Declines in Woodland Salamander Abundance Associated with Non-Native Earthworm and Plant Invasions

JOHN C. MAERZ,*‡ VICTORIA A. NUZZO,† AND BERND BLOSSEY*

*Department of Natural Resources, Cornell University, Ithaca, NY 14851, U.S.A. †Natural Area Consultants, 1 West Hill School Road, Richford, NY 13835, U.S.A.

Abstract: Factors that negatively affect the quality of wildlife babitat are a major concern for conservation. Non-native species invasions, in particular, are perceived as a global threat to the quality of wildlife babitat. Recent evidence indicates that some changes to understory plant communities in northern temperate forests of North America, including invasions by 3 non-native plant species, are facilitated by non-native earthworm invasion. Furthermore, non-native earthworm invasions cause a reduction in leaf litter on the forest floor, and the loss of forest leaf litter is commonly associated with declines in forest fauna, including amphibians. We conducted a mark-recapture study of woodland salamander abundance across plant invasion fronts at 10 sites to determine whether earthworm or plant invasions were associated with reduced salamander abundance. Salamander abundance declined exponentially with decreasing leaf litter volume. There was no significant relationship between invasive plant cover and salamander abundance, independent of the effects of leaf litter loss due to earthworm invasion. An analysis of selected salamander prey abundance (excluding earthworms) at 4 sites showed that prey abundance declined with declining leaf litter. The loss of leaf litter layers due to non-native earthworm invasions appears to be negatively affecting woodland salamander abundance, in part, because of declines in the abundance of small arthropods that are a stable resource for salamanders. Our results demonstrate that earthworm invasions pose a significant threat to woodland amphibian fauna in the northeastern United States, and that plant invasions are symptomatic of degraded amphibian habitat but are not necessarily drivers of babitat degradation.

Keywords: Alliaria petiolata, Berberis thunbergii, earthworm invasion, forest leaf litter, invasive plants, salamander

Declinaciones en la Abundancia de Salamandras Asociadas con Invasiones de Lombrices y Plantas No Nativas

Resumen: Los factores que afectan negativamente a la calidad del bábitat de vida silvestre son una preocupación mayor para la conservación. Las invasiones de especies no nativas en particular, son percibidas como una amenaza global para la calidad del bábitat. Evidencias recientes indican que algunos cambios en las comunidades de plantas de sotobosque en bosques templados de Norte América, incluyendo invasiones por tres especies de plantas no nativas, son facilitados por la invasión de lombrices de tierra no nativas. Más aun, las invasiones de lombrices de tierra no nativas pueden causar una reducción en la capa de bojarasca en el suelo del bosque, y la pérdida de bojarasca comúnmente se asocia con declinaciones en la fauna forestal, incluyendo anfibios. Realizamos un estudio de marca-recaptura para determinar si las invasiones de lombrices o plantas se asociaban con la abundancia de salamandras. La abundancia de salamandras declinó exponencialmente con la disminución del volumen de bojarasca. No bubo relación significativa entre la cobertura de plantas invasoras y la abundancia de salamandras independientemente de los efectos de la pérdida de hojarasca debido a la invasión de lombrices de tierra. El análisis de la abundancia de presas

‡Current address: Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, U.S.A., email jmaerz® *warnell.uga.edu Paper submitted April 30, 2008; revised manuscript accepted October 16, 2008.*

> *Conservation Biology*, Volume 23, No. 4, 975-981 ©2009 Society for Conservation Biology DOI: 10.1111/j.1523-1739.2009.01167.x

selectas de salamandras (excluyendo lombrices de tierra) en cuatro sitios mostró que la abundancia de presas declinó con la declinación de bojarasca. La pérdida de capas de bojarasca debido a las invasiones de lombrices no nativas parece estar afectando negativamente a la abundancia de salamandras, en parte porque las declinaciones en la abundancia de artrópodos pequeños que son un recurso estable para las salamandras. Nuestros resultados demuestran que las invasiones de lombrices representan una amenaza significativa para la fauna de anfibios en el noreste de Estados Unidos y que las invasiones de plantas son sintomáticas de un bábitat de anfibios degradado, pero no necesariamente son las causas de esa degradación.

