Elevated native terrestrial snail abundance and diversity in association with an invasive understory shrub, *Berberis thunbergii*, in a North American deciduous forest

Ryan M. Utz[a],[*], Timothy A. Pearce[b], Danielle L. Lewis[a], Joseph C. Mannino[a]

[a] *Falk School of Sustainability, Chatham University, 6035 Ridge Rd., Gibsonia, PA, 15044, USA*
[b] *Carnegie Museum of Natural History, 4400 Forbes Ave., Pittsburgh, PA, 15213, USA*

ARTICLE INFO

ABSTRACT

Invasive terrestrial plants often substantially reshape environments, yet how such invasions affect terrestrial snail assemblages remains understudied. We investigated how snail assemblages in deciduous forest soils with dense *Berberis thunbergii* (Japanese barberry), an invasive shrub in eastern North America, differ from forest areas lacking the shrub. Leaf litter and soil samples were collected from forest patches with dense *B. thunbergii* understories and adjacent control areas within two exurban forest tracts in western Pennsylvania, U.S.A. Snails were identified to species and quantified by standard diversity metrics. Contrary to our expectations, snails were significantly more abundant and diverse in *B. thunbergii*-invaded areas. Despite differences in abundance, the snail community composition did not differ between invaded and control habitats. The terrestrial snail assemblage we observed, which was composed entirely of native species, appears to respond favorably to *B. thunbergii* invasion and therefore may not be negatively impacted by physicochemical changes to soils typically observed in association with the plant. Such findings could reflect the fact that *B. thunbergii* likely creates more favorable habitat for snails by creating cooler, more humid, and more alkaline soil environments. However, the snail assemblages we retrieved may consist mostly of species with high tolerance to environmental degradation due to a legacy of land use change and acid deposition in the region.

1. Introduction

Invasive species rank among the top causes of biodiversity decline worldwide due to myriad direct and indirect species interactions (McGeoch et al., 2010). In particular, invasive plant species often change ecosystems by outcompeting native flora with similar ecological attributes for limiting resources (Gioria and Osborne, 2014), which can cause holistic environmental changes that impact entire biological communities (Ehrenfeld, 2010). Under certain circumstances, invasive plants can become dominant in floral assemblages (Lundgren et al., 2004; Burton et al., 2005). Such conditions can result in significant reductions in biodiversity and biomass of faunal assemblages in understory and soil environments (Gerber et al., 2008).

One invasive plant increasingly found in forests of the northeastern United States that likely exerts ecological effects on fauna is *Berberis thunbergii* (Japanese barberry), a shrub native to Asia. Several attributes of *B. thunbergii* allow it to successfully invade deciduous forest understories, including the ability to propagate via rhizomes (DeGasperis and Motzkin, 2007), tolerance of very low light and soil nitrogen levels

(Cassidy et al., 2004), and resistance to browsing by herbivores such as whitetail deer (*Odocoileus virginianus*; Silander and Klepeis, 1999). Soils in forests invaded by *B. thunbergii* exhibit altered physicochemical properties relative to reference conditions, including elevated pH levels (Kourtev et al., 1998), altered microbial community composition (Kourtev et al., 2002, 2003), and elevated nitrogen concentrations (Ehrenfeld et al., 2001). Invertebrate communities have also been shown to change following *B. thunbergii* invasion, with elevated densities of non-native annelid worms (Nuzzo et al., 2009) and ticks (Williams et al., 2009) observed in invaded plots.

Terrestrial snails represent an ecologically important invertebrate assemblage that has not previously been investigated for compositional changes following *B. thunbergii* invasion. Multiple ecosystem functions are supported by terrestrial snails, including providing a source of calcium for avian reproduction (Graveland, 1996; Pabian and Brittingham, 2011) and performing leaf litter decomposition (De Oliveira et al., 2010; Meyer et al., 2013). Although terrestrial mollusks comprise a large proportion of biodiversity in many ecosystems, a disproportionately large number of species within this group are

threatened or endangered due to anthropogenic environmental stressors (Régnier et al., 2009, 2015). The few studies that have investigated how invasive plants affect snail assemblages suggest that effects may be species-specific. Some have reported declines in the abundance and diversity of snails following a plant invasion (Horáčková et al., 2014), while others report the opposite trend (Ruckli et al., 2013) or an increase in locally rare species (Stoll et al., 2012).

