Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: Impact on leaf litter decomposition

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Summary

This study examined an 'invasional meltdown', where the invasion of a Midwestern woodland by an exotic shrub (*Rhamnus cathartica* L.P. Mill) and the invasion by Eurasian earthworms facilitated one another. Using a litterbag approach, we examined mass loss of four substrates (*R. cathartica*, *Acer saccharum*, *Quercus rubra*, and *Quercus alba)* along a gradient of Eurasian earthworm density and biomass throughout a 40.5 ha oak woodland in Glencoe, Illinois. Earthworm densities and biomass were greatest in patches where *R. cathartica* prevailed, and populations were lowest in an upland forest subcommunity within the woodland. At each of three points along this earthworm gradient, we placed replicated litterbags constructed either to permit or to deny access to the litter by earthworms. The treatments were, therefore, plot treatments (low, medium and high earthworm density and biomass) and litterbag treatments (earthworm access and earthworm excluded). We found that earthworms promoted a very rapid loss of litter from *R. cathartica* bags. Within 3 months greater than 90% of this litter was lost from the litterbags. Earthworm impacts on other substrates followed the sequence *A. saccharum* > *Q. alba* = *Q. rubra*. Effects of both litterbag and plot treatments were found within 3 months for *A. saccharum* but *Quercus* species were affected only after a year. We propose that the impact of earthworms on litter breakdown creates conditions that promote and sustain invasion by *R. cathartica*. Previous work has demonstrated that *R. cathartica* may alter soil properties in a way that promotes and sustains invasion by earthworms. These findings have implications for the restoration management of these systems, since the legacy of *R. cathartica* on soil properties and earthworm populations may persist even after the plant has been physically removed.

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Introduction

Invasive species can be major stressors of the ecosystems that they invade (Gordon, 1998; Mack et al., 2000). Local extinction can be an outcome of a successful invasion; in fact invasive species are regarded as second only to habitat loss as a factor involved in modern human-caused extinctions (Soule, 1990). Much of the research emphasis on invasion biology has focused on the biology and impacts of individual species (Williamson, 1996). This approach yields useful information not only on the process of invasion itself, but can also lead to proposed mitigation strategies for the most problematic species (Anderson et al., 1996; Levine and D'Antonio, 1999; Tilman, 1999). Despite the value of single species studies there is a growing awareness of the potential for synergy between invaders, where one species facilitates the spread of another, typically unrelated, species (Simberloff and Von Holle, 1999; Adams et al., 2003; O'Dowd et al., 2003). The 'invasional meltdown' hypothesis has two dimensions: one is that rather than there being competitive interactions between invaders, invasive species facilitate each other; and secondly, the hypothesis predicts that invasion rates should accelerate over time (Simberloff and Von Holle, 1999; Ricciardi, 2001). Since explicit studies on the invasional meltdown hypothesis are rare (Simberloff and Von Holle, 1999; Bourgeois et al., 2005) generalizations would be premature. However, it is clear that facilitation between invaders can be the result of one invader indirectly affecting ecosystem processes in such a way as to facilitate invasion by other species (Kourtev et al., 1998). Investigations on the impact of invasive species on ecosystem structure and processes are, therefore, important for a mechanistic understanding of the consequences of invasion. Such explorations of the ecosystem impacts of invasion have become more widespread (Rapport et al., 1985; Ehrenfeld, 2003; Allison and Vitousek, 2004; Brooks et al., 2004).

We report here on work undertaken in woodlands in the Chicago area on the interaction between a major plant pest, *Rhamnus cathartica* (European buckthorn) and invasive Eurasian earthworms. Preliminary results of surveys conducted in oak woodlands in the area indicated that invasive earthworms achieved their highest abundance and greatest biomass in woodland patches dominated by European buckthorn. The distributions of earthworm populations were suggestive that they were responsible for a very rapid incorporation of forest floor material into the soil – plots where earthworm populations were highest had virtually no litter cover for much of the year. These observations indicated that the potential for measurable below-ground impacts were substantial and might result in a modification of system functioning. Modified soil processes will, in turn, have implications for the management of these systems. We briefly review the status on Midwestern US invasion by Eurasian earthworms and by *R. cathartica* before outlining the objectives of the present study, which examines synergy between the two.