Palabras Clave: Alliaria petiolata, Berberis thunbergii, hojarasca de bosque, invasión de lombrices de tierra, plantas invasoras, salamandra

Introduction

The spread of non-native species is a significant component of anthropogenic environmental change (Vitousek et al. 1997). Whether invasions by non-native species are a primary cause of the decline or extirpation of populations of native species is an area of active debate (Gurevitch & Padilla 2004; Clavero & García-Berthou 2005). One reason for the debate is that invasions by a particular species often coincide with other environmental changes, such as habitat fragmentation, habitat alteration, and invasions by other species, that may have their own direct or indirect contribution to declines (Gurevitch & Padilla 2004). For example, declines in coastal horned lizard populations (Phrynosoma coronatum) are linked to habitat loss and fragmentation and to the invasion of Argentine ants (Linepithema humile), which tend to occur in heavily fragmented habitats (Suarez et al. 1998; Suarez et al. 2000; Suarez & Case 2002). Similarly, studies show that increased predation rates on bird nests in heavily fragmented habitats may be linked to the greater abundance of invasive shrubs in those habitats (Schmidt & Whelan 1999; Borgmann & Rodewald 2004). In both cases the roles of either fragmentation or invasion in population declines cannot be fully understood without considering the other factors and their potential interactions.

Such is the case with plant invasions of northern temperate forests of North America. A suite of European and Asian plant species are invading mature forests, raising concerns about their impacts on wildlife habitat. For example, we received anecdotal reports of apparent declines in woodland salamander abundance coincident with invasions by garlic mustard (Alliaria petiolata). Because non-native plant invasions can negatively affect amphibian habitat (e.g., purple loosestrife [Lythrum salicaria] can reduce wetland quality for larval American toads [Bufo americanus] (Brown et al. 2006), and Japanese knotweed [Fallopia japonica] in old fields is linked to reduced amphibian foraging success) (Maerz et al. 2005a), it is possible that perceived associations are accurate, and that non-native plant invasions are contributing to declines in woodland salamander populations. However, it is also possible that a decline in salamander abundance is coincidental with non-native plant invasion, and that separate processes explain the concurrent patterns.

Nuzzo et al. (2009), report that garlic mustard and 2 other non-native plant invasions are positively associated with non-native earthworm invasions and concurrent reductions of forest leaf litter layers (see also Bohlen et al. 2004a, 2004b; Hale et al. 2005, 2006). Other processes that contribute to litter loss, such as deforestation, lead to declines in plethodontid salamander abundance (Pough et al. 1987; Petranka et al. 1993; Ash 1997). The loss of leaf litter may alter forest floor microclimates, which have a significant impact on plethodontid salamander abundance (Feder 1983). Among the known impacts of leaf litter loss driven by earthworms is the decline in invertebrate soil fauna (reviewed by Bohlen et al. 2004b; Migge-Kleian et al. 2006), including small invertebrates such as springtails (Collembola), mites (Acarina), ants (Hymenoptera: Formicidae), beetles (Coleoptera), and Lepidopteran and Dipteran larvae that compose the more stable constituents of adult and juvenile salamander diets (Maglia 1996; Maerz et al. 2005c). Therefore, the loss of leaf litter due to earthworm invasions may be the actual cause of declines in salamander abundance and the simultaneous cause of invasions by non-native plants.

We used comparative mark-recapture studies at *A. petiolata* and *Berberis thunbergii* (*B. thunbergii*; Japanese barberry) sites described in Nuzzo et al. (2009) to test the hypothesis that non-native plant cover and reduced leaf litter volume are associated with reduced abundance of woodland salamanders. We also hypothesized that salamander prey abundance, excluding earthworms, declines with a reduced litter layer and an increased non-native plant cover.

