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Local- Vs. Landscape-Scale Indirect Effects of an Invasive Weed on Native Plants

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Local- Vs. Landscape-Scale Indirect Effects of an Invasive Weed on Native Plants[1]

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Abstract: Insect-mediated indirect interactions between native plant species recently have been shown to be important determinants of plant performance in a number of ecological communities. However, the potential indirect effects of exotic plant invasion on native plant species are not well understood. We examined whether the presence or proximity of the targeted exotic weed, musk thistle, influences the magnitude of attack on native thistles by the introduced biological control, flowerhead weevil. At the local scale, we quantified weevil egg densities on heads of the native wavyleaf thistle growing at different distances (0 to 100 m) from patches of the exotic thistle. Densities were significantly higher when the native thistle occurred within, vs. 30 to 50 m or 80 to 100 m from, patches of the exotic thistle, indicating a strong local "spillover effect." At larger scales, we measured egg densities on wavyleaf thistle within grassland landscapes (2.4×2.4 km^2) with varying infestation densities of the invasive musk thistle. We found that egg densities increased significantly with increasing invasive thistle densities measured at larger site and landscape scales. Because flowerhead weevil feeding substantially reduces seed production of wavyleaf thistle, exotic thistle populations are likely to have indirect negative effects on these native thistles. Our results provide strong empirical evidence that exotic plants can increase the attack on native plant species by maintaining populations of a shared insect herbivore. This finding suggests that persistence of exotic weeds in less-successful biocontrol programs will magnify the nontarget effects of weed biocontrol insects.

Nomenclature: Musk thistle, *Carduus nutans* spp. *leiophyllus* (Petrovic) Stoj. & Stef. #[3] CRUNU; wavyleaf thistle, *Cirsium undulatum* (Nutt.) Spreng. # CIRUN; flowerhead weevil, *Rhinocyllus conicus* Frölich.

Additional index words: Associational susceptibility, biological control, indirect effects, nontarget effects, spillover effects, thistles.

INTRODUCTION

Indirect interactions between species are increasingly recognized to be important in determining the dynamics of natural populations and communities (Strauss 1991; Wooton 1994). It is highly probable that they are likewise important in invasion dynamics, but we are still in the relatively early stages of enumerating and quantifying these effects. In plant–herbivore systems, neighboring vegetation in some cases can indirectly affect a host plant species by increasing its susceptibility to attack by insect herbivores, a process generally referred to as "associational susceptibility" or "associational damage" (Karban 1997; Thomas 1986). If herbivore damage affects plant performance, associational damage can result in a negative indirect interaction between the two host plant species that is mediated by their shared herbivore (i.e., result in "apparent competition," Holt 1977).

Theory suggests that such shared predation could be important in generating negative indirect effects between invasive weeds targeted for biological control and nontarget native plants, when the herbivore agent can feed on both (Holt and Hochberg 2001). If so, one would predict that the presence of an abundant invasive species within a habitat would lead to an increase in the degree of nontarget attack on the associated susceptible native species. In this article, we contrast two studies across two different spatial scales that examined the influence

of the invasive musk thistle on the magnitude of non-target attack on a native thistle, wavyleaf thistle, by the exotic flowerhead biocontrol weevil in the mixed grass prairie of central Nebraska.

Natural History Background. The focal invasive weed in our study was musk thistle, a Eurasian species that was first recorded in North America in the mid-1800s (Dunn 1976). It subsequently spread west and was considered a major economic weed, especially in rangelands of the central United States, prompting the search for a suitable biological control agent.

The flowerhead weevil was identified as a promising biocontrol agent and was introduced into the United States from Canada in 1968 and into Nebraska in 1969 to 1972 (Gassmann and Louda 2001; McCarty and Lamp 1982; Zwölfer and Harris 1984). However, nontarget feeding on native North American thistles by flowerhead weevil has been reported (Louda 2000; Louda and Arnett 2000; Louda et al. 1997; Turner et al. 1987). In the spring, overwintered adults of the flowerhead weevil mate and lay eggs on the bracts of developing thistle flower heads. After the larvae hatch, they burrow into the receptacle, feed for 25 to 40 d, and then pupate in hardened cells within the flower head (Zwölfer and Harris 1984). In the process, they significantly reduce thistle seed production (Louda 2000; Louda and Arnett 2000).

