Plant Ecol (2011) 212:1655–1662
DOI 10.1007/s11258-011-9938-7

Indirect positive effects ameliorate strong negative effects of *Euphorbia esula* on a native plant

Daniel Z. Atwater · Carolyn M. Bauer ·
Ragan M. Callaway

Received: 13 March 2011 / Accepted: 7 June 2011 / Published online: 21 June 2011

Abstract Invasive plant species can have strong direct negative effects on native plants. Depending on the nature of interactions among competitors and consumers within a community, strong indirect interactions may either augment or offset direct effects. We used path analysis to estimate the relative importance of direct and indirect effects of *Euphorbia esula*, an unpalatable invasive plant, on *Balsamorhiza sagittata*, a native forb, through "shared defense" and by suppression of native competitors. Our results indicate that *E. esula* had strong direct negative effects on *B. sagittata*, but also that its net effect was reduced by 75% because of indirect positive effects. This reduction was because in equal parts of lessened competition from other native plants eliminated from *E. esula* stands and to lower levels of herbivory inside *E. esula* stands, apparently caused by indirect defense of *B. sagittata* by *E. esula*. To our knowledge, this is the first evidence that invaders may indirectly reduce herbivory on native plants, a phenomenon that may commonly occur with unpalatable invaders. Furthermore, our results highlight the potential complexity of interactions between native and invasive plants.

Keywords Associational resistance · Indirect interactions · Leafy spurge · Plant invasion · Path analysis · Shared defense

Introduction

Invaders often dominate communities in their introduced ranges, causing losses in native species abundance and diversity (Braithwaite et al. 1989; Memmott et al. 2000; Grigulis et al. 2001) and reducing growth and reproduction of surviving native species. Direct negative interactions between native and invasive plants are recognized as important drivers of these community changes (Levine et al. 2002; Hierro and Callaway 2003; Maron and Marler 2008). However, indirect interactions between native and invasive plants may also play an important and potentially complex role in the ecology of an invaded community, particularly because indirect interactions with invasive plants may have strong inhibitory and facilitative effects.

D. Z. Atwater (✉) · R. M. Callaway
Division of Biological Sciences, The University
of Montana, 104 Health Sciences, Missoula,
MT 59812, USA
e-mail: danatwater@gmail.com

C. M. Bauer
Department of Biology, University of Washington,
Seattle, WA 98195, USA

Present Address:
C. M. Bauer
Department of Biology, Tufts University, Medford,
MA 02155, USA

Indirect interactions can have substantial effects on the organization of uninvaded plant communities (Miller 1987; Levine 1999; Callaway 2007), but have only recently attracted the attention of researchers studying plant invasions. Indirect interactions between native and invasive plants can be mediated by native plants (Saccone et al. 2010), soil microbes (Callaway et al. 2003; Klironomos 2002; Inderjit et al. 2007) or by pollinators (Munoz and Cavieres 2008), but perhaps most importantly by herbivores (Parker et al. 2006; White et al. 2006; Meiners 2007; Orrock et al. 2008; Pearson and Callaway 2008). Because herbivores can have such powerful indirect effects on community composition in uninvaded systems, understanding their indirect effects in invaded systems is also likely to be important. To our knowledge, previous studies on the indirect effects of native herbivores in plant invasions have focused on their role as causes of invader success, but two other potential *positive* indirect interactions between native and invasive plants are "shared defense" and "associational resistance." Defenses are considered to be "shared" when a palatable beneficiary is protected by a nearby unpalatable species. The positive effect of growing with many other species that limit herbivory by other mechanisms, such as visual or olfactory masking, is called "associational resistance" (Tahvanainen and Root 1972; Atsatt and O'Dowd 1976; Feeny 1976; Callaway 2007).