Given the capacity of *B. thunbergii* to dominate forest understories and to comprehensively change soil ecosystems, we sought to determine how such an invasion affects terrestrial snail assemblages. We quantitatively compared the abundance and diversity of snails collected from control and *B. thunbergii*-invaded plots of exurban deciduous forest tracts in western Pennsylvania, U.S.A. and hypothesized that understories with heavy *B. thunbergii* infestation would possess fewer and less diverse assemblages of native snail species. To our knowledge, our study represents the first to quantitatively consider the effects of an invasive plant on terrestrial snails in North America.

2. Methods

2.1. Site selection

We executed the study in two ecologically similar forest reserves in southwestern Pennsylvania, U.S.A.: Eden Hall campus (EHC) and Irwin Run. Both sites are small (157 and 31 ha, respectively) protected reserves in regenerating deciduous forest tracts surrounded by agricultural and light urban development. The two sites are separated by a distance of 6 km, feature forests with similar species composition and size structure, and are located about 20 km north of the Pittsburgh metropolitan region. The region is humid temperate with a mean annual precipitation of 88 cm. Prior to European settlement, forests in the region consisted mainly of *Tsuga canadensis*, *Pinus strobus*, and *Castanea dentata* but forested areas are currently dominated by *Quercus* spp., *Prunus serotina*, and *Acer* spp. due to widespread and repeated logging, tree pathogen introductions, and land use conversion (typical of nearly all forests in the region; Hall et al., 2002; Lovett et al., 2006).

All samples collected to quantify snail assemblages were retrieved from locations classified as invaded by *B. thunbergii* or from control forest understories. Invaded plots were identified by surveying both properties on foot with a global positioning system and mapping the areas of contiguous *B. thunbergii* understory using ArcGIS 10.3 (ESRI, 2014). Although the plant can be found in isolated patches, the majority of *B. thunbergii* cover in our study sites consisted of dense, nearly impenetrable patches.

Once contiguous barberry patches were georeferenced, we randomly selected 24 locations among both reserves to serve as replicates (Fig. 1). Twelve sites were located 15–100 m within *B. thunbergii* patches. The other twelve sites, randomly chosen to serve as control replicates, were located outside, but within 50 m of, the *B. thunbergii* patch edges. All randomly selected locations were positioned at least 15 m apart. To assess the degree of invasion, we surveyed *B. thunbergii* stem density within a 1 m^2 plot at the sampling location. An average *B. thunbergii* stem density of 8.8 ± 4.6 (mean ± standard deviation) per square meter was observed in invaded plots and the shrub was entirely absent in all control plots. All sites were located at least 25 m away from streams or other bodies of water.

2.2. Soil sampling and laboratory processing

Snail samples were collected using the soil and leaf litter sampling method, which adequately recovers minute species and allows for comparisons of relative abundance across a given habitat gradient (Pearce and Örstan, 2006). To sample, we placed a 0.25 × 0.25 m PVC quadrat on the forest floor at the randomly selected location. The top 5 cm of soil and leaf litter inside the quadrat were collected using a garden trowel and placed into a cotton canvas bag.

Soil and leaf litter samples were dried at 50 °C in a drying oven for 24–36 h. Once all samples were thoroughly dried, all contents were filtered through stacked sieves with 8, 4, 2, 1.4, 1.0, and 0.7 mm mesh to improve the detectability of snails. Sieved sample contents were checked for snail shells under a dissecting microscope. Both fresh and empty shells were collected from samples so that we did not omit species likely present locally so that we could tally species even if they were not recovered alive. Although some studies caution against including empty shell specimens when quantifying communities since shells can degrade at different rates (Cameron and Pokryszko, 2005), shells of several species in similar environments have been found to degrade at comparable rates (Pearce, 2008). Furthermore, we assumed that the presence of *B. thunbergii* would be unlikely to significantly affect shell decomposition rates or bias the primary study objectives. Each individual was identified to species.

2.3. Statistical analyses

Differences in snail abundance and community composition between control and *B. thunbergii* plots were quantified by contrasting control versus invaded samples. We chose to treat these as a dichotomous categorical independent variable., rather than use *B. thunbergii* stem density or dry mass estimates as a continuous variable, due to the observation that *B. thunbergii* exhibits a very patchy and sprawling growth form. Consequently, even in heavily infested, mature *B. thunbergii* patches, a single random m^2 plot may not include the number of *B. thunbergii* stems that accurately reflects the degree of invasion.