It has been hypothesized that, after the most recent Pleistocene glaciations, the forested ecosystems north of the furthest extent of the glaciers had no native postglacial earthworm populations (Gates, 1977; James, 2004). Most of the earthworms present in natural areas in the Midwest are invasive Eurasian species. There is a growing literature confirming that invasive earthworms have negative impacts on these woodlands (Gundale, 2002; Bohlen et al., 2004; Groffman et al., 2004). Gundale (2002), for instance, reported a negative correlation between *Lumbricus rubellus*, a worm, and *Botrychium mormo*, an endangered fern. The suggested mechanism underlying this relationship is the loss of mycorrhiza required by *B. mormo* from the litter layer as a consequence of rapid incorporation of detritus by earthworms.

European buckthorn (*R. cathartica*) is native to Eurasia and North Africa and was introduced to North America in the late 1880s as an ornamental shrub. It has become naturalized throughout much of the northeastern US, the Great Plains and throughout Canada. In Illinois it dominates many oak woodlands in the vicinity of Chicago. Surveys of *R. cathartica* populations reveal that it dominates the understory of some *Quercus rubra* L. forests and has been implicated in decimating populations of native herbaceous plants (Gourley and Howell, 1984; Boudreau and Willson, 1992).

In recent years, we have been examining the impact of *R. cathartica* on some ecosystem properties in woodlands in Chicago. The results indicate that *R. cathartica* may modify some processes in the soils, and that the legacy of *R. cathartica* may, in some circumstances, have implications for subsequent conservation management of these areas (Heneghan et al., 2002, 2004a). *R. cathartica* leaf litter has relatively high N content and decomposes very rapidly. Patches within woodlands where *R. cathartica* prevails have soils with elevated nitrogen, higher pH, and higher water content compared with uninvaded parts of the woodland. Since all of these soil properties are important to plant community development, soil legacies of the growth of *R. cathartica* may present unforeseen obstacles for the success of restoration, subsequent to the removal of this species.

In this paper, we quantify populations of earthworms in several subcommunities within Mary Mix McDonald Woods, Glencoe, Illinois. Since initial observations showed that populations appeared to be highest in areas of the woodland where buckthorn density was greatest, we exploited this 'natural' gradient to establish a decomposition experiment to evaluate the potential effect of earthworm populations of varying density upon the breakdown of litter of varying substrate quality. The litters we employed in this experiment were *R. cathartica*, *Acer saccharum*, *Q. rubra*, and *Quercus alba*. The expectation was that *Rhamnus* and *Acer*, the higher quality substrates, would decompose more rapidly than the two *Quercus* species. We hypothesized that the differences in the density of earthworm populations along the gradient would result in greater mass loss in plots where earthworm density was high, and that mass loss from litterbags constructed in a way that permitted colonization by earthworms would be greater than from those where earthworm access was denied.

Materials and methods

Site description

Our study areas were located in Mary Mix McDonald Woods – a 40 ha site near Chicago, composed of a variety of different subcommunity types, classified according to the Chicago Wilderness community classification system (Chicago Region Biodiversity Council, 1999). The Upland Forest at McDonald Woods is dominated by white oak (*Q. alba*) with red oak (*Q. rubra*) and sugar maple (*A. saccharum*) as sub-dominants. *Q. alba* dominates the dry-mesic woodland with *Q. rubra* and *Fraxinus* species as sub-dominants. *Q. rubra* dominates the mesic woodland with *Q. alba* and *A. saccharum* being sub-dominants. All sites had a depauperate herbaceous flora consisting of a few shade tolerant and less palatable native species. The lack of vegetation in the herbaceous layer appears to be due to a combination of fire suppression, dense shading from invasive woody species, a history of domestic livestock grazing, and an over abundant white-tailed deer population. *R. cathartica* is very common in what is described below as "highly degraded areas".

Earthworm population study

Estimates of the abundance and biomass of earthworms were made in the following subcommunities within McDonald Woods: upland forest, mesic ($\times 2$), dry-mesic, and highly degraded areas. The survey was conducted between April 18 and May 22, 2002. Earthworms were extracted within 10 replicated $45\,cm \times 45\,cm$ plots within each community. An open steel sampling quadrat was placed on the soil and all litter was carefully removed. We applied an extractant composed of 38.1 g of ground oriental mustard seed suspended in 125 ml of water then diluted in 5 l of water in field immediately prior to application. Earthworms that emerged into the sampling square were collected and returned to laboratory, where abundance and biomass were recorded.