Shared defense and associational resistance may be important processes in some plant invasions. Although some exotic plant species evolve lower levels of defense when released from herbivore pressure (Siemann and Rogers 2003), other invasive plant species decrease investment in defense against specialist herbivores but increase investment in defense against generalists (Müller-Schärer et al. 2004; Joshi and Vrieling 2005), or increase overall investment in defense (Ridenour et al. 2008). Also, some plants may possess defensive compounds that are novel to generalist herbivores in the introduced range and thus experience lower rates of herbivory (Callaway and Ridenour 2004; Branson and Sword 2008; Jogesh et al. 2008; Tallamy et al. 2010; but see Lind and Parker 2010). Regardless of the underlying mechanisms, herbivores avoid some invasive species, resulting in dramatically lower rates of herbivory on exotic plants than native plants in some systems (Cappuccino and Carpenter 2005; Cappuccino and Arnason 2006). If invasive plant species are avoided by native herbivores in the invaded range, palatable native plant species may benefit indirectly by growing closely to these invaders. This might also happen any time an invasive species forms a dense thicket that obscures plants from visual herbivores. In such a case, invaders might release native plants from predation by visual but not olfactory herbivores (as in Hambäck et al. 2003).

Euphorbia esula (leafy spurge) is one of North America's most problematic invasive plants because of its competitive ability and vigorous vegetative habit, but also to its toxicity and unpalatability to grazers (Dittberner and Olson 1983; Cyr and Bewley 1989; Trammell and Butler 1995). *Euphorbia esula* reduces native diversity in many community types (Belcher and Wilson 1989); nonetheless, some native species persist during the early stages of *E. esula* invasion. We observed that the North American native *Balsamorhiza sagittata* (arrowleaf balsamroot) maintains substantial populations in low-to-moderate density *E. esula* stands. *Balsamorhiza sagittata* is a large dominant native forb whose shoots, flowers and seeds are commonly eaten by native generalist herbivores, such as pronghorn, bighorn sheep, mule deer and deer mice (Wikeem and Pitt 1979, 1991; Burell 1982; USDA 1988). Seeds of *B. sagittata* are also consumed by specialist insects (Amsberry and Maron 2006) that live in the seed head (capitulum) and feed as larvae.

We hypothesized that *B. sagittata* growing within *E. esula* patches experiences strong direct negative effects from *E. esula*, but that *E. esula* also has indirect effects in the form of shared defense because of its unpalatability, as well as through reduction in the density of native competitors. We used a path analysis to estimate the relative strength of these effects using observational data.

Materials and methods

We chose five sites in montane grasslands around the Missoula Valley in Western Montana, and at each of the five sites, we established a 10 m × 10 m plot in both an *E. esula* invaded area and in a nearby uninvaded area. The uninvaded plot was always within 20 m of the *E. esula* plot and did not differ noticeably in elevation, slope or aspect. We chose sites where the general plant community resembled the remnants in the *E. esula* patch. All of these sites were historically used for cattle grazing, but had been set aside for conservation and were only experiencing natural grazing by the time *E. esula* invasion occurred. Intense *E. esula* invasion occurred relatively recently in the Missoula Valley, and we estimate that dense patches became common only within the past 15 years. *Euphorbia esula* is clonal and expands vegetatively from the center of the colony. We located plots within several meters of the edge of active expansion fronts; thus, our plots were probably situated where *E. esula* had been present for only a few years. We also chose plots that contained relatively uniform, but moderate densities of *E. esula*.

Our sites were located at the Cox Property (46°50′12″N;113°57′59″W, elev. 1,265 m, slope 13°, aspect S), the Rocky Mountain Elk Foundation reserve (46°56′17″N;114°01′01″W, 1,130 m, 21°, W), Waterworks Hill (46°52′53″N;113°59′08″W, 1,090 m, 18°, ENE), the North Hills (46°53′34″N;113°58′45″W, 1,085 m, 16°, E) and Mt. Jumbo (46°51′55″;113°58′03″, 1,030 m, 39°, SSW). All sites had grassland plant communities dominated by *B. sagittata*, *Pseudoroegneria spicata* (bluebunch wheatgrass), *Bromus tectorum* (cheatgrass) and *Bromus japonicus* (Japanese brome).