We assessed several metrics related to snail abundance and alpha richness as dependent variables. Snail density was quantified by the number of counts per sampled. Diversity was quantified in terms of species density (number of species per sample) and Shannon-Weiner biodiversity (H'). All abundance and diversity metrics were compared using regular or generalized linear models (GLMs), with metrics representing counts (such as species density) modeled in a GLM assuming a Poisson distribution. All models included the forest plot (Eden Hall versus Irwin Run) as a randomized blocking variable to account for any variation observed due to differences in snail assemblages between the two forest tracts.

Snail assemblage composition among sample types was also compared by ordination and indicator species analyses. We modeled snail assemblages using non-metric multidimensional scaling (NMDS) on Bray-Curtis dissimilarity distances of snail counts per sample. Differences in community composition were assessed using a permutational multivariate analysis of variance (PERMANOVA) model with invasion status and location as independent variables and Bray-Curtis dissimilarity as the distance metric. Finally, indicator species analysis (Dufrêne and Legendre, 1997) was also applied on snail counts to identify if certain species represented significant indicators of control or *B. thunbergii*-invaded plots.

All statistical analyses were performed in R (3.2.1; R Development Core Team, 2017). NMDS coordinates were calculated using the vegan package (Oksanen et al., 2017) and indicator species analysis was conducted through the indicspecies package (De Caceres and Jansen, 2016).

3. Results

We retrieved 275 snail shells representing 11 species (Fig. 2), all of which were native to the study region. One sample from a control plots lacked snails. All individuals were identifiable to species. The three most common species, *Punctum minutissimum*, *Ventridens virginicus*, and *Glyphyalinia wheatleyi*, comprised 70.5% of all collected specimens.

Samples from *B. thunbergii*-invaded plots contained greater abundances of snails and harbored more snail diversity relative to those from control plots. More snails were retrieved from invaded samples relative to control samples as standardized by sample area (Table 1, Fig. 3A).
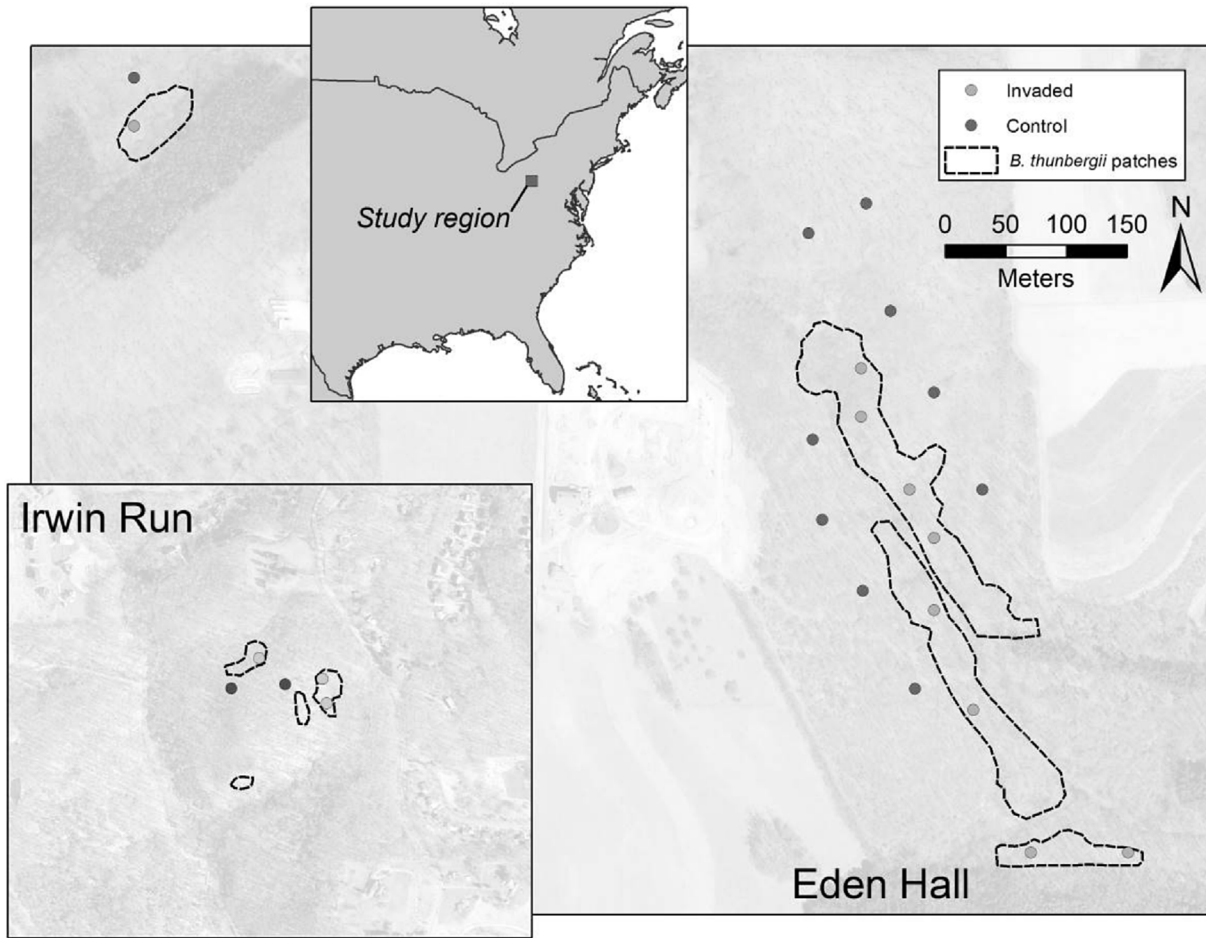
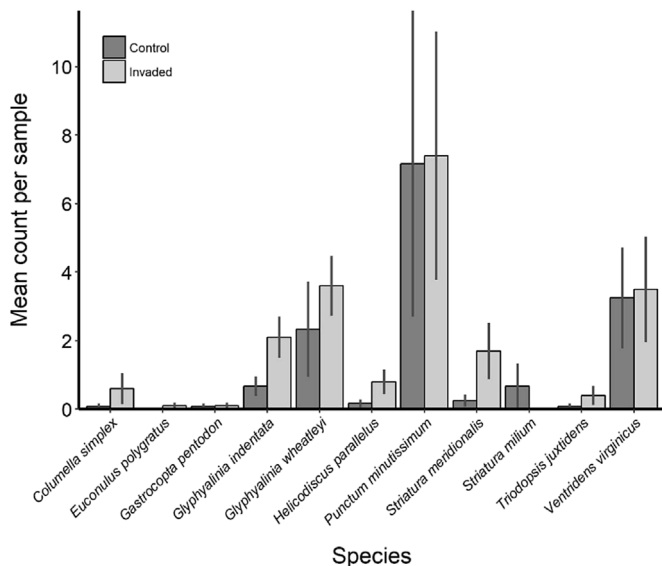**Fig. 1.** Map of study location, plots, and contiguous *B. thunbergii* patches.

Fig. 2. Mean (±1 standard error) count of snails by species per sample collected from control and invaded plots. Counts reflect the number of snails retrieved from twelve 0.0625 m² plots per plot type.

Table 1

Model parameters for linear or generalized linear models (GLMs) testing the effects of *B. thunbergii* invasion on snail assemblages. GLM models are italicized and both assumed a Poisson distribution. Coefficients are provided only if the factor was statistically significant.

Model	Factor	Coefficient	z- or t-value	p-value
Snail count (n/sample)				
	B. thunbergii present	0.24	2.4	.018
	Location: Irwin	−1.45	6.6	<.001
Species density (n/sample)				
	B. thunbergii present	0.50	2.1	.032
Diversity				
	B. thunbergii present	0.47	2.2	.036

Invaded samples harbored an average of 1.6 more species than those from control plots, a difference that was statistically significant (Fig. 3B). Snail Shannon-Weiner diversity was approximately 1.8 times greater in *B. thunbergii*-invaded plots and the difference was statistically

significant (Fig. 3C).

Despite the differences in species density and diversity, we detected few community-scale differences between *B. thunbergii*-invaded and control samples. Ordination coordinates largely overlapped between treatment types (Fig. 4) and a PERMANOVA did not detect differences in snail community composition between invaded and control sites (F-value = 1.31, p = .230) nor the interaction between location and invasion status (F-value = 1.03, p = .418), though there a difference in community composition was detected between locations (F-value = 2.99, p = .004). Indicator species analysis suggested that no species were statistically significant indicators for invasion status.
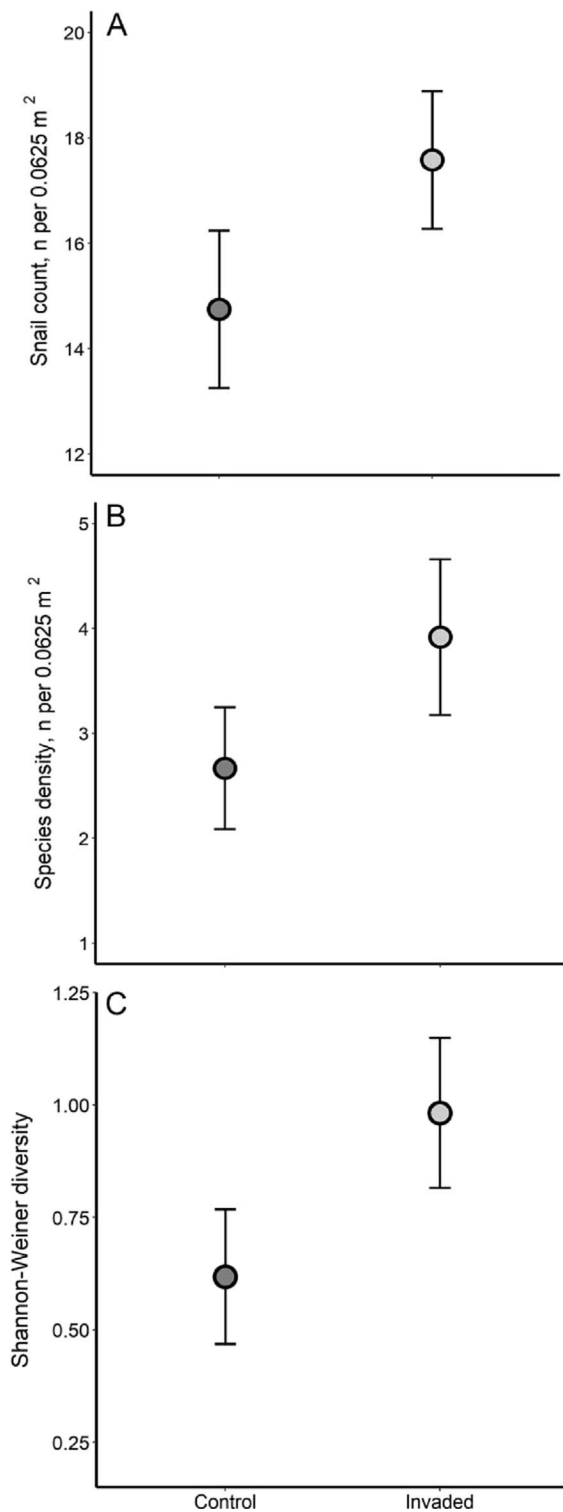
Fig. 3. Mean (± 1 standard error) (A) snail count per sample, (B) species density and (C) Shannon-Weiner diversity between control and *B. thunbergii*-invaded samples.

Fig. 4. Non-metric multidimensional scaling ordination coordinates of snail assemblages delineated by site type and location. One control sample is absent because it lacked any snails and two control samples perfectly overlap.

4. Discussion

In contrast to our expectation, we detected no negative effects of *B. thungbergii* understory infestation on snail assemblages. In fact, forest understories with dense *B. thunbergii* cover appear more likely to harbor a greater degree of snail diversity, species density, and, by some metrics, greater densities of individuals relative to control areas. The mechanisms lead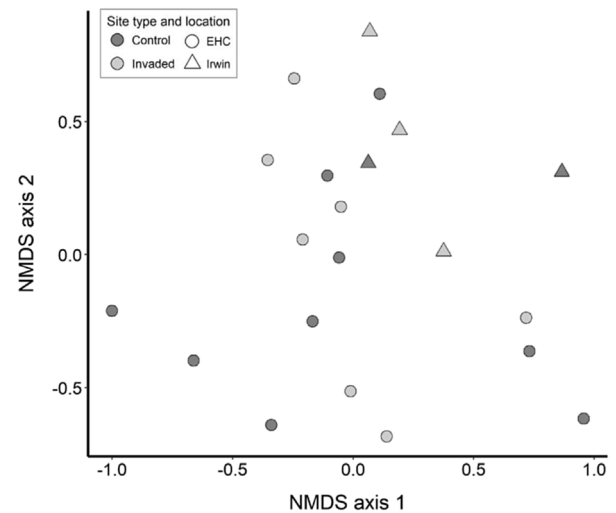ing to such findings were not tested and remain speculative, but shading provided by *B. thunbergii*, which may result in lower temperatures, elevated soil moisture, and elevated pH relative to control areas, may serve to create favorable conditions. In a related study executed at the same locations, temperatures at the forest floor were about 0.7 °C cooler on average relative to control plots due to shading by *B. thunbergii* (Daugherty and Utz, *in preparation*). Such microclimatological effects may serve to improve conditions for snail communities (Ruckli et al., 2013). Regardless of the mechanism, we suggest that terrestrial snail assemblages in western Pennsylvania forests may be resilient to the ecological effects induced by this invasive plant species and, in fact, may benefit from the invasion.