Methods

Study Sites

We used 10 of the 15 mature hardwood forests described previously in Nuzzo et al. (2009) for our study: 5 in central New York with established invasions of *A. petiolata*,

and 5 in northeastern Pennsylvania with established invasions of B. thunbergii. All sites were north of the southern limit of the Wisconsin Glacial Boundary, which is within the region of northern hardwood forests that are believed to be historically earthworm-free (Hendrix & Bohlen 2002). The A. petiolata sites were generally lowelevation forests dominated by sugar maple (Acer saccharum), red oak (Quercus rubra), white ash (Fraxinus americanus), sweet birch (Betula lenta), and white oak (Q. alba). The B. thunbergii sites were high-elevation sites in the Pocono Mountains and were dominated by black oak (Q. nigra), chestnut oak (Q. prinus), sugar maple, white ash, and tulip poplar (Liriodendron tulipifera). Native understory plant communities were dominated by tree seedlings, perennial and annual herbs, and ferns at the A. petiolata sites, and by native shrubs (primarily Ericaeceae) at the B. thunbergii sites (Nuzzo et al. 2009). Mature trees were generally shorter, with smaller crowns at the *B. thunbergii* sites compared with the A. petiolata sites, resulting in greater light penetration and consequently drier soils at the B. thunbergii sites. Some sites had a history of limited logging but not within the past 60 years, which is sufficient time (assuming no other disturbance) to restore forest organic layers and salamander populations to precut levels (Petranka et al. 1993; Ash 1997). Each site had a well-developed invasion front (a clearly delineated transition from a habitat invaded by non-native plants to an area without non-native plants), with no other apparent features correlated with that transition. We designated the areas on each side of the invasion front as invaded or uninvaded, depending on the presence of the target non-native plant species.

Salamander and Environmental Monitoring

At each site, we established 15, 1×1 m study plots on each side of the invasion front. We placed 2, 100 \times 25×6 cm coverboards made from rough-cut, untreated sugar maple on opposing sides of each plot (one board per side). To install coverboards, we cleared away all leaf litter and duff, tamped the mineral soil, and placed boards directly on the mineral soil. We redistributed the leaf litter that we had removed around the perimeter of each board. All coverboards were installed at least 5 months prior to sampling. We checked coverboards on 12 occasions (every 2-4 weeks) from early April to late October. We collected all salamanders present under a coverboard, identified the species and sex, measured them (snout-vent length and wet mass), marked each individual uniquely using visible implant elastomers (Northwest Marine Technologies, Shaw Island, Washington, D.C.) (Davis & Ovaska 2001; Bailey et al. 2004b), and released them immediately at the edge of the coverboard.

The measures of native and non-native plant cover, leaf litter levels, and earthworm biomass are described in Nuzzo et al. (2009). In brief, we measured the percent cover of all native and non-native plant species in each plot repeatedly for 2-4 years (depending on the site) to determine maximum cumulative cover. We measured leaf litter volume in early autumn when annual cumulative litter loss due to soil fauna was greatest but fresh litter had not yet fallen to the forest floor. The volume was determined by measuring litter depth at 4 locations within each plot, calculating the mean depth of all nonzero values, and multiplying that mean by the percent cover of organic matter within the plot. While sampling for salamanders under coverboards, we also counted the number of earthworms in each of 3 size classes (small, <5 cm; medium, 5-10 cm; large, >10 cm) for each of 3 guilds: epigeic, anecic, and endogeic (Hendrix 1995; Hendrix & Bohlen 2002; see descriptions by Hale et al. 2006). We multiplied count data by the mean fresh mass of earthworms for that guild and size class to determine the fresh biomass of worms for each plot during each visit. We then estimated the "mean active earthworm fresh biomass" for 1 year for each plot (from this point forward, the term earthworm biomass refers to active fresh weight).

We do not know whether salamanders or earthworms exhibit diel activity patterns, and the logistics of covering 600 coverboards over 10 sites across 2 states limited our ability to standardize sampling times or conditions. Multiple sites were seldom covered in a single day, so most sampling took place in the early morning. We reversed the order of visits when we were able to visit 2 sites in a single day. To minimize transport of invasive species, we always sampled uninvaded plots before sampling invaded plots at a site.