From 27 June 2008 to 7 July 2008, we measured 1,041 individual *B. sagittata* plants at the five sites. We counted each *B. sagittata* individual within our plots and measured canopy height, the longest diameter of the leafy canopy (plant width), number of leaves, number of flower heads, and number of damaged leaves and gave each plant a subjective leaf damage rating based on a scale from 0 to 10. We also measured the distance to the nearest *B. sagittata* neighbor, distance to nearest *Lupinus sericeus* (if within 2 m) and distance to nearest *Pseudoroegneria spicata* (if within 2 m). *Lupinus sericeus* and *P. spicata* are prominent native plants that, together with *B. sagittata*, covered a majority of the landscape at the study sites (D. Atwater, personal observation). We also recorded the presence of any other plant species within a 50-cm radius of the target plant. Local *E. esula* density was measured as the number of living stems within a 1 m × 1 m square centered on each *B. sagittata* plant.

We collected one capitulum, or seed head, from each flowering *B. sagittata* plant (total $n = 357$) and dissected it to look for signs of herbivory. Capitula were scored positively for herbivory if they contained an intact seed herbivore, boring holes or frass (insect excreta) produced by insect seed predators. We performed a chi-square test of homogeneity to determine whether herbivory was contingent on the presence of *E. esula*.

To generate integrative variables for *B. sagittata* performance, we performed a principal components analysis (PCA) on plant height, plant width and number of leaves to create a single score for plant size (S_{PCA}). These variables were log transformed to improve normality and because herbivory is hypothesized to affect plant performance on a logarithmic scale (Rees and Brown 1992, Hambäck and Beckerman 2003). Likewise, we performed a PCA to generate a single integrative variable for plant damage (D_{PCA}) because neither the proportion of leaves damaged per plant nor the subjective damage rating alone was a satisfactory indicator of overall leaf damage. Factors were generated using a correlation matrix. We used a variance explained criterion (retain enough factors to explain 70% of variance) to determine whether the data reduction was appropriate and how many factors to retain. For both S_{PCA} and D_{PCA}, this resulted in a single factor being retained for further analysis. This analysis and all other analyses reported here were performed with SPSS (SPSS, Inc., 2008–2010), unless otherwise indicated.

To determine the importance of direct and indirect effects, we conducted a path analysis (model illustrated in Fig. 1). For this analysis, we used only data from flowering plants because young non-flowering plants were almost entirely absent inside of *E. esula* patches and would have caused inappropriate reduction in our estimate of plant size outside of *E. esula* patches (Fig. 2). In the analysis, we modeled the effects of *E. esula* density on the performance of *B. sagittata* (S_{PCA}), allowing it to have both a direct effect and indirect effects through changes in leaf herbivory (D_{PCA}) and proximity of the target *B. sagittata* to other native plants ($-1 \times$ nearest-neighbor distance). In our initial model, we allowed proximity of neighbors to have an effect on herbivory but removed these effects from the final model because they did not significantly contribute to the model. We used logical inference rather than model