The host range of flowerhead weevil is not restricted to *Carduus* spp. thistles. The weevil also develops in *Cirsium* spp. flower heads, including over 30% of the native *Cirsium* spp. in North America (Pemberton 2000). In addition, severe population declines of one native species, Platte thistle (*Cirsium canescens*), have followed the invasion by flowerhead weevil into two intensively studied preserves in the Nebraska Sand Hills (Louda 2000; Louda et al. 2003). In this study, we quantified the interactions of the native wavyleaf thistle in mixed grass prairie; it is likely that flowerhead weevil affects wavyleaf thistle populations in Nebraska (Louda 2000; S. M. Louda, personal observation). Seed production of wavyleaf thistle is reduced by more than 80% in flower heads with flowerhead weevil feeding compared with those without (Louda 2000; F. L. Russell and S. M. Louda, unpublished data). Furthermore, weevil egg load is significantly negatively correlated with seed production in flower heads of a given size for this species ($r = -0.24$, $P < 0.0001$). Thus, egg density is a good proxy for insect floral damage to wavyleaf thistle. Finally, wavyleaf thistle has significant distributional and habitat overlap with the invasive musk thistle, suggesting her-bivore-mediated indirect interactions between these two thistle species might be important.

In this study, we contrast data from two field studies in which we addressed the following two questions. First, does the susceptibility of wavyleaf thistle to attack by the introduced flowerhead weevil vary locally as a function of distance from patches of the invasive musk thistle? Second, we scaled up and asked: Does the level (density) of the musk thistle invasion, either across large study sites or in the even larger surrounding landscape, influence the magnitude of weevil attack on the native wavyleaf thistle?

MATERIALS AND METHODS

To quantify the variation in flowerhead weevil attack on native thistles locally, in relation to distance from patches of the invasive thistle, nine sites with musk thistle patches and naturally occurring wavyleaf thistle plants were selected in 2002 in midgrass prairie across south central and southwestern Nebraska in the vicinity around the town of North Platte (100°45′W, 45°10′N: nine sites in Custer, Dawson, Gosper, Keith, and Lincoln counties). Musk thistle patches were defined as aggregations of flowering musk thistles (>200 m²) that greatly exceeded background musk thistle density; patch densities ranged from 0.12 to 1.74 plants per m² ($\bar{x} = 0.63$, SE $= 0.18$), and patch areas ranged from 283 to 4,716 m² ($\bar{x} = 1,395$, SE $= 426$). At each site, flowerhead weevil egg densities, measured as the mean number of weevil eggs per flowerhead for a given plant, were quantified on 10 wavyleaf thistle plants that occurred: (1) in a musk thistle patch, (2) 30 to 50 m from the musk patch, and (3) 80 to 100 m from the musk thistle patch. Split-plot ANOVA was used to analyze the effects of distance from the musk patch on level of attack on the native wavyleaf thistle by the flowerhead weevil.

To quantify variation in weevil use of native thistles in response to invasive exotic thistle densities at the site-to-landscape scale, we quantified weevil egg load on the native wavyleaf thistle in 14 landscapes with varying levels of infestation of the invasive musk thistle in south central Nebraska in 2002. Each study area consisted of a central 800 × 800 m grassland site, surrounded by the eight adjacent land parcels of equivalent size that we refer to as the surrounding landscape. Densities of bolting (flowering) individuals of the invasive musk thistle and the native wavyleaf thistle were quantified within each site in five 30-m-wide by 800-m-long transects for the invasive thistle and five 4-m-wide by 800-m-long transects for the native thistle. Transects were spaced at
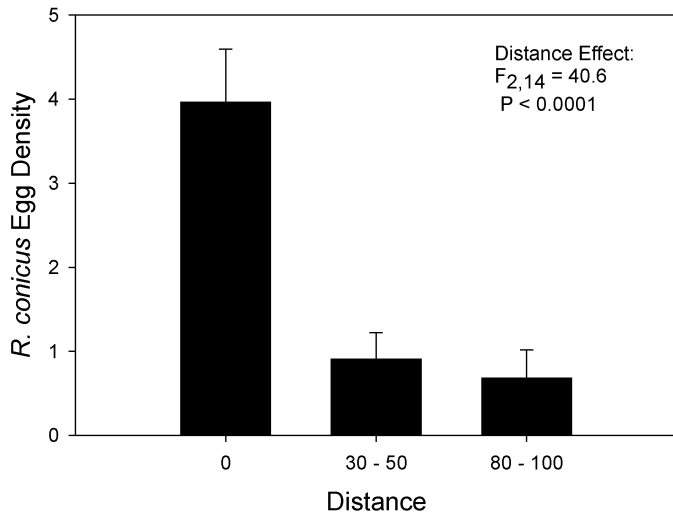
Figure 1. Flowerhead weevil egg load on the native wavyleaf thistle in relation to distance from patches of the invasive exotic musk thistle (F. L. Russell, S. M. Louda, and T. A. Rand, unpublished data).

200-m intervals; invasive densities in the surrounding landscape matrix were also estimated using quantitative point counts in 100-m-radius arcs at 16 locations, 200 m apart, along the perimeter of the central site.

Weevil attack was measured as oviposition on the native species. Flowerhead weevil egg densities, which are correlated with adult weevil densities on a plant (S. M. Louda and F. L. Russell, unpublished data), were quantified on 20 native wavyleaf thistle plants in each of the 14 landscapes. Plants were sampled along transects into each target site in the order encountered with the caveat that they were >10 m from the last plant measured; when several plants were encountered at >10 m, only one randomly selected individual in the group was measured. We calculated the site level mean flowerhead weevil egg load per head per plant, and used regression analyses to examine the relationship between egg load on the native species and exotic thistle density (for statistical details, see Rand and Louda 2004).

RESULTS AND DISCUSSION

Local Pattern in Egg Load. Locally, flowerhead weevil egg density on the native thistle (mean number of eggs per flower head) declined significantly with increasing distance from patches of the invasive musk thistle (distance: $F_{2,14} = 40.66$, P < 0.0001; Figure 1). Egg density on wavyleaf thistle plants in musk thistle patches was 4.3 and 5.8 times greater than egg densities on native thistles 30 to 50 m and 80 to 100 m from musk patches, respectively. The effect of musk thistle patches on levels of flowerhead weevil attack of native thistles diminished

rapidly with increasing distance from the patch. Egg loads on native thistles in musk patches were significantly higher than egg loads on native thistles 30 to 50 m and 80 to 100 m from musk patches in post hoc comparisons, and there was no significant difference in egg load between native thistles 30 to 50 m and 80 to 100 m from musk patches (Figure 1). Thus, we found a strong ''spillover effect'' of flowerhead weevils onto native thistles when they occurred in close proximity to patches of the invasive, and the effect was relatively localized.

Landscape Pattern in Egg Load. At the larger landscape scale, univariate regression models revealed that flowerhead weevil egg densities increased significantly with increasing densities of the invasive thistle (Figure 2), both within the central site as well as within the surrounding landscape ($R^2 = 0.53$, P = 0.003 and $R^2 = 0.34$, P = 0.03, respectively; Rand and Louda 2004). In fact, within-site invasive thistle density explained over 50% of the site–site variation in levels of flowerhead weevil attack. In contrast to the strong effects of invasive thistle density, there was no significant relationship between the density of the native wavyleaf thistle within a site and weevil egg density on it ($R^2 = 0.02$, P = 0.64, Rand and Louda 2004). Thus, the levels of nontarget attack of the native wavyleaf thistle were more closely linked to densities of the invasive weedy thistle than its own densities.

''Spillover'' Despite Lower Preference Ranking. Overall, we found that the nontarget use of native thistles increased significantly both with local proximity to patches of the invasive species, musk thistle, and with site–landscape densities of this invasive weed. Thus, invasive thistles appear to serve as a ''reservoir'' of the biocontrol weevil. The buildup of weevils on large populations of the invasive plant species likely results in an indirect negative effect of the invasive plant on the native plant species because it led to an increased magnitude of herbivore attack on the native. It is noteworthy that this spillover effect occurs in this system, given the fact that flowerhead weevil has a documented preference for, and a superior performance on, the invasive musk thistle (Arnett and Louda 2002; Gassmann and Louda 2001; Zwölfer and Harris 1984). Thus, our results support the suggestion from the modeling studies that host preference is likely to be a poor predictor of the level of nontarget effects (Holt and Hochberg 2001).