Once in spring and once in autumn of 2001, we measured salamander prey availability in the invaded and uninvaded habitats of 4 of the A. petiolata sites. In each season we placed a 25×25 cm frame at 4 random locations around the perimeter of each 1-m² plot and collected all leaf litter down to the mineral soil. The 4 samples were homogenized into a single sample for each plot and stored in a cotton pillowcase in a cooler for transport to the laboratory. At the laboratory we placed each sample in a Berlese funnel under a 25-watt incandescent bulb for 5 d (large samples were subdivided into multiple funnels). Invertebrates were collected in whirlpacks containing 15% EtOH. The invertebrates were identified to the highest taxonomic resolution possible. For each sample we counted the number of invertebrates in 2 select groups that are volumetrically important in salamander diets at similar sites in the region (Maerz et al. 2005c): ants (Hymenoptera: Formicidae) and beetles (Coleoptera: Carabidae, Curculionidae, and Staphylinidae).

Salamander Abundance Estimation

We used closed population models in program CAPTURE to estimate the mean salamander abundance for each habitat (for a detailed description and justification for using these models in studies of plethodontid salamanders, see Bailey et al., 2004*a*). We used the "appropriate" function in CAPTURE to compare different closed population models, and then we estimated salamander abundance with each model. Although a single model was often determined "most appropriate," other models were often relatively similar in their weight. Furthermore, the M_{tbb} model, which other studies indicate is the best-fit model for plethodontids, does not allow for population size estimation (Bailey et al. 2004*a*). Therefore, rather than using a single abundance estimate from the most appropriate model, we used an average of all abundance estimates, with each estimate weighted by its relative appropriate ness.

Statistical Analyses

We used estimated mean values for both habitats at each site in all our analyses. We used paired t tests to determine whether earthworm biomass and leaf litter volume differed between non-native plant-invaded and adjacent uninvaded habitats. We used a 2-factor analysis of variance (ANOVA) to test the hypothesis that non-native plant invasions are associated with reduced salamander abundance. We treated measures of salamander abundance in invaded and uninvaded habitats within sites as repeated measures, and because the study sites for our focal invasive plant species were distributed in 2 different regions, we included target invasive plant as a second fixed factor. Then we used a general linear model, again with target invasive plant as a fixed factor, to test the hypotheses that salamander abundance is positively correlated with native plant cover and litter volume and negatively correlated with invasive plant cover. We used this model to test only for main effects and treated habitats within sites as independent replicates because measures of plant cover and litter volume were generally different between habitats. We also used a general linear model to determine whether litter volume was negatively correlated with earthworm biomass in both focal regions. Finally, we used a general linear model with season as a repeated measure to determine whether the salamander prey abundance, excluding earthworms, declined with decreasing litter volume among habitats. When necessary, dependent variables were log-transformed for linear analyses (Zar 1999).

Results

Independent of invasion, leaf litter volume was significantly greater among *Berberis* study sites compared with *Alliaria* study sites (mean squares [MS] = 0.0003, $F_{1,16}$ = 9.233, p = 0.008; Fig. 1a), but declined similarly with increasing non-native earthworm biomass (MS = 0.0005, $F_{1,16}$ = 15.712, p = 0.001; Fig. 1a) in both regions (fo

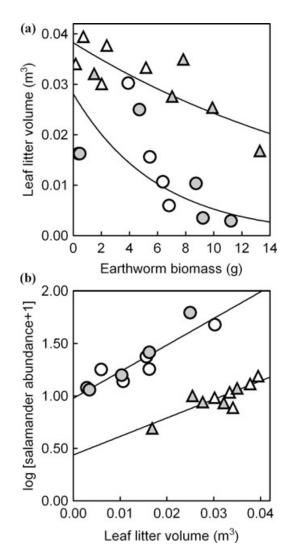


Figure 1. Correlations between (a) the mean "annual active earthworm biomass" and the mean autumn leaf litter volume and (b) the mean autumn leaf litter volume and P. cinereus abundance among forest babitats in central New York and northeastern Pennsylvania (U.S.A.) (circles, Alliaria petiolata sites; triangles, Berberis thunbergii sites; gray, babitats invaded by non-native plants; white, babitats without invasive plants).

cal plant/region × earthworm biomass interaction: MS = 0.000012, $F_{1,16} = 0.344$, p = 0.566; Fig. 1a). Estimated earthworm biomass tended to be greater (paired *t* test: t = -3.900, df = 9, p = 0.004) and, consequently, leaf litter volume tended to be lower (paired *t* test: t = 4.258, df = 9, p = 0.002) in habitats invaded by non-native plants compared with adjacent uninvaded habitat.