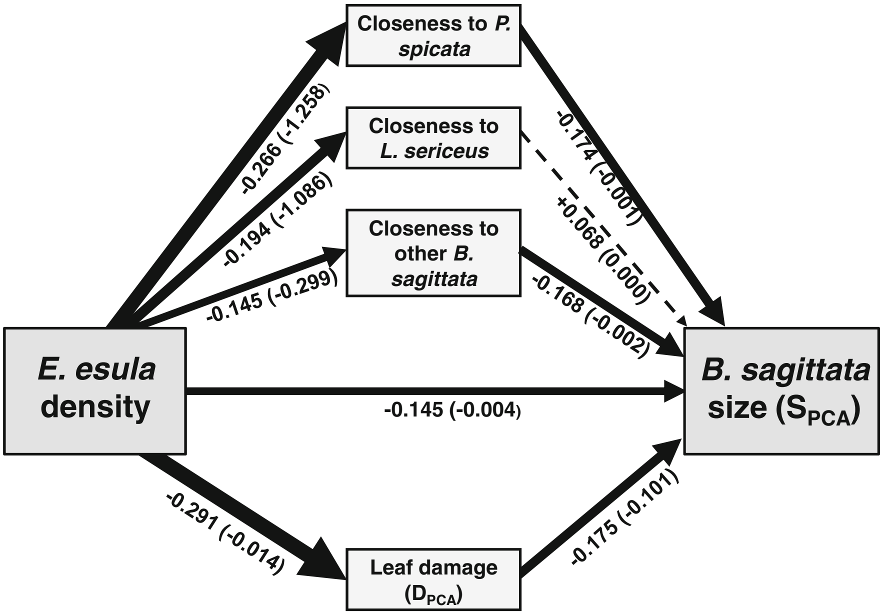

Fig. 1 Path analysis diagram. *Arrows* indicate effects of effect variables on response variables from effect → response variable. *The size of the arrow* indicates the strength of the effect. Standardized path coefficients are shown on each *arrow*, with unstandardized coefficients in *parentheses*. All paths are significant ($P < 0.05$) except "Proximity to *L. sericeus*" → D_{PCA} (*dotted line*). Direct random effects of site were also modeled for each endogenous variable (*paths not shown*)

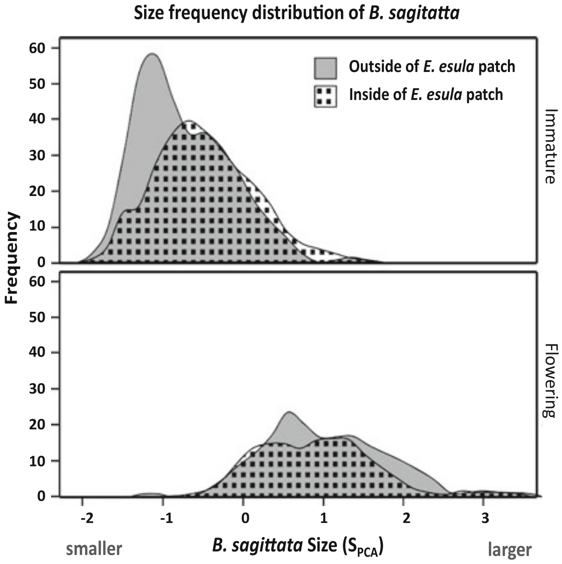

Fig. 2 Frequency distribution of *Balsamorhiza* size PCA score. The *upper panel* shows the frequency distribution for immature plants, and the *lower panel* shows the distribution for flowering plants. *Color* indicates whether plant was located outside (*solid gray*) or inside (*stippled*) of a *Euphorbia* patch. The distributions are similar, except that very small young plants (one or two leaves) are conspicuously absent from *Euphorbia* patches

comparison to construct the final model, and we used random site effects for each of the endogenous variables.

In our path analysis, we conducted a series of multiple linear regressions of effect variables against response variables. The *arrows* in the diagram represent effect paths from one variable to another (effect variable → response variable). The path coefficients on the diagram are regression coefficients (β). A large value for the path coefficient indicates that changes in the effect variable cause large changes in the response variable. To estimate the indirect effect of A on C through B ($A \rightarrow B \rightarrow C$), we take the product of the path coefficients of A on B and of B on C ($A \rightarrow B \times B \rightarrow C$). The total effect of A on C is the sum of all direct and indirect effects of A on C. For example, the indirect effect of *E. esula* density on *B. sagittata* size through herbivory is the product of the path coefficient from *E. esula* to herbivory and from herbivory to size. To calculate the total effect of *E. esula* on size, we added the coefficient of the direct path from *E. esula* to size to the products of the coefficients along each of the indirect paths.