Litterbag study

Two types of litterbags were used for this experiment. One type was constructed using a plastic mesh that permitted earthworm colonization (mesh size approximately $4\,cm \times 4\,cm$) and the other type with a finer mesh ($1.6\,cm \times 1.6\,mm$) was designed to exclude earthworms. At each of three plots in the woodland (designated as low, medium, and high earthworms biomass sites), 12 litterbags of each mesh type containing litter from each one of the four plant litter types were placed on the soil surface. These monospecific bags contained 5 g of air-dried litter from the following species: *Q. rubra*, *Q. alba*, *R. cathartica*, and *A. saccharum*. Weights were recorded to the nearest 0.01 g. The bags were put in the field on March 23, 2003. The first collection was on May 23, 2003 at which time five *R. cathartica* litterbags from both litterbag treatments, and from all plots were collected. These were collected sooner than we had originally scheduled after visual inspection revealed that mass loss was proceeding very rapidly. On June 5, 2003 all remaining bags of *R. cathartica* were collected and five litterbags of other substrates from both treatments and all sites were collected. Analysis on mass remaining at that time revealed that despite very rapid loss of *R. cathartica* litter, decomposition of the *Quercus* litter was proceeding slowly. We, therefore, decided to let the *Quercus* and *Acer* litterbags remain in the field until July 23, 2004 at which time we collected all remaining litterbags. To avoid the confounding effects of having fragments being lost disproportionately from the litterbags with large mesh size, we closely inspected the soil surface under the litterbags during removal from the bare soil upon which the bags had been placed. It was never the case that fragments were found under these bags in a quantity that caused concern.

Statistical analysis

Differences between mass remaining among two treatments (treatment 1: "earthworm level": high, medium and low populations; and treatment 2: "litterbag type": large mesh versus small mesh) were analyzed using a two-way analysis of variance (ANOVA) with mass remaining as the dependent variable (% mass remaining was arcsine transformed before statistical analysis). Differences in biomass and density of earthworms were each analyzed using a single-factor analysis of variance, testing a null hypothesis that no differences existed between the woodland communities surveyed. In all cases, differences between means were analyzed using Tukey's HSD test when the ANOVA had shown the treatment effects to be significant at $P < 0.05$.

Results

Earthworm population study

Differences were found in earthworm densities and biomass between subcommunities within McDonald Woods ($F = 17.89$, $P < 0.001$; $F = 20.55$, $P < 0.001$, respectively (Fig. 1)). Highest earthworm density and biomass were found in plots dominated by *R. cathartica*. Lowest earthworm density and biomass were found in the upland forest subcommunity. Mesic and dry-mesic subcommunities had similar earthworm populations although they had higher densities and biomass than the upland forest; all of these subcommunities had lower biomass than the plot dominated by *R. cathartica*, although the densities in the dry mesic and in "mesic 2" were not statistically different from the *R. cathartica* plot.

Litterbag study

Earthworms had a dramatic impact of litter disappearance (Fig. 2a–h). Rates of mass loss were found in the following order: *R. cathartica* > *A. saccharum* > *Q. rubra* = *Q. alba*. Treatment effects on each litter type will be discussed in turn.

Within 4 weeks of the start of this experiment less than 20% of *R. cathartica* litter remained in litterbags to which earthworms had access compared with 70% remaining in earthworm exclusion bags (differences between litterbag types was significant, $F = 212.82$, $P < 0.001$). There were differences between the plots also ($F = 4.92$, $P < 0.02$), and litterbags placed in plots with highest earthworm densities had the greatest mass loss (Fig. 2a). At the second collection date the same effects were also noted; the mass
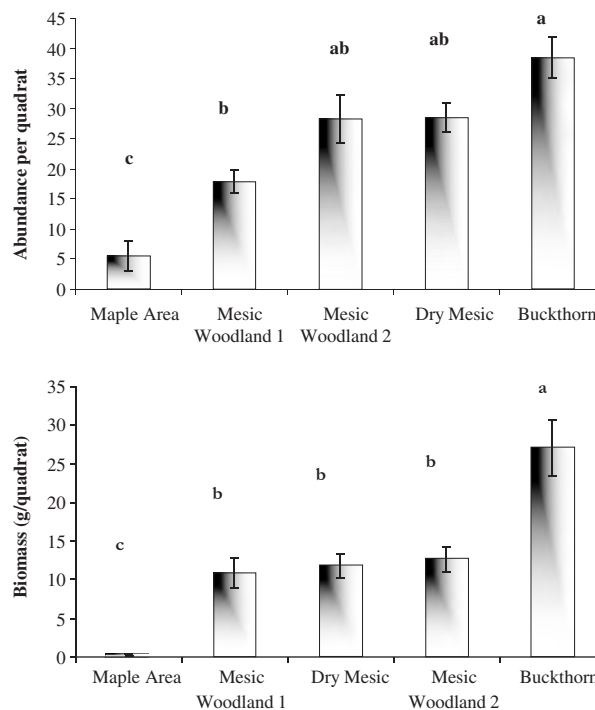
Figure 1. Earthworm populations from subcommunities within McDonalds Woods: (a) earthworm densities (means and standard error) and (b) earthworm biomass (means and standard error). Population characteristics that differ between subcommunities are indicated by different letters (tested using Tukey's HSD).