Salamander communities were dominated by a single plethodontid species, the eastern red-backed salamander *(Plethodon cinereus)*, which accounted for 80–99% of all individuals captured across sites. Other plethodontid species encountered in low abundance were the northern slimy salamander (P. glutinosus), Allegheny mountain dusky salamander (Desmognathus ochrophaeus), northern two-lined salamander (Eurycea bislineata), four-toed salamander (Hemidactylium scutatum), northern spring salamander (Gyrinophilus porphyriticus), and northern red salamander (Pseudotriton ruber). Two salamander species that were not plethodontids were encountered in low abundance: yellow-spotted salamander (Ambystoma maculatum) and eft stages of the eastern red-spotted newt (Notophthalmus viridescens). The capture rates of species other than P. cinereus were too low to estimate whether species composition differed among sites or between invaded and uninvaded habitats. Limited captures and the fact that many of the subordinate species (except P. glutinosus) migrate seasonally made mark-recapture estimates of abundance untenable for these species, so we used data only on P. cinereus abundance in our subsequent analyses.

The paired analysis indicated that P. cinereus abundance among Alliaria sites was significantly higher than among *Berberis* sites (MS = 0.563, $F_{1,8} = 7.682$, p =0.024; Fig. 1b), but within-site abundance did not differ significantly between invaded and uninvaded habitats $(MS = 0.026, F_{1,8} = 2.178, p = 0.178)$ in either region (focal plant × habitat: MS = 0.009, $F_{1.8} = 0.709$, p = 0.424). Within sites, P. cinereus abundance in invaded and uninvaded habitats was highly positively correlated (r =0.872, p = 0.001). Within both regions, *P. cinereus* abundance declined exponentially with decreasing leaf litter volume (Alliaria sites: r = 0.918, p < 0.001; Berberis sites: r = 0.850, p = 0.002; Fig. 1b). General linear analysis in which transformed ($\log_{10}[abundance + 1]$) abundance estimates were used also showed that P. cinereus abundance differed regionally (MS = $1.057, F_{1,15} = 116.878,$ p < 0.001; Fig. 1) as a positive function of leaf litter volume (MS = 0.581, $F_{1,15} = 64.199$, p < 0.001; Fig. 1) but was not correlated with percent cover of native (MS $< 0.001, F_{1.15} = 0.006, p = 0.939$) or non-native plants (MS = 0.010, $F_{1,15} = 1.093$, p = 0.312).

P. cinereus prey (ants and beetles) availability varied significantly between seasons and within and among sites as a function of leaf litter volume. Spring prey abundance was exponentially positively correlated with leaf litter volume, so we used transformed ($\log_{10}[abundance + 1]$) prey abundance measures for the analysis. Prey abundance was significantly greater in spring samples compared with autumn samples (MS = 0.340, $F_{1.4} = 7.980$, p = 0.048; Fig. 2), primarily because of the high abundance of the non-native weevil, Barypeithes pellucidus (Coleoptera: Curculionidae) (Maerz et al. 2005c). Weevils were absent in autumn samples, and available preys were dominated by ants (Hymenoptera: Formicidae) and rove beetle (Coleoptera: Staphylinidae) species. Within both seasons, prey abundance declined significantly with decreasing leaf litter volume (leaf litter volume: MS = 1.047,

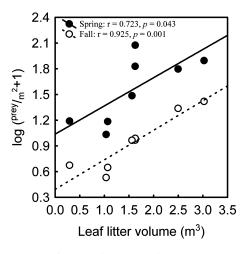


Figure 2. Correlations between the mean P. cincreus prey abundance, excluding non-native earthworms, and leaf litter volume among forest babitats in 4 central New York sites (black, spring samples; white, autumn samples).