Results

One factor (S_{PCA}) was extracted from the PCA for plant size and 85.5% of variance in the initial variables was explained by that single factor. Component loadings were: leaves = 0.903, height = 0.885 and width = 0.935; plants with high S_{PCA} scores were wider, taller and had more leaves than plants with low S_{PCA} scores. We also extracted one factor from the PCA for leaf damage, and 72.7% of variance in the initial variables was explained by that factor. Component loadings were: subjective damage = 0.853 and proportion of leaves damaged = 0.853; plants with higher D_{PCA} scores had higher subjective damage ratings and more leaves damaged than plants with lower scores.

Relatively few small immature plants were present inside of *E. esula* patches; therefore, we only considered data from flowering adult plants in further analysis (Fig. 2). Among mature plants, those inside *E. esula* patches were smaller but also experienced about a 25% reduction in herbivory compared with mature plants outside of *E. esula* patches (Table 1).

The path analysis (Fig. 1) suggested that *B. sagittata* adult size was negatively affected by the degree of leaf herbivory ($\beta = -0.175$, $P = 0.001$), proximity to neighboring *P. spicata* ($\beta = -0.174$, $P = 0.002$) and conspecific *B. sagittata* plants ($\beta = -0.104$, $P = 0.004$), and importantly, *E. esula* density ($\beta = -0.168$, $P = 0.002$). However, because *E. esula* density also had strong direct negative effects on leaf herbivory ($\beta = -0.291$, $P < 0.001$), and on proximity to *P. spicata* ($\beta = -0.266$, $P < 0.001$) and conspecific *B. sagittata* plants ($\beta = -0.145$, $P = 0.004$), the *indirect* effects of *E. esula* density on *B. sagittata* size were positive. As a result, the overall negative effect of *E. esula* on *B. sagittata* size was reduced by ≈75% (from −0.145 to −0.036). Our model indicated that indirect effects caused by changes in herbivory and in proximity to other competitors contributed equally to the 75% amelioration of direct effects caused by *E. esula* (Table 2). Plants in *E. esula* patches did not have reduced seed herbivory ($\chi^2 = 0.106$, df = 1, $n = 1{,}041$, $P = 0.744$).

Discussion

In this study, we estimated the relative strengths of direct and indirect effects of invasive *Euphorbia esula* on Montana native *Balsamorhiza sagitatta* plants. We hypothesized that negative effects of association with *E. esula* would be reduced through protection from herbivores and through reduction in the density of native competitors. To estimate the importance of these effects, we used observational data to perform a path analysis to quantify the interactions between these plant species. Our model required the following assumptions: (1) *E. esula* density affected native plant abundance, (2) *E. esula* density influenced herbivory on natives and not the opposite and (3) herbivory negatively influenced the size of natives and not the opposite.

Our model indicated that strong indirect benefits of association with *E. esula* reduced the cost of association with *E. esula* by about 75%. Roughly half of

Table 1 Effect of *E. esula* on *B. sagittata* size and herbivory

	Outside *E. esula*	Inside *E. esula*	*P*-value
Number of leaves per plant	21.96 (±12.33)	22.09 (±11.75)	0.690
Number of flowers per plant	9.92 (±11.41)	7.76 (±7.09)	0.029
Canopy height (cm)	41.7 (±11.56)	39.06 (±10.43)	0.034
Canopy width (cm)	70.75 (±16.1)	70.11 (±14.35)	0.862
Plant size (S_{PCA})	0.96 (±0.42)	0.93 (±0.39)	0.408
Number of damaged leaves	8.01 (±4.25)	6.04 (±3.6)	<0.001
Proportion of leaves damaged (%)	41.31 (±19.00)	30.32 (±16.54)	<0.001
Subjective damage rating	2.42 (±1.07)	1.63 (±0.72)	<0.001
Leaf damage (D_{PCA})	−0.06 (±0.71)	−0.64 (±0.55)	<0.001
Distance to nearest *P. spicata* (cm)	64.2 (±59.21)	98.68 (±72.89)	<0.001
Distance to nearest *L. sericeus* (cm)	103.18 (±80.56)	139.91 (±75.68)	<0.001
Distance to nearest conspecific (cm)	53.35 (±27.49)	58.8 (±31.69)	0.087