Mixed effects of invasive plants on snail assemblages have been noted outside of North America, though the response trajectory appears to be species-specific with respect to the invader and/or snail. For example, Horáčková et al. (2014) found that snail abundance was negatively affected by only one out of four species of invasive plants in eastern European riparian forests, while snail assemblages under two of the four invasive plant species were found to be less species-rich. Some have found that rare species were found to be more densely populated under invaded plots. In Switzerland, forest plots with heavy cover of the invasive herbaceous plant *Impatiens glandulifera* harbored greater densities of native snails, possibly due to elevated soil moisture (Ruckli et al., 2013). Although Stoll et al. (2012) found substantially reduced snail species density and abundances of long-lived and large species in soils invaded by *Fallopia japonica* (Japanese knotweed) in Swiss forests, a locally threatened species, *Vertigo pusilla*, was significantly more abundant in invaded plots.

Unlike what was reported in other studies, we did not detect species that were statistically significantly associated with control or invaded plots. Although several species, including *Columella simplex*, those in the genus *Glyphyalinia* and *Striatura meridionalis*, were found to be more abundant in invaded plots, the fidelity and relative abundance of each such species to the respective plot type (Dufrêne and Legendre, 1997) was not high enough to suggest these species significantly respond more favorably to invasion than others. Community ordination of the samples concurred with this finding. The lack of compositional difference coupled with higher abundances of snail communities in invaded plots may suggest that environmental conditions in invaded plots benefit the assemblage as a whole. Invasions of *B. thunbergii* can lead to cooler soil environments due to shading (Daugherty and Utz, *in preparation*). Soils under *B. thunbergii* typically become more alkaline due to chemical changes associated with the leaf litter, with pH rising by up to 1.2 in invaded understories (Ehrenfeld et al., 2001). Considering such

environmental changes, benefits to snails might be expected.

Environmental legacy effects may have influenced the results we observed. Acid and nitrogen deposition caused by concentrated industrialization was acutely severe in the region over the past century and both stressors continue to shape regional forest ecosystems to date (Driscoll et al., 2001; Aber et al., 2003). Forests throughout eastern North America were cleared for agricultural and industrial purposes throughout the region, in some cases multiple times over the past three centuries (Hall et al., 2002). Invasive pathogens have also effectively eliminated formerly dominant canopy species such as *C. dentata* and *Fraxinus* spp. (Gandhi and Herms, 2010) and top predator extirpation has resulted in overabundant populations of herbivores, especially *Odocoileus virginianus* (white-tailed deer). Resulting trophic cascades have led to widespread loss of understory plant biodiversity (Banta et al., 2005; Knight et al., 2009). The cumulative effects of such stressors very likely impacted populations of environmentally sensitive snail species: more species of snails have been found in old growth forest stands relative to recently clearcut stands (Douglas et al., 2013). Additionally, the region-wide acidification resulting from industrialization (Driscoll et al., 2001) typically reduces snail density and biodiversity (Wareborn, 1992; Gärdenfors et al., 1995). Therefore, the snail assemblages present when *B. thunbergii* spread into our study areas may have already been depauperate: the 11 species we retrieved from study sites represents a small fraction of the 129 species found within Pennsylvania (Pearce, 2015).

Although our findings suggest that *B. thunbergii* may support higher densities and diversity of snails, the study was not designed to demonstrate causal mechanisms supporting such a theory. If environmental conditions that favor *B. thunbergii* colonization also favor higher densities or diversity of gastropods, our observational study design would not be able to distinguish such a phenomenon from cause and effect. However, our original hypothesis, that invading barberry should represent degraded habitat for snail populations, appears to lack support regardless of the mechanisms supporting elevated snail densities.