 $F_{1,4} = 9.766, p = 0.035$; leaf litter volume × season interaction term: MS = 0.003, $F_{1,4} = 0.068, p = 0.807$; Fig. 2).

Discussion

The difficulty in determining whether invasion by a particular non-native species is affecting native species is that invasions are often correlated with other factors that may be the primary or a contributing cause of decline (Gurevitch & Padilla 2004). In some cases invasive species may increase the effects of other factors (e.g., habitat fragmentation) on wildlife (e.g., Schmidt & Whelan 1999; Suarez & Case 2002; Borgmann & Rodewald 2004). Our research and the research of others suggests that any apparent effects of non-native plant invasions on native plant communities (Bohlen et al. 2004b; Nuzzo et al. 2008) and P. cinereus abundance in north temperate North American forests are largely the result of invasions by non-native earthworms. Our results suggest that earthworm impacts on leaf litter have a strong negative effect on P. cinereus abundance, and that the apparent association between non-native plant invasions and P. cinereus declines is an artifact of the high likelihood that sites with high earthworm biomass are invaded by non-native plants. That is, plant invasions appear to be symptomatic rather than a cause of degraded forest habitats for salamanders.

Although earthworms were associated with leaf litter loss and declining *P. cinereus* abundance in both focal plant regions, there were consistent regional differences in these relationships that suggest that the magnitude of earthworm impacts can vary geographically. For example, the same biomass of non-native earthworms was associated with less leaf litter among the sites in central New York compared with northeastern Pennsylvania sites, and P. cinereus abundance was greater for a given amount of leaf litter among the central New York sites. The higher amounts of leaf litter in northeastern Pennsylvania are not the result of greater leaf inputs. These sites are more stunted, with greater canopy gaps and smaller crowns. It is more likely that the differences in canopy composition and moisture account for these regional differences. The northeastern Pennsylvania sites were more xeric, had greater light penetration, and were dominated by oak species, whereas the central New York sites were more mesic and were dominated by highly dense canopies of sugar maple. Compared with maple litter, oak litter is less susceptible to breakdown by earthworms (Suárez et al. 2006). In addition, drier soil conditions among our northeastern Pennsylvania sites are likely to limit earthworm activity, further slowing the breakdown of leaf litter. Moisture conditions would also explain why salamander abundance is greater among the central New York sites despite less leaf litter. Cooler temperatures and increased moisture enable salamanders to forage more frequently (Feder 1983), remain active during the warmer summer months, and potentially be slightly less dependent on leaf litter to remain moist and cool.

Although invasive species are considered an important contributing factor in amphibian population declines, empirical evidence of such impacts is relatively limited (Kiesecker 2003). Introductions of predatory fishes or other amphibians that may compete with or prey upon native species are the primary examples of invader impacts on amphibians. There are no studies demonstrating bottom-up impacts of invasive species on amphibian abundance. Recent evidence suggests that some plant invasions may negatively affect larval amphibian performance (Maerz et al. 2005b; Brown et al. 2006; Leonard 2008) and terrestrial foraging success of frogs (Maerz et al. 2005a) but none of these studies has linked invaders to population declines. We suggest that the loss of leaf litter due to earthworm invasion negatively impacts P. cinereus, in part, because of the reduced abundance of small arthropods such as ants, beetles, and Collembola. Although we did not quantify Collembola abundance in this study, the results of many other studies show that these also decline with litter loss due to earthworm invasion (Migge-Kleian et al. 2006). Small arthropods are important stable resources for adult and juvenile P. cinereus (Maerz et al. 2005c). Earthworms are potentially important prey for adult P. cinereus and so may compensate somewhat for the loss of other taxa in salamander diets; however, P. cinereus predation on earthworms is generally restricted to larger adults and foraging on cool, rainy nights (Maerz et al. 2005c).