Data (mean ± s.d.) are only shown for flowering *B. sagittata* plants. *P*-values for differences in trait means, with respect to *E. esula* presence, were calculated using *T*-tests ($n = 357$). These *P*-values are provided for general information only, as the path analysis presented elsewhere in this manuscript provides a more rigorous test of the effects of *E. esula* on *B. sagittata*

Table 2 Direct and indirect effects of *E. esula* on *B. sagitatta* size (S_{PCA})

	Direct effect	−0.145 (−0.004)
+	Total indirect effect	0.109 (0.003)
	Indirect effect through plant community	0.057 (0.002)
	Indirect effect through herbivory	0.051 (0.001)
=	Total effect	−0.036 (−0.001)

Standardized coefficients are shown with unstandardized coefficients in parentheses

the indirect positive effect was because of relief from competition with native plants inside of *E. esula* patches, and half was because of reduced herbivory inside of *E. esula* patches, probably because native ungulates avoided grazing in *E. esula* patches. Although the positive effects we observed were strong, we do not believe that they ultimately allow *B. sagittata* to persist within *E. esula* patches, as the overall effect of *E. esula* on *B. sagittata* was still negative despite the strength of the indirect positive effects.

Instead, our results suggest that, for the adult plants that survived initial *E. esula* invasion, the indirect effects of *E. esula* provided substantial benefits and may allow them to persist for longer than might be expected if only direct costs of association with *E. esula* were measured. This may be a common feature of many species invasions; such indirect benefits could occur any time an invader was less palatable than neighbors, any time an invader reduced the abundance of native competitors or any time an invader obscured native plants from herbivores.

According to our model, half of the indirect benefits of association with *E. esula* resulted from reduced competition from native plants. Because invasive plants often reduce the abundance of native competitors, remaining native plants may experience relief even while experiencing intense competition from the invader. These indirect interactions are important to acknowledge because native plants species may respond differently to invasive species, and may have different competitive effects on other natives. For example, two of the three species we identified as native competitors in this experiment appeared to have similar negative effects on the performance of target *B. sagittata* plants. In contrast, the nitrogen-fixing *Lupinus sericeus* trended toward a weak positive effect. Therefore, the overall cost of association with *E. esula* could be expected to differ depending on the initial abundance of *L. sericeus* and depending on the degree to which these three species were affected by *E. esula*.

Our model also indicated that *E. esula* indirectly facilitated *B. sagittata* because of reduced rates of leaf—but not seed—herbivory on plants inside of *E. esula* patches. Because it is hypothesized that invasive plants often evolve increased defense against generalist herbivores (Müller-Schärer et al. 2004; Joshi and Vrieling 2005), and that native generalists sometimes cannot tolerate the chemical defenses of novel species, associational resistance could be an important but overlooked aspect of the interactions between many native and invasive plants.

To properly test for causal relationships among the variables we measured, experimental manipulation of native plant competition, herbivory and *E. esula* density over multiple seasons is necessary. However, in this study, path analysis allowed us to explore interactions between *B. sagittata* size, herbivory, native plant abundance and *E. esula* density using purely observational data. Such analyses may prove powerful in systems where logistical constraints or conservation concerns prohibit experimental manipulation. Our results indicated that indirect interactions among native and invasive plants can be strong, and can be an important component of the net effects of invasive plants. A complete understanding of the ecology of species invasions, and prediction of how native plants respond to invasion, may therefore require consideration of the strong indirect effects that invaders can have on native species.

Acknowledgments This work was partially funded by the Howard Hughes Medical Institute and the NSF Graduate Research Fellowship Program. The authors would also like to thank Bert Lindler and the Rocky Mountain Elk Foundation, Morgan Valliant and the City of Missoula Parks and Recreation Department, and Joy Sherry for use of their lands for our research. Ragan M. Callaway thanks the NSF for funding.

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