The spatiotemporal scales in our work, which was limited to a small geographic area, within a 6 km² radius and a single field season, must be considered when interpreting our results. However, the forest overstory and soil structure in our study was relatively homogeneous, and including additional study areas would have likely introduced confounding factors. For example, the leaf litter of different native trees are known to support disparate snail assemblages and varying densities in the region (Hotopp, 2002; Nation 2007). Geologic heterogeneity associated with calcium content would also be expected to cause snail assemblages to vary (Beier et al., 2012). Consequently, the limited spatial scale of our study likely served to isolate the effects of *B. thunbergii* invasion.

5. Conclusion

Our findings contribute to a small but growing body of evidence that suggests terrestrial snail assemblages exhibit heterogeneous and species-specific responses to plant invasions with potential consequences for ecological processes. To our knowledge, ours is the only study in North America to consider how snails and invasive plants interact. We suggest that future efforts consider how changes to snail abundance associated with invasive plant species affects important ecological functions, such as how passerine birds might respond to elevated calcium availability (Graveland et al., 1994) or the effects on leaf litter decomposition rates (Astor et al., 2015).

Acknowledgements

References

Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.-L., Magill, A.H., Martin, M.E., Hallett, R.A., Stoddard, J.L., 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? BioScience 53, 375–389.

Astor, T., Lenoir, L., Berg, M.P., 2015. Measuring feeding traits of a range of litter-consuming terrestrial snails: leaf litter consumption, faeces production and scaling with body size. Oecologia 178, 833–845.

Banta, J.A., Royo, A.A., Kirschbaum, C., Carson, W.P., 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Nat. Area. J. 25, 10–18.

Beier, C.M., Woods, A.M., Hotopp, K.P., Gibbs, J.P., Mitchell, M.J., Dovčiak, M., Leopold, D.J., Lawrence, G.B., Page, B.D., 2012. Changes in faunal and vegetation communities along a soil calcium gradient in northern hardwood forests. Can. J. For. Res. 42, 1141–1152.

Burton, M.L., Samuelson, L.J., Pan, S., 2005. Riparian woody plant diversity and forest structure along an urban-rural gradient. Urban Ecosyst. 8, 93–106.

Cameron, R.A.D., Pokryszko, B.M., 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. J. Conchol. 38, 529.

Cassidy, T.M., Fownes, J.H., Harrington, R.A., 2004. Nitrogen limits an invasive perennial shrub in forest understory. Biol. Invasions 6, 113–121.

De Caceres, M., Jansen, F., 2016. Indicspecies: Relationship between Species and Groups of Sites. R Package Version 1.7.6. .

DeGasperis, B.G., Motzkin, G., 2007. Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. Ecology 88, 3115–3125.

De Oliveira, T., Hättenschwiler, S., Tanya Handa, I., 2010. Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. Funct. Ecol. 24, 937–946.

Douglas, D.D., Brown, D.R., Pederson, N., 2013. Land snail diversity can reflect degrees of anthropogenic disturbance. Ecosphere 4, 1–14.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience 51, 180–198.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. Annu. Rev. Ecol. Evol. Systemat. 41, 59–80.

Ehrenfeld, J.G., Kourtev, P., Huang, W., 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecol. Appl. 11, 1287–1300.

ESRI, 2014. ArcGIS. Environmental Systems Resource Institute (Redlands, CA). .

Gandhi, K.J.K., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions 12, 389–405.

Gärdenfors, U., Waldén, H.W., Wäreborn, I., 1995. Effects of soil acidification on forest land snails. Ecol. Bull. 259–270.

Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., Schaffner, U., 2008. Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. Biol. Conserv. 141, 646–654.

Gioria, M., Osborne, B.A., 2014. Resource competition in plant invasions: emerging patterns and research needs. Front. Plant Sci. 5.

Graveland, J., van der Wal, R., van Balen, J.H., van Noordwijk, A.J., 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. Nature 368, 446–448.

Graveland, J., 1996. Avian eggshell formation in calcium-rich and calcium-poor habitats: importance of snail shells and anthropogenic calcium sources. Can. J. Zool. 74, 1035–1044.

Hall, B., Motzkin, G., Foster, D.R., Syfert, M., Burk, J., 2002. Three hundred years of forest and land-use change in Massachusetts, USA. J. Biogeogr. 29, 1319–1335.

Horáčková, J., Juřičková, L., Šizling, A.L., Jarošík, V., Pyšek, P., 2014. Invasiveness does not predict impact: response of native land snail communities to plant invasions in riparian habitats. PLoS One 9, e108296.

Hotopp, K.P., 2002. Land snails and soil calcium in central Appalachian mountain forest. SE. Nat. 1, 27–44.

Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J., Kalisz, S., 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat. Area J. 29, 110–116.

Kourtev, P.S., Ehrenfeld, J.G., Häggblom, M., 2002. Exotic plant species alter the microbial community structure and function in the soil. Ecology 83, 3152–3166.

Kourtev, P.S., Ehrenfeld, J.G., Häggblom, M., 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. Soil Biol. Biochem. 35, 895–905.

Kourtev, P.S., Ehrenfeld, J.G., Huang, W.Z., 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. In: Wieder, R.K., Novák, M., Černý, J. (Eds.), Biogeochemical Investigations at Watershed, Landscape, and Regional Scales. Springer Netherlands, pp. 493–501.

Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. BioScience 56, 395–405.

Lundgren, M.R., Small, C.J., Dreyer, G.D., 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeast. Nat. 11, 313–332.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A.,

Chanson, J., Hoffmann, M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Divers. Distrib. 16, 95–108.

Meyer, W.M., Ostertag, R., Cowie, R.H., 2013. Influence of terrestrial molluscs on litter decomposition and nutrient release in a Hawaiian rain forest. Biotropica 45, 719–727.

Nation, T.H., 2007. The influence of flowering dogwood (*Cornus florida*) on land snail diversity in a southern mixed hardwood forest. Am. Midl. Nat. 157, 137–148.

Nuzzo, V.A., Maerz, J.C., Blossey, B., 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conserv. Biol. 23, 966–974.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. R Package Version 2.4-3. .

Pabian, S.E., Brittingham, M.C., 2011. Soil calcium availability limits forest songbird productivity and density. Auk 128, 441–447.

Pearce, T.A., 2008. When a snail dies in the forest, how long will the shell persist? Effect of dissolution and micro-bioerosion. Am. Malacol. Bull. 26, 111–117.

Pearce, T.A., 2015. Pennsylvania land snails susceptible to climate change, with imperilment ranks and updated distribution maps. In: Final Report to the Wild Resources Conservation Program Grant Contract WRCP-10379 (Project #441161), pp. 41. on web at. http://www.carnegiemnh.org/uploadedFiles/CMNH_Site/Mollusks/Downloads/PA%20Land%20Snails%202015_Climate%20Change_Imperilment%20Ranks_Distribution%20Maps_Final%20Report.pdf.

Pearce, T.A., Örstan, A., 2006. Terrestrial gastropoda. In: Sturm, C.F., Pearce, T.A., Valdés, Á. (Eds.), The Mollusks: a Guide to Their Study, Collection, and Preservation. Universal-Publishers.

R Development Core Team, 2017. R: a language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria.

Régnier, C., Achaz, G., Lambert, A., Cowie, R.H., Bouchet, P., Fontaine, B., 2015. Mass extinction in poorly known taxa. Proc. Natl. Acad. Sci. U. S. A. 112, 7761–7766.

Régnier, C., Fontaine, B., Bouchet, P., 2009. Not Knowing, not recording, not listing: numerous unnoticed mollusk extinctions. Conserv. Biol. 23, 1214–1221.

Ruckli, R., Rusterholz, H.-P., Baur, B., 2013. Invasion of *Impatiens glandulifera* affects terrestrial gastropods by altering microclimate. Acta Oecol. 47, 16–23.

Silander, J.A., Klepeis, D.M., 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biol. Invasions 1, 189–201.

Stoll, P., Gatzsch, K., Rusterholz, H.-P., Baur, B., 2012. Response of plant and gastropod species to knotweed invasion. Basic Appl. Ecol. 13, 232–240.

Wareborn, I., 1992. Changes in the land mollusc fauna and soil chemistry in an inland district in southern Sweden. Ecography 15, 62–69.

Williams, S.C., Ward, J.S., Worthley, T.E., Stafford, K.C., 2009. Managing Japanese barberry (Ranunculales: Berberidaceae) infestations reduces blacklegged tick (Acari: Ixodidae) abundance and infection prevalence with *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae). Environ. Entomol. 38, 977–984.