Earthworm impacts on *P. cinereus* may also be linked to effects of leaf litter loss on forest floor microclimates. Plethodontid salamanders are lung less and, like many other organisms, depend on leaf litter as a moist substrate to buffer them from extreme temperatures and dehydration (Feder 1983). The loss of litter may promote water evaporation from forest soils, placing additional hydric constraints on salamanders.

Our results contribute to a growing body of research demonstrating the potentially large impacts of earthworm invasions on communities and ecosystem function in northern temperate forests of North America (reviewed by Bohlen et al. 2004b). By rapidly reducing forest leaf litter and mixing historically well-layered forest soils, earthworms affect nutrient cycling, microbial abundance and activity, and, consequently, soil invertebrate community structure. Earthworm invasions alter plant communities, causing declines or extinctions in some flora and increasing the relative importance of historically subordinate native and non-native plant species. Finally, earthworm invasions may alter resource dynamics (Maerz et al. 2005c) and be a source of soil pollution that affects vertebrate populations (Ireland 1977; Reinecke et al. 2000), both of which may contribute to population declines.

With the realization that earthworm invasions are major drivers of change in temperate forests comes the question of whether there are management options to control earthworms and their effects. The spread of earthworms to temperate forests that remain earthworm-free should be a high management priority. Because earthworm introductions are a legacy of agricultural landscapes, earthworm-free areas are likely to be more remote landscapes that are not utilized for agriculture. Earthworms are, however, also spread through their use as bait and increasingly as contaminants of ornamental plants (Cameron et al. 2008). Intervention to prevent the spread of earthworms through these pathways may be an important management objective (Hendrix & Bohlen 2002; Hale 2008). For areas currently invaded by earthworms, management options are far more limited. At present there are no published effective means of control for earthworms at the large scale. Within invaded landscapes, recognizing that earthworms are major drivers of forest change can better inform other management priorities. Specifically, it is important to realize that investment in the control of major herbivores, such as deer, or non-native plants may not result in the protection or restoration of native forest plants and animals affected by earthworm invasions. Finally, additional non-native earthworm species (e.g., Amynthas spp.) from other parts of the globe such as Asia are arriving and spreading within the United States. These new species reflect new patterns of global trade, and how these new invaders are affecting recipient ecosystems is not well understood. With a growing and compelling body of evidence on the impacts of earthworm invasions, there is a need for greater vigilance about the deliberate and accidental introduction and spread of new earthworm fauna (Hendrix & Bohlen 2002).

Acknowledgments

The funding for this research was provided by U.S. Environmental Protection Agency (NCER 828902) and was also made possible with logistical support from the Hawk Mountain Sanctuary's Acopian Center for Conservation Research, Pennsylvania Natural Lands Trust, Forest Lake Club, Pennsylvania Department of Conservation and Natural Resources, City of Syracuse, New York Department of Environmental Conservation, and the National Park Service. The use of vertebrates in the research was approved by the Cornell University Institutional Animal Care and Use Committee and by permit to J.C.M. from New York Department of Environmental Conservation and Pennsylvania Fish and Boat Commission.

Literature Cited

- Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conservation Biology 11:983-989.
- Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004a. Comparing population size estimators for plethodontid salamanders. Journal of Herpetology 38:370–380.
- Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004b. Estimating detection probability parameters for *Plethodon* salamanders using the robust capture-recapture design. Journal of Wildlife Management 68:1–13.
- Bohlen, P. J., P. M. Groffman, T. J. Fahey, M. C. Fisk, E. Suárez, D. M. Pelletier, and R. T. Fahey. 2004a. Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems 7:1–12.
- Bohlen, P. J., S. Scheu, C. M. Hale, M. A. McLean, S. Migge, P. M. Groffman, and D. Parkinson. 2004b. Non-native invasive earthworms as agents of change in northern temperate forests. Frontiers in Ecology and the Environment 2:427-435.
- Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14:1757-1765.
- Brown, C. J., B. Blossey, J. C. Maerz, and S. J. Joule. 2006. Invasive plant and experimental venue affect tadpole diet and performance. Biological Invasions 8: 327–338.
- Cameron, E. K., E. M. Bayne, and D. W. Coltman. 2008. Genetic structure of invasive earthworms *Dendrobaena octaedra* in the boreal forest of Alberta: insights into introduction mechanisms. Molecular Ecology 17:1189-1197.
- Clavero, M., and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20: 110.
- Davis, T. M., and K. Ovaska. 2001. Individual recognition of amphibians: effects of toe clipping and fluorescent tagging on the salamander *Pletbodon vehiculum*. Journal of Herpetology 35:335– 338.
- Feder, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39:291–310.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19:470–474.
- Hale, C. M. 2008. Evidence for human-mediated dispersal of exotic earthworms: support for exploring strategies to limit further spread. Molecular Ecology 17:1165–1169.
- Hale, C. M., L. E. Frelich, and P. B. Reich. 2005. Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA. Ecological Applications 15:848–860.
- Hale, C. M., L. E. Frelich, and P. B. Reich. 2006. Changes in hardwood