remaining being, of course, less than it had on the previous occasion (Fig. 2b).

Mass loss of *A. saccharum* at the time of first collection was influenced by the presence of worms with statistically significant differences between litterbag types ($F = 22.78$, $P < 0.001$), but not by plot type. There was, however, an interaction effect between litterbag type and plot ($F = 20.51$, $P < 0.001$) derived from the very conspicuous litterbag type effect in plots where earthworm densities were high (Fig. 2c). On the second collection date, approximately 1 year after the previous collection, there was no overall effect of litterbag type but a strong plot effect ($F = 33.06$, $P < 0.001$). There was an interaction effect ($F = 3.74$, $P < 0.04$), indicating that despite the similarity of remaining mass in the two litterbag types in the plots with low earthworm densities, there was a litterbag type effect in the other plots (Fig. 2d).

Mass loss of *Q. rubra* litter was unaffected by either the litterbag type or by plot on the first collection date (3 months after the start of the experiment) (Fig. 2g). One year later, there was a litterbag effect ($F = 24.56$, $P < 0.001$) and a plot effect ($F = 13.08$, $P < 0.001$). There was also a

significant interaction effect ($F = 8.06$, $P < 0.01$) between litterbag type and plot – the effect of earthworm exclusion (litterbag type effect) being very pronounced in the plots where earthworm densities were high or medium, but no litterbag effects where earthworm populations were low (Fig. 2h).

The patterns observed for *Q. alba* were similar to those reported above for *Q. rubra*. No significant effects of litterbag type or plot were noted for the first date (Fig. 2e). One year later, there were significant effects of litterbag type ($F = 77.58$, $P < 0.001$) and plot ($F = 7.05$, $P < 0.01$) (Fig. 2f). There were no interaction effects.

Discussion

We found that there were differences in the earthworm density and biomass in the different subcommunities investigated. Thus, litterbags in-stalled in the *R. cathartica* dominated, mesic, and upland forest plots were, as we had anticipated, subjected to a gradient of earthworm impact – from relatively modest (means of 26.9 ind m^{-2} and biomass of 1.32 g m^{-2}) in the upland forest to high (means of 188.16 ind m^{-2} and biomass of 132.74 g m^{-2}) in plots dominated by *R. cathartica*. Plots in the mesic subcommunity had moderate density and biomass (means of 87.71 ind m^{-2} and biomass of 57.36 g m^{-2}). Earthworm populations are variable in space and time (Curry, 2004), therefore the numbers reported for each subcommunity are not assumed to be static in the plots throughout the period of the study. However, reinvestigations of the earthworm populations were made during the course of the study, and the relative abundance and biomass remained the same across the plots (Heneghan and Fagen, unpubl. data).

The highest abundance and biomass of earthworms was found where *R. cathartica* was prevalent, thus suggesting that there was a
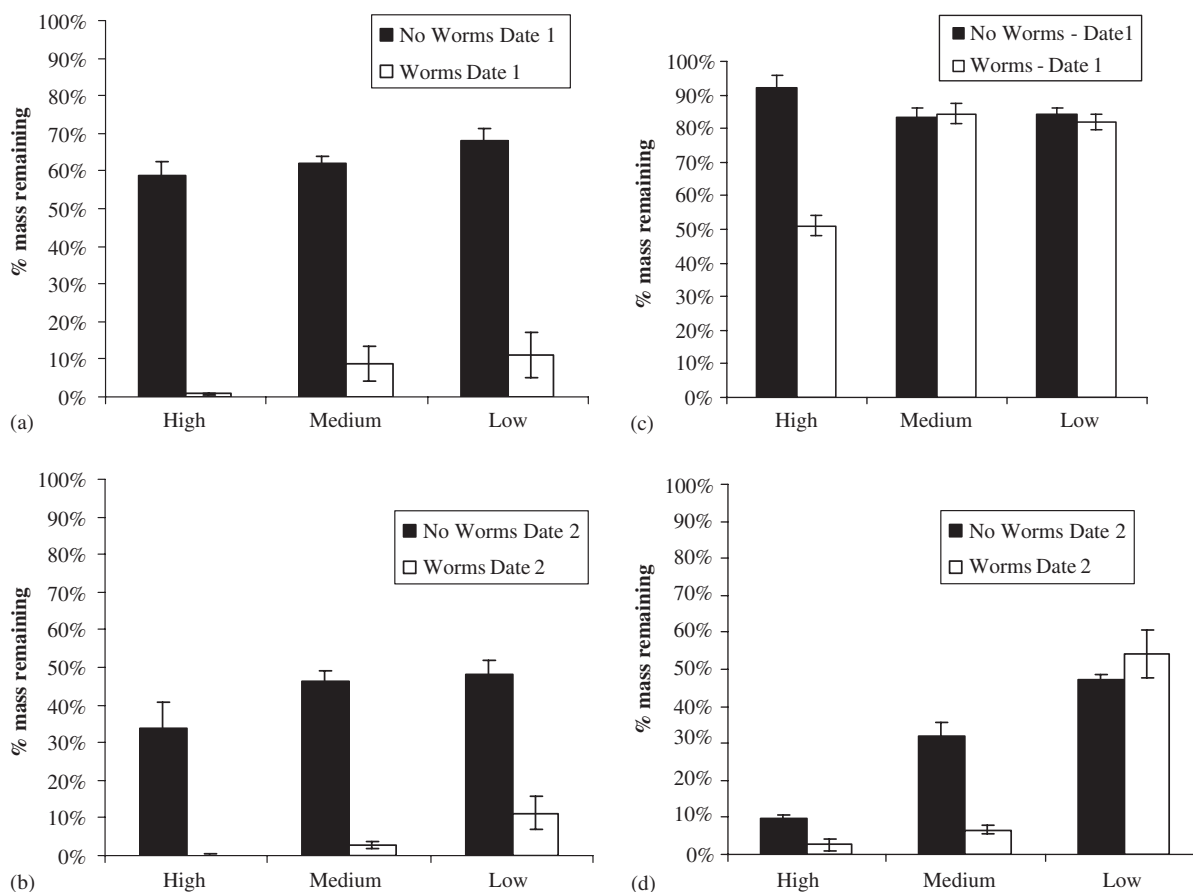
Figure 2. Percent mass remaining (means and standard error) in litterbags which either allowed earthworm colonization, or excluded earthworms: (a) *R. cathartica* on first collection date, (b) *R. cathartica* on second collection date, (c) *A. saccharum* on first collection date, (d) *A. saccharum* on second collection date, (e) *Q. alba* on first collection date, (f) *Q. alba* on second collection date, (g) *Q. rubra* on first collection date, and (h) *Q. rubra* on second collection date.
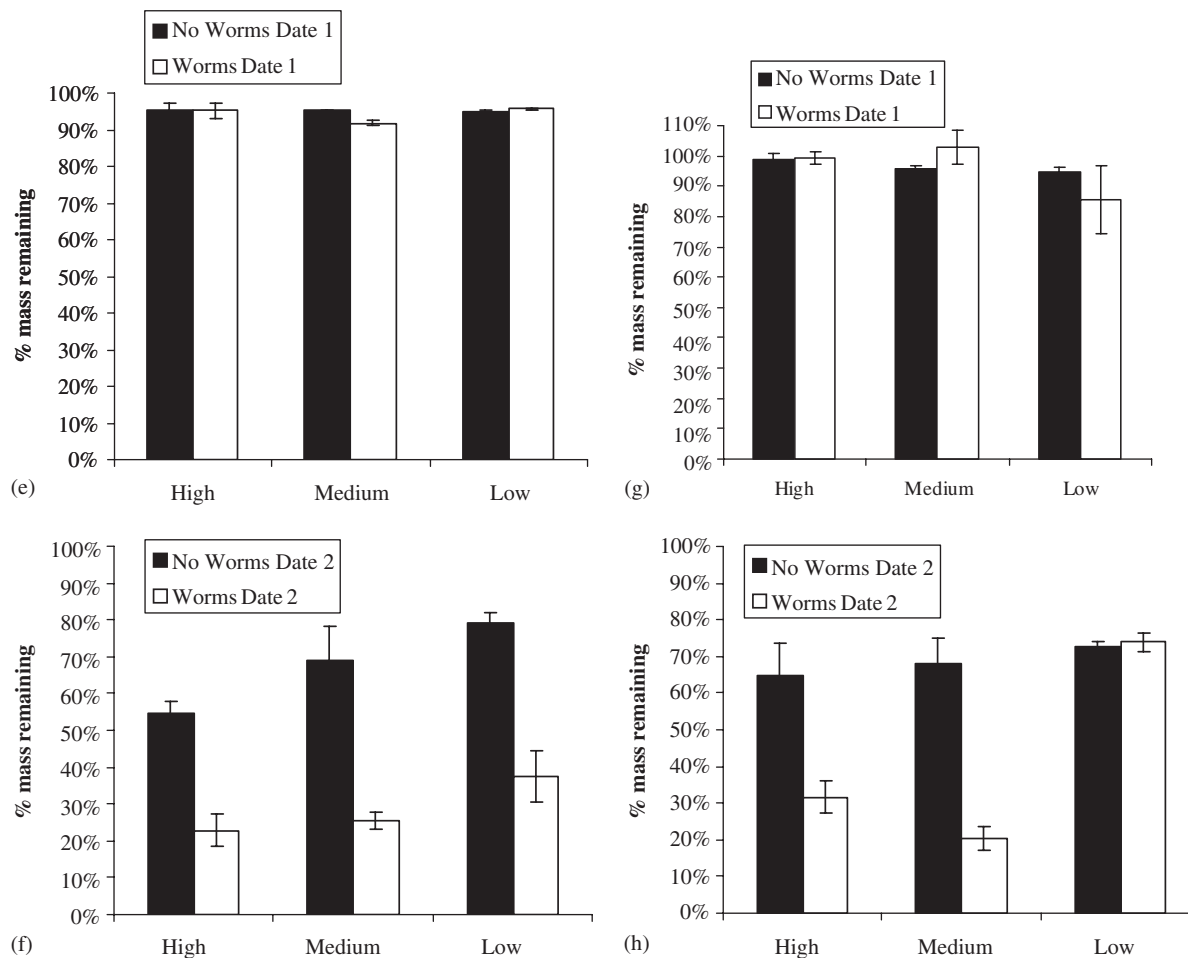
Figure 2. (*Continued*)

relationship between the success of one invader and the success of the other invader – a modest invasional meltdown. Determining the mechanism generating the facilitation of one of the invaders by the other is difficult as it is not clear if earthworms are enhancing the spread of *R. cathartica*, or if the growth of *R. cathartica* promotes larger earthworms populations, or, alternatively, if the species are involved in a mutually reinforcing positive feedback loop. There are good reasons for hypothesizing the last of these three proposals. Well-established *R. cathartica* populations are associated with soils that have elevated total nitrogen, modified nitrogen cycling, and elevated soil moisture and pH. That invasive shrubs can drive such changes in soil properties has been shown by other studies (Stock et al., 1995; Ehrenfeld, 1997, 2003; Ehrenfeld et al., 2001; Kourtev et al., 2002; Ashton et al., 2005). In studies on *Berberis thunbergii*, which like *R. cathartica* is not N-fixing, similar changes in soil were reported and invaded plots were also associated with enhanced earthworm populations (Kourtev et al., 1998). Thus *B. thun-*

bergii promotes soil conditions that favor earthworm populations. On the other hand, earthworms are major contributors to important ecosystem processes – they are direct comminutors of leaf material, and are therefore a major direct contributor to litter breakdown (Edwards, 2004). The presence of earthworms accelerates the mineralization of nitrogen (Robinson et al., 1992; Saetre, 1998), and invasive earthworms are implicated in modifying key aspects of soil functioning (James, 1991; Lavelle et al., 1997; Lachnicht et al., 2002; Bohlen et al., 2004). Since invasive plant species colonization is often associated with resource availability in excess of utilization by the native plant community (Davis et al., 2000), it may be hypothesized that changes in resource availability as a consequence of earthworm invasion might result in opportunities for the invasion by aggressive plants, such as *R. cathartica*. Thus, both earthworms and *R. cathartica* can conceivably form a positive feedback loop resulting in their promoting a coordinated spread throughout a landscape. This also may facilitate the population recovery of

the invasive shrub after management intervention (removal of *R. cathartica* by cutting, chemical treatment of stumps or prescribed fire are common management practices (Boudreau and Willson, 1992)). After management for removal of *R. cathartica*, populations of earthworms remain high (Heneghan and Umek, personal observations) arguably allowing for reinvasion by the shrub, which appears to grow vigorously in plots even after management.

Two principal findings emerged from the litterbag experiment. Firstly, there is a strong effect of litterbag type, i.e. litterbags into which earthworms have access generally have lower litter mass remaining. This was the case for *R. cathartica* and *A. saccharum* on the first collection dates, and for the *Quercus* species after a year in the field. The effect of litterbag type persisted for *R. cathartica* after its second collection, but not for *A. saccharum* (although there was still a strong interaction between litterbag type and the plot type (low, medium and high earthworms)). Thus overall, the presence of earthworms resulted in acceleration of litter loss from the soil surface for two of the examined litter types, whereas the impact of earthworms on both *Quercus* spp. was slower. This is consistent with the notion that *Quercus* litter is of a lower quality and therefore decomposes relatively slowly (Blair and Crossley, 1988; Heneghan et al., 1999, 2004b). Generally fresh litter has lower palatability for earthworms than aged litter (Curry, 2004). The aging of litter is assumed to leach out unpalatable chemical constituents of the litter and to allow time for the colonization of litter by microbial populations which, in turn, increase the nutrient quality of the litter. Since substrate quality determines microbial succession (Witkamp, 1963), litter of lower quality may have slower microbial succession and be less preferable to earthworms than litter of higher quality. Assuming that this was the case for the litters chosen in this study, these factors would explain the emergence of the worm litterbag effect only after the *Quercus* spp. litter had been in the field for a year.

The second significant finding from the litterbag study was that, in conformity with our expectations, the plots that diverged in the dimensions of their earthworm populations had significantly different mass remaining in litterbags as the experiment progressed. These plot effects were significant for *R. cathartica* litter at the first collection date; this effect persisted at the time of second collection, and was present for all other litters when they were collected after a year in the field. It is clear that there is typically a 'dose dependence' in the effect, especially at the extremes of earthworm density and

biomass (confirmed by Tukey HSD tests showing consistent difference between the high and the low earthworm density plots). It is noteworthy that even in the plots with low earthworm activity there is a substantial and rapid mass loss of *R. cathartica* litter from litterbags that permitted earthworm access. Perhaps this substrate is so palatable that even when numbers are very low earthworms will preferentially feed on it.

Trends in mass loss from litterbags from which earthworms were excluded often followed the same response to the plots treatments (low, medium, and high earthworm populations) as from litterbags with earthworm access, although mass loss from litterbags with earthworm access was usually greatest (i.e. the same trend is present, but the magnitude of the response is smaller in the absence of earthworms). There may be a number of reasons for this. Litterbags with small mesh size can be colonized by smaller fauna, including juvenile earthworms. As the latter grow they may comminute the litter resulting in a response to plot treatments. Alternatively, or perhaps complementary to this, plots with *R. cathartica* have different microbial activity to adjacent area without this invasive plant, and these differences in microbial populations may be manifested in modified decomposition rates (Heneghan et al., 2004a). The activity of microbial decomposers is often limited by nitrogen, thus the microbial populations may track the nitrogen availability across the gradient of plots and produce the observed trends.

The results of this experiment explain a conspicuous phenomenon found in many urban woodlands, namely a loss of the litter layer during the growing season (Heneghan et al., 2002; Steffen and Heneghan, personal observation). Typically, in the woodlands around Chicago in the very extensive thickets of *R. cathartica* the soil is exposed within the first few weeks of spring. The high impact of earthworms on the decomposition of litter, particularly that of *R. cathartica*, explains why this is the case. This substantial impact on *R. cathartica* litter is suggestive that the autocatalytic impact of the two species will be greatest in the very prevalent and extensive thickets of *R. cathartica*, where the breakdown of this nutrient-rich litter provides ample resources for large earthworm populations. The fact that the impact is not as substantial where *Quercus* litter is preponderant encourages a hope that the successful management of these woodlands (which is aimed at reducing invasion by *R. cathartica* and sustaining the oak population) will reduce the earthworm populations by minimizing the amount of palatable litter available to them.

Acknowledgments

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