In addition, although the results of the first study suggested that spillover appeared to be relatively localized
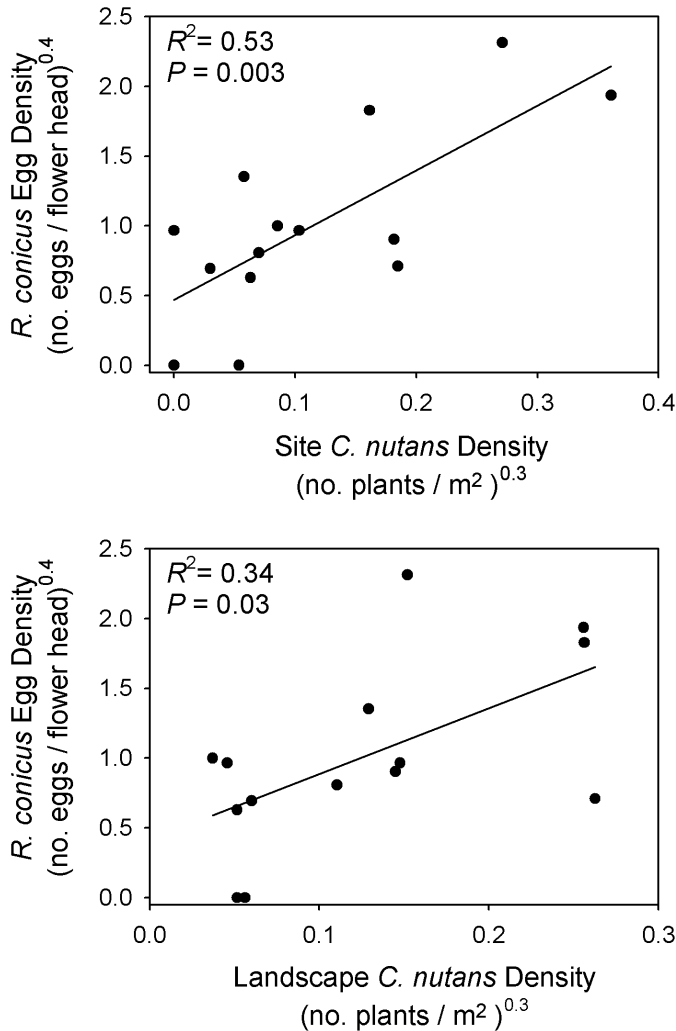
Figure 2. Flowerhead weevil egg load on the native wavyleaf thistle in relation to site-level exotic musk thistle density ($R^2 = 0.53$, $F = 13.56$, $P = 0.003$) and landscape level exotic musk thistle density ($R^2 = 0.34$, $F = 6.28$, $P = 0.028$). Transformed data are plotted for both thistle density ($x^{0.3}$) and flowerhead weevil egg load ($y^{0.4}$). Adapted from Rand and Louda (2004).

(i.e., occur at distances <30 m), the fact that we also found higher use of natives as invasive densities increased at the larger landscape scale indicates that spillover damage to vulnerable native species may also be substantial wherever invasive plants remain relatively abundant within a system. These data, showing that populations of flowerhead weevil are maintained by persistent musk thistle infestations and supplementing the data that show flowerhead weevil feeding reduces seed production per flower head and per plant (Louda 2000; S. M. Louda, unpublished data), lead to the inference that the weevil will likely affect populations of this native thistle.

Spatial Scale. Theory suggests that the proximity of prey species that share a predator and the dispersal dy-

namics of the shared predator are critical in determining the strength of indirect effects among the prey resource species (Holt 1984, 1987). Our results, which simultaneously show a sharp decline in weevil egg load on native thistles within meters of musk thistle patches, yet a significant increase in egg load with increasing site-to-landscape level musk thistle abundance as well, suggest that associational susceptibility of wavyleaf thistle to musk thistle mediated by flowerhead weevil operates at multiple, overlaid spatial scales in landscapes where musk thistle, native thistles, and flowerhead weevils are all present. For example, high egg densities on native thistles in or near musk thistle patches may be the cumulative result of strong, local indirect effects of musk thistle on wavyleaf thistle, overlaid on a background level of flowerhead weevil use that reflects the larger scale abundance of musk thistle.

Interestingly, whereas proximity to musk thistle at the local scale of meters or landscape scale of kilometers resulted in greater herbivory in this study, spillover did not explain the use of flowerhead weevil of another thistle, Platte thistle, at an even larger biogeographic scale of tens of kilometers (T. A. Rand and S. M. Louda, unpublished data). In sum, incorporating the concept that predator-mediated indirect effects of exotic species on native species may result from overlaid spatial processes and the recognition that the importance of specific factors might shift across scales is likely to be productive in predicting spatial variation in the magnitude of indirect effects of invasive species on native species, similar to the use of incorporating overlaid dispersal processes in modeling geographic patterns of invasion (Suarez et al. 2001).

Finally, it has been estimated that only about 20% of insect introductions for biological control actually show evidence of significant limitation of targeted weed populations (Williamson and Fitter 1996). Thus, in many cases, invasive plants and their associated exotic insects remain in the environment. In the absence of strict host specificity of biocontrol insects, i.e., the complete absence of feeding on any native species, this combination creates the potential for negative synergistic effects of invasive plants and introduced herbivores on native plant species and communities. Thus, the bottom line from a conservation perspective is that indirect effects, such as those documented in this study, need to be carefully considered before the release of biocontrol insects within natural areas, especially if there is any evidence that native species within targeted areas can serve as even less preferred secondary hosts.

ACKNOWLEDGMENTS

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