plants (e.g., apparent competition, Orrock et al., 2010) our work clearly shows that alien ecosystem engineers can have community-level impacts on organisms with which they lack both competitive and predatory interactions: *L. maackii* density was negatively associated with species richness and evenness, and species composition varied significantly between invaded and uninvaded forest. The shift in species composition in invaded forest may have been partially related to *L. maackii*-associated changes in microclimate, because counts of one of the species driving the shift in community composition, *L. clamitans*, were inversely correlated with temperature, which tended to be cooler in invaded forest compared with uninvaded forest.

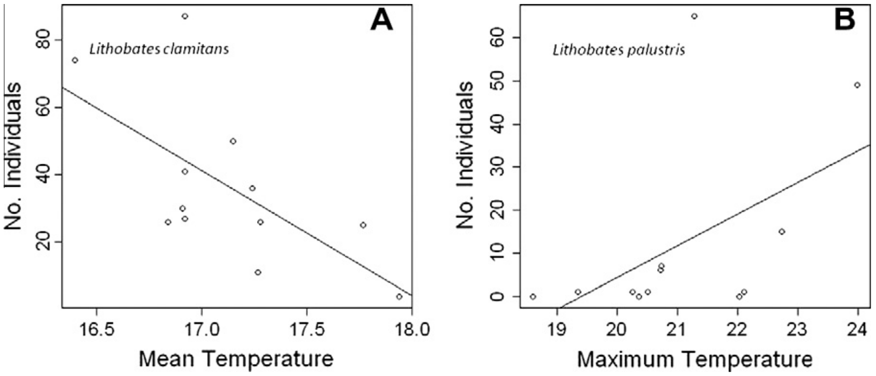

Fig. 3. (A) Decline in counts of the Green frog, *Lithobates clamitans*, in forest plots ($N = 12$) with increasing mean daily temperature (April–June 2009) and (B) increase in counts of the Pickerel frog, *L. palustris*, in forest plots with increasing mean daily maximum temperature.

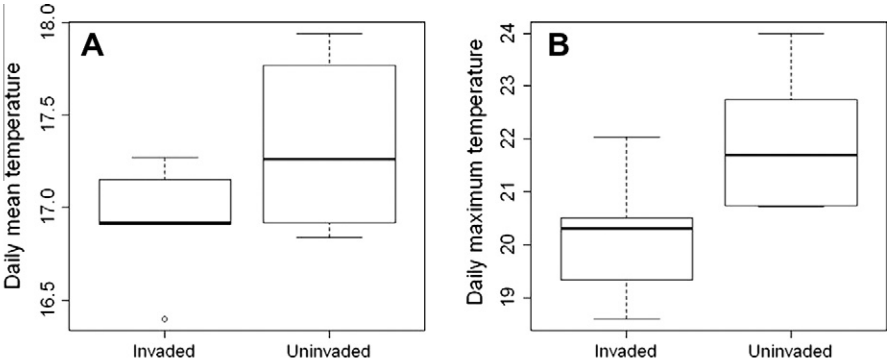

Fig. 4. (A) Decrease in mean daily temperature in forest plots invaded by the Amur Honeysuckle, *Lonicera maackii* ($N = 6$) compared with uninvaded plots ($N = 6$) and (B) decrease in mean daily maximum temperature in the same forest plots described in (A).

Abundant data attest to increased germination (Luken and Goessling, 1995) and growth (Luken et al., 1997) of *L. maackii* in high-light environments that typically experience increased temperatures relative to interior forest (Herrera, 1997). *L. maackii* interrupts infiltration of radiation to the ground surface (McKinney and Goodell, 2010), and here we show that ground temperatures are cooler in areas with dense *L. maackii* relative to uninvaded areas. The change in microclimate precipitated by invasion may represent one potentially important pathway by which the plant acts as an ecosystem engineer in invaded habitats (Jones et al., 1997; Crooks, 2002). Elsewhere we have discussed the chemical changes to aquatic environments associated with *L. maackii* and related effects on larval amphibians (Watling et al., 2011a,b). Declines of a woodland salamander in forest invaded by garlic mustard (*Alliaria petiolata*) have been linked to diminished prey resources (Maerz et al., 2009). Thus, multiple pathways have been implicated to explain invasive plant effects on amphibians. As an increasing number of studies describe amphibian responses to plant invasion (e.g., McEvoy and Durtsche, 2004; Brown et al., 2006; Maerz et al., 2009), elucidating the mechanisms underlying these responses is key to evaluating the magnitude of invasive plant effects on communities where they invade.

The shift in species composition we observed between invaded and uninvaded plots was attributable to increased numbers of one species associated with relatively cool forest plots. *L. clamitans* was the only species to increase substantially in number with increasing *L. maackii* density, possibly because it prefers the relatively cool temperatures associated with *L. maackii* invasion. Studies of thermal optima in *L. clamitans* indicate decreased jumping performance at temperatures above approximately 25 °C (Huey and Stevenson, 1979; Knowles and Weigl, 1990), whereas sympatric species studied show a leveling off or continued increase in jumping ability between 20 and 30 °C (Knowles and Weigl, 1990). In fact, counts of one species (*L. palustris*) increased in uninvaded plots, where average daily maximum temperatures were over 1.5 °C greater than in invaded plots. However, the increase in *L. clamitans* counts in invaded plots and relationships between counts and average temperature were marginally non-significant, suggesting that changes in microclimate may only be a partial explanation for invasive plant effects on amphibians.

It is also possible that our results are driven by differences in detectability between invaded and uninvaded plots; if *L. clamitans* are equally abundant but less likely to move where *L. maackii* density is low, counts from pitfall sampling will be lower than counts from invaded plots (e.g., Hyde and Simons, 2001). Nonetheless, decreased mobility likely comes at a biological cost because it implies limited access to resources (Werner, 1992). Because landscape changes associated with altered microclimate (e.g., forest clearing) can affect amphibian movement (Todd et al., 2009), and because amphibians may be particularly negatively impacted by decreased connectivity (Cushman, 2006), a deeper understanding of how plant invasion alters movement dynamics may be warranted.

In conclusion, we find that invasion by *L. maackii* is associated with relatively depauperate and homogenized amphibian communities. *Lonicera maackii* changes the distribution of thermal refugia in the environment by creating localized patches of relatively cool habitat favored by the Green frog, *L. clamitans*. More generally, our results demonstrate how invasive ecosystem engineers can contribute to the erosion of biodiversity for organisms with which they lack competitive or trophic interactions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.07.005.

References

Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Glob. Change Biol. 15, 196–208.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677–688.

Brown, C.J., Blossey, B., Maerz, J.C., Joule, S.J., 2006. Invasive plant and experimental venue affect tadpole performance. Biol. Invas. 8, 327–338.

Canhoto, C., Laranjeira, C., 2007. Leachates of *Eucalyptus globulus* in intermittent streams affect water parameters and invertebrates. Int. Rev. Hydrobiol. 92, 173–182.

Chen, J., Saunders, S.C., Crow, T.T., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. BioScience 49, 288–297.

Civitello, D.J., Flory, S.L., Clay, K., 2008. Exotic grass invasion reduces survival of *Amblyomma americanum* and *Dermacentor variabilis* ticks (Acari: Ixodidae). J. Med. Entomol. 45, 867–872.

Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, United Kingdom.

Collier, M.H., Vankat, J.L., Hughes, M.R., 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am. Midl. Nat. 147, 60–71.

Conant, R., Collins, J.T., 1998. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin, New York.

Corn, P.S., 1994. Straight-line drift fences and pitfall traps. In: Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S. (Eds.), Measuring and Monitoring Biological Diversity Standard Methods for Amphibians. Smithsonian Institution Press, Washington DC, pp. 109–117.

Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153–166.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol. Conserv. 128, 231–240.

Gotelli, N.J., Entsminger, G.L., 2009. EcoSim: null models software for ecology. Version 7.72. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT 05465. <http://garyentsminger.com/ecosim.htm>.

Herrera, C.M., 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos 78, 601–611.

Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. 19, 357–366.

Hyde, E.J., Simons, T.R., 2001. Sampling plethodontid salamanders: sources of variability. J. Wildlife Manage. 65, 624–632.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kimbro, D.L., Grosholz, E.D., Baukus, A.J., Nesbitt, N.J., Travis, N.M., Attoe, S., Coleman-Hulbert, C., 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. Oecologia 160, 563–575.

Knowles, T.W., Weigl, P.D., 1990. Thermal dependence of anuran burst locomotor performance. Copeia 3, 796–802.

Leibold, M.A. et al., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. Proc. Roy. Soc. London B 270, 775–781.

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7, 975–989.

Luken, J.O., Goessling, N., 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. Am. Midl Nat. 133, 124–130.

Luken, J.O., Kuddes, L.M., Tholemeier, T.C., Haller, D.M., 1997. Comparative responses of *Lonicera maackii* (Amur Honeysuckle) and *Lindera benzoin* (Spicebush) to increased light. Am. Midl Nat. 138, 331–343.

Maerz, J.C., Brown, C.J., Chapins, C.T., Blossey, B., 2005. Can secondary compounds of an invasive plant affect larval amphibians? Funct. Ecol. 19, 970–975.

Maerz, J.C., Nuzzo, V.A., Blossey, B., 2009. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. Con. Biol. 23, 975–981.

McEvoy, N.L., Durtsche, R.D., 2004. Effect of the invasive shrub *Lonicera maackii* (Caprifoliaceae; Amur honeysuckle) on autumn herpetofauna biodiversity. J. Kent. Acad. Sci. 65, 27–32.

McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biol. Invas. 12, 2751–2763.

Orrock, J.L., Holt, R.D., Baskett, M.L., 2010. Refuge-mediated apparent competition in plant-consumer interactions. Ecol. Lett. 13, 11–20.

R Development Core Team. 2005 R: a language and environment for statistical computing, reference index version 2.2.1. Vienna: R Foundation for Statistical Computing <http://www.R-project.org>.

Rothermel, B.B., Luhring, T.M., 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested stands. J. Herpetol. 39, 619–626.

Rouget, M., Richardson, D.M., Nel, J., Le Maitre, D.C., Egoh, B., Mgidi, T., 2004. Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climate suitability. Divers. Distrib. 10, 475–484.

Todd, B.D., Luhring, T.M., Rothermel, B.B., Gibbons, J.W., 2009. Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. J. Appl. Ecol. 46, 554–561.

Watling, J.I., Hickman, C.R., Orrock, J.L., 2011a. Predators and invasive plants affect performance of amphibian larvae. Oikos 120, 735–739.

Watling, J.I., Hickman, C.R., Lee, E., Wang, K., Orrock, J.L., 2011b. Extracts of the invasive shrub *Lonicera maackii* increase mortality and alter behavior of amphibian larvae. Oecologia 165, 153–159.

Werner, E.E., 1992. Individual behavior and higher-order species interactions. Am. Nat. 140, S5–S32.