forest understory plant communities in response to European earthworm invasions. Ecology **87:**1637–1649.

- Hendrix, P. F., editor. 1995. Earthworm ecology and biogeography in North America. CRC Press, Boca Raton, Florida.
- Hendrix, P. F., and P. J. Bohlen. 2002. Exotic earthworm invasions in North America: ecological and policy implications. BioScience 52:801-811.
- Ireland, M. P. 1977. Lead retention in toads *Xenopus laevis* fed increasing levels of lead-contaminated earthworms. Environmental Pollution 12:85–92.
- Kiesecker, J. M. 2003. Invasive species as a global problem: toward understanding the worldwide decline of amphibians. Pages 113-126 in R. D. Semlitsch, editor. Amphibian conservation. Smithsonian Institution, Washington, D.C.
- Leonard, N. E. 2008. Native and exotic leaf litter controls on the performance of larval amphibians. Biology Department, University of New Orleans, New Orleans, Louisiana.
- Maerz, J. C., B. Blossey, and V. Nuzzo. 2005a. Green frogs show reduced foraging success in habitats invaded by Japanese knotweed. Biodiversity and Conservation 14:2901–2911.
- Maerz, J. C., C. J. Brown, C. T. Chapin, and B. Blossey. 2005b. Can secondary plant compounds of an invasive plant affect larval amphibians? Functional Ecology 19:970–975.
- Maerz, J. C., J. M. Karuzas, D. M. Madison, and B. Blossey. 2005c. Introduced invertebrates are important prey for a generalist predator. Diversity and Distributions 11:83–90.
- Maglia, A. M. 1996. Ontogeny and feeding ecology of the red-backed salamander, *Pletbodon cinereus*. Copeia **1996**:576-586.
- Migge-Kleian, S., M. A. McLean, J. C. Maerz, and L. Heneghan. 2006. The influence of invading earthworms on indigenous fauna in ecosystems previously uninhabited by earthworms. Biological Invasions 8:1275–1285.
- Nuzzo, V., J. C. Maerz, and B. Blossey. 2009. Earthworm invasion as the Driving Force Behind Plant Invasion and Community Change in Northeastern North American Forests. Conservation Biology 23: in press.[this issue]
- Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7:363-370.
- Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20:1–9.
- Reinecke, A. J., S. A. Reinecke, D. E. Musilbono, and A. Chapman. 2000. The transfer of lead (Pb) from earthworms to shrews (*Myosorex varius*). Archives of Environmental Contamination and Toxicology 39:392-397.
- Schmidt, K. A., and C. J. Whelan. 1999. Effects of exotic *Lonicera* and *Rhamus* on songbird nest predation. Conservation Biology 13:1502-1506.
- Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041-2056.
- Suarez, A. V., and T. J. Case. 2002. Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. Ecological Applications 12:291–298.
- Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. Ecological Applications 10:711–725.
- Suárez, E., T. J. Fahey, J. B. Yavitt, P. M. Groffman, and P. J. Bohlen. 2006. Patterns of litter disappearance in a northern hardwood forest invaded by exotic earthworms. Ecological Applications 16:154–165.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmánek, and R. Westbrooks. 1997. Introduced species as a significant component of human-caused global change. New Zealand Journal of Ecology 21:1-16.
- Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey.