

Trait- and Density-Mediated Indirect Interactions Initiated by an Exotic Invasive Plant Autogenic Ecosystem Engineer

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ABSTRACT: Indirect interactions are important for structuring ecological systems. However, research on indirect effects has been heavily biased toward top-down trophic interactions, and less is known about other indirect-interaction pathways. As autogenic ecosystem engineers, plants can serve as initiators of nontrophic indirect interactions that, like top-down pathways, can involve both trait-mediated indirect interactions (TMIs) and density-mediated indirect interactions (DMIs). Using microcosms, I examined a plant → predator → consumer interaction pathway involving the exotic autogenic ecosystem engineer *Centaurea maculosa*; native *Dictyna* spiders (which exhibit density and trait [web-building] responses to *C. maculosa*); *Dictyna*'s insect prey, *Urophora affinis*; and *Urophora*'s host plant (a secondary receiver species) to quantify DMIs and TMIs in an autogenic engineered pathway. Both DMIs and TMIs were strong enough to reduce *Urophora* populations, but only DMIs, which were 4.3 times stronger than TMIs, were strong enough to also reduce *Urophora*'s fecundity and increase the fecundity of its host plant. Prior field studies support these results, suggesting that the differences between DMIs and TMIs are even stronger in nature. This study illustrates that autogenic ecosystem engineers can initiate powerful indirect interactions that generally parallel predator-initiated interactions but also differ in important functional ways.

Keywords: biological control, ecosystem engineer, indirect effects, feedbacks, plant architecture, spiders.

Introduction

Indirect interactions are powerful forces structuring ecological systems. This notion gained prominence when Hairston et al. (1960) posed their seminal hypothesis that the world is green because predators exhibit strong cascading effects by suppressing consumers that would otherwise decimate vegetation communities. Early work validated this idea by showing that even a single top predator functioning as a keystone species can initiate trophic cascades that transform lower trophic levels and dramatically alter primary

productivity (Paine 1966; Estes and Palmisano 1974). Whole-ecosystem studies produced more comprehensive support, showing that entire lakes could be turned from green to clear and back again through manipulation of top predators: an explicit test of the green-world hypothesis (Carpenter et al. 1985). These studies, and more recent ones (Power 1990; Silliman and Bertness 2002; Kurle et al. 2008; Schmitz 2008), have illustrated the profound roles that indirect effects can have in ecological systems. However, they have also set strong precedence in emphasizing predators and top-down effects in indirect interactions by focusing on predator → consumer → producer pathways.

Indirect effects transmit through a wide variety of pathways. As several authors have recently noted, plants play ubiquitous but largely underappreciated roles in indirect interactions (Ohgushi 2005; Ohgushi et al. 2007; Pringle et al. 2007; Pearson 2009). In fact, an extensive body of work has been quietly developed that illustrates the many ways in which herbivores can affect other species via indirect interactions transmitted through plants (Karban and Baldwin 1997; Martinsen et al. 1998; Agrawal et al. 1999; Van Zandt and Agrawal 2004; Ohgushi et al. 2007; Pringle et al. 2007; Huntzinger et al. 2008). Some such interactions are entirely trophically mediated, such as herbivores indirectly affecting other herbivores through resource competition. In contrast, other indirect effects transmitted through plants are not trophic or are only partially trophic, particularly those arising from ecosystem engineering (Jones et al. 1994). For example, through allogenic engineering, plants become important transmitters of indirect interactions when herbivores and other organisms change plant morphology in ways that alter, for example, thermal conditions, hiding and escape cover, and nesting substrate for other species (Lill and Marquis 2003; Ohgushi 2005; Bailey and Whitham 2006; Pringle et al. 2007; Huntzinger et al. 2008). Additionally, as autogenic ecosystem engineers, plants can be initiator species in indirect interactions because they create substrates for many biotic interactions and specific plant architectures can influence interaction outcomes (Crooks 2002; Ohgushi 2005; Callaway 2007; Pearson 2009). Such

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autogenic engineering may be a particularly important mechanism by which architecturally unique exotic plants impact invaded communities through both direct and indirect effects (Crooks 2002). Importantly, many plant species may commonly participate in multiple such indirect interactions, influencing one or many species of organisms simultaneously or sequentially (Ohgushi 2005; Ohgushi et al. 2007). Hence, plants commonly serve as initiator and transmitter species in indirect interactions (fig. 1), and relegating them to only the role of receiver species greatly limits understandings of indirect effects.

A primary focus of current indirect-effects research has been to quantify the relative influence of the two functionally distinct types of indirect interactions (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005): density-mediated indirect interactions (DMIIs) and behavioral or trait-mediated indirect interactions (TMIIs). DMIIs arise when an initiator species indirectly affects the abundance of a receiver species through its direct effects on the abundance or density of a transmitter species (Abrams et al. 1996). In contrast, TMIIs arise when the initiator species indirectly affects the abundance of the receiver species by altering the behavior or traits (e.g., morphological, physiological, chemical, etc.) of the transmitter species. Both density- and trait-mediated interactions commonly transmit simultaneously through the same pathway and can have additive, synergistic, or opposing effects on net interaction

outcomes (Werner and Peacor 2003; Griffin and Thaler 2006). Additionally, TMIIs commonly result in less predictable outcomes and can produce highly nonlinear effects that magnify their strength relative to DMIIs (Wootton 1994; Krivan and Schmitz 2004). Thus, decomposing these components and evaluating their individual and joint contributions is necessary to fully understand indirect effects.

Consistent with the general top-down emphasis in indirect-interaction studies, current research on TMIIs and DMIIs has focused on interactions where predators are the initiators, their consumer prey are the transmitters, and lower trophic levels, usually primary producers, are the receiver species, that is, predator → consumer → producer pathways (e.g., Werner and Peacor 2003; Schmitz et al. 2004). However, the theoretical framework applied is not limited to top-down trophic interactions. Theoretically, any organism at any taxonomic level can act as an initiator, a transmitter, or a receiver species (Wootton 1994; Abrams et al. 1996). Moreover, both density- and trait-mediated interactions are likely to occur concurrently in many interaction pathways. All species are presumably capable of density responses, and most organisms are capable of exhibiting some degree of plasticity that can result in trait-mediated interactions (Miner et al. 2005). Thus, DMIIs and TMIIs are not restricted to predator → consumer → producer pathways. Moreover, understanding the relative contributions of TMIIs and DMIIs to net interaction outcomes

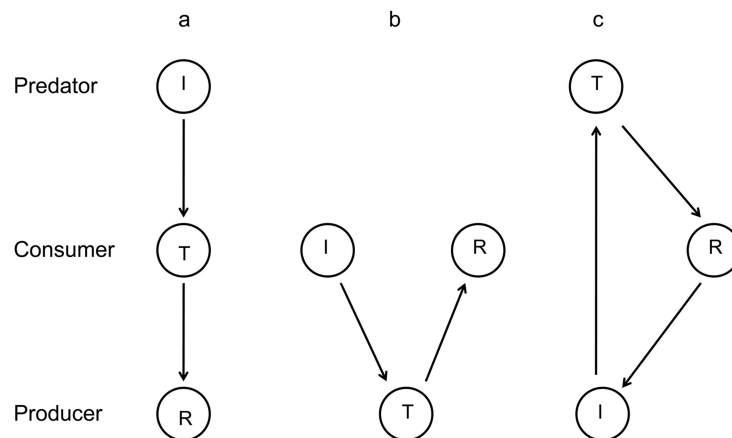


Figure 1: Indirect-interaction pathways depicting initiator, transmitter, and receiver species in different trophic positions. Research to date examining density-mediated indirect interactions (DMIIs) and trait-mediated indirect interactions (TMIIs) has focused on top-down trophic pathways where the initiator (I) is a predator, the transmitter (T) is a consumer, and the receiver (R) is a primary producer (a). However, initiator, transmitter, and receiver species can theoretically occur at all trophic levels. The scenario presented in b represents a classic exploitation-competition pathway where the initiator and receiver species are both herbivores and the transmitter is a plant. In this case, feedbacks are likely. The scenario presented in c represents a poorly recognized case involving an autogenic engineer as the initiator that directly affects a predator through a nontrophic linkage; the primary receiver is a consumer and the secondary receiver is a plant. In this particular case, the secondary receiver is also the initiator, but more commonly it would be a different plant species. These pathways are not exhaustive: they focus on illustrating the fact that transmitter species, which are key to understanding DMIIs and TMIIs, can occur at all trophic levels. The labels “predator,” “consumer,” and “producer” indicate the trophic levels across scenarios. Arrows indicate direction of the interactions.

is as important in other types of interaction pathways as it is in predator → consumer → producer pathways (Wootton and Emmerson 2005). Yet, studies have not attempted to partition and quantify DMIs and TMIs in other interaction pathways, as is currently done in predator → consumer → producer pathways.

Here I examine an exotic plant invader that serves as an autogenic ecosystem engineer initiating indirect interactions via both DMIs and TMIs that are transmitted by a native predator to both primary and secondary receiver species. Spotted knapweed (*Centaurea maculosa*) is an exotic perennial forb that has invaded millions of hectares of grassland in the western United States (Sheley et al. 1998). Within grasslands in western Montana, *C. maculosa* differs architecturally from native forbs in that it generates larger, more expansive, and more persistent stems and establishes substantially higher overall stem densities (Pearson 2009; D. E. Pearson, Y. K. Ortega, and S. J. Sears, unpublished data). As a result, *C. maculosa* invasion has increased densities of native *Dictyna coloradensis* and *Dictyna major* web spiders by ≥46-fold (density effect) relative to uninvaded sites by increasing availability of a limited substrate (Pearson 2009). The novel substrates have also altered *Dictyna* behavior by producing more expansive architectures that enable spiders to build larger webs that double their per capita prey capture rates (trait effect). Thus, in this system, the initiator species is a plant, *C. maculosa*, that engineers vegetation architecture; the transmitter species is a predator, *Dictyna* spp., that exhibits density and trait responses to the initiator; and the receiver species are *Dictyna* prey, primarily Diptera and Hymenoptera (plant → predator → consumer pathway). Field studies suggest that ecosystem engineering by the plant has had substantial indirect effects in this system, elevating spider predation rates on their prey by ≥90-fold via combined density- and trait-mediated pathways (Pearson 2009). In this study, I developed microcosms to fully partition and quantify the independent and interactive effects of the trait and density interactions in this plant → predator → consumer pathway parallel to approaches commonly used in predator → consumer → producer pathways. I also examined how DMIs and TMIs affected the fecundity of the prey's host plant: a secondary receiver species (fig. 1c).

Material and Methods

Experiments were conducted in microcosms within a fenced outdoor space at Diettert Gardens on the University of Montana campus in Missoula. Microcosms comprised four components: (1) models representing plant substrates (the initiator species), (2) *Dictyna coloradensis* spiders (the transmitter species), (3) *Dictyna* prey (the receiver species), and (4) a plant host for the prey species (a secondary receiver species). Native and exotic forbs in this system have very

different architectures and occur at very different stem densities (D. E. Pearson, Y. K. Ortega, and S. J. Sears, unpublished data). Variation in plant architecture influences web size, an important component of web-spider foraging behavior (the trait effect), while variation in substrate density influences spider density (the density effect; Pearson 2009). In my experiments, I varied substrate size to influence TMIs and manipulated substrate abundance to influence DMIs in a two-by-two full-factorial design (see below). I used the gallfly biological control agent, *Urophora affinis* (Tephritidae), and its live host plant, *C. maculosa*, for the primary and secondary receiver species, respectively. Hence, the initiator and secondary receiver species were the same. However, I selected these species because the biology of this system is well studied and readily manipulated and because *U. affinis* is commonly consumed by *Dictyna* in the field (Story et al. 1995; Pearson 2009). My primary objective was to quantify the strength of autogenically engineered indirect interactions. Inferences about feedbacks in this particular biocontrol system were secondary.

Centaurea maculosa is a widespread perennial forb (Asteraceae) that produces one to many persistent panicle-shaped flowering stems that are approximately 4–15 dm tall. Individual *C. maculosa* stems from the previous growing season were collected near Missoula to serve as experimental substrates. All primary stems were cut to a height of 50 cm, and all lateral stems were trimmed back to emulate either small substrates or large substrates. In constructing arenas, I simulated natural conditions by setting treatment effects for the density and trait treatments on the basis of field estimates for these parameters. Pilot work indicated that a substrate width of approximately 4 cm resulted in web sizes that were comparable to *Dictyna*'s primary native substrate, *Achillea millefolium*. Thus, small substrates were designed to emulate natural conditions experienced by spiders before invasion. Larger substrates were trimmed to widths of approximately 20 cm to emulate typical *C. maculosa* plants in the field. Trait effects approximated field parameter estimates well (see "Results"). Substrate densities were set at one stem for low density (the biological minimum) and 16 stems for high density (the highest density that could be achieved while keeping stems separated). The difference between low- and high-density treatments was conservative (16-fold) relative to natural conditions, where stem densities in *C. maculosa*-invaded areas were on average 47 times higher than those in native habitat (D. E. Pearson, Y. K. Ortega, and S. J. Sears, unpublished data).

Dictyna coloradensis (Dictynidae) are small (carapace length, ≤1 mm), univoltine spiders that construct irregular, cribellate webs and are active from about April to October. These spiders build up their webs over several days but do not reconstruct webs daily like some orb weavers (Jackson 1978). Webs are constructed within, not among, substrates.

Dictyna spp. capture and feed on a variety of taxa ranging from about 1 to 20 mm in length, but most prey are Diptera and Hymenoptera (Pearson 2009). They retain prey items in their webs, so captures can be readily quantified. Adult and late-instar female *D. coloradensis* individuals (adult males do not construct webs) were collected in the Missoula valley and randomly introduced onto model substrates in a greenhouse. *Dictyna coloradensis* cannot be distinguished from *Dictyna major* when alive (J. Slowik, Denver Museum of Nature and Science, Denver, CO), so it is possible that a few experimental individuals were *D. major*. However, prior identification of spiders from the collection areas produced only *D. coloradensis*, and the spiders are ecologically similar (Jackson 1978) and exhibit similar responses to plant architecture (Pearson 2009). Thus, the study species is referred to as *D. coloradensis*.

Urophora affinis larvae overwinter within galls in *C. maculosa* seed heads (Story et al. 1992). They pupate in spring and emerge as adults from May to July. Adults display and copulate on *C. maculosa* plants or nearby substrates, and females oviposit within immature *C. maculosa* flowerheads. The eggs hatch into larvae and induce gall formation in the plants, which reduces seed production via an energy sink (Harris 1980). Thus, *U. affinis* impact their host by reducing fecundity. *Urophora affinis* individuals were reared for the study by collecting and caging *C. maculosa* seedheads before the emergence of *U. affinis*. *Urophora affinis* individuals were randomly collected from the rearing cage without regard to sex when introduced into experimental arenas.

I gathered live *C. maculosa* plants from a wild population in the Missoula valley in May to serve as host plants. Similarly sized plants that had not initiated bolting were selected and placed in 1-gal pots with a 50 : 50 sand and potting soil mix in the bottom third of the pot to facilitate drainage. The remainder of each pot was filled with soil from the root zone of the collected plants. Plants were reared in a greenhouse until they bolted and initiated flowering. When flowers began to reach a stage suitable for *U. affinis* oviposition, plants were transferred to experimental arenas.

Each experimental arena (fig. 2) consisted of an oversized 1.9-cm-thick plywood base covered with a 1-m-wide \times 1-m-wide \times 0.75-m-tall frame of 1.3-cm-diameter PVC pipe overlaid with insect netting (Wondermesh, Garvock, Laurencekirk, Scotland). The cloth mesh size was 0.8 mm, and it allowed wind, precipitation, and 85% natural light to pass through but prevented the passage of all but extremely small invertebrates. In the high-density treatment, the stems were placed in a 4 \times 4 array with 20-cm spacing, with a little extra space in the center for the live host plant. In the low-density treatment, the single stem was randomly placed in one of the four central points on the array. Stems were plastered into holes drilled in the wooden bases. One live host plant was placed in the center of each arena before the



Figure 2: Experimental arenas. The upper panel shows an arena being prepared for the high-density, small-substrate treatment. The lower panel shows a low-density, large-substrate arena out in the field, toward the end of the experiment. The arrow in the lower panel points to the spider.

spiders were introduced, with plants standardized by size and flower development within each block. I placed *D. coloradensis* on substrate models (one spider per substrate) and allowed them to establish and begin constructing webs overnight before the arenas were covered and placed outdoors. Twenty *U. affinis* were added to each cage when microcosms were first set out, and 20 more were added every 2 days to offset natural mortality (non-spider-inflicted mortality) and to maintain populations at around 20–30 flies per arena over the course of the study. I ran experiments for 8 days, with each arena receiving 60 total *U. affinis* over the course of the experiment. Field studies indicated that this period was long enough for web size and prey captures to equilibrate (Pearson 2009) but short enough to avoid confounding effects (Preisser et al. 2005; Abrams 2008). I initiated arenas over a 2-week period in June to allow all host plants to reach the proper developmental stage for *U.*

affinis oviposition. Arenas were set out in blocks of four cages representing the full combination of treatments ($n = 18$ blocks). Each day, I examined all webs, noting the presence or absence of spiders and counting new prey captures. Spiders that abandoned substrate models (often as a result of wind or rain events occurring before they were fully established) were immediately removed from the arenas to prevent them from moving to the covers and killing prey independent of experimental substrates.

At the end of the experiment, I measured webs (following Pearson 2009), tallied final prey captures, and maintained live plants in the greenhouse so flowers could mature and set seed and *U. affinis* larvae could develop. Plants remained covered with insect netting in the greenhouse to preclude further access by *Urophora*. I pollinated the experimental plants using live flowers collected from wild plants in the field, because netting excluded pollinators. Once all flowers on a plant set seed, seed heads were collected and dissected to count the seeds and *U. affinis* larvae within.

To evaluate the indirect effects of plant architecture on *D. coloradensis* prey (the primary receiver species), I used the total number of adult *U. affinis* captured in all webs in each arena over the 8-day study as the response variable in a generalized mixed linear model, with density (1 vs. 16 stems) and trait (large vs. small stems) effects and their interaction entered as fixed factors and experimental block treated as a random factor (PROC MIXED; SAS Institute 2003). Since the total number of *U. affinis* introduced into each cage was the same across treatments, total captures provided a direct measure of impact on the prey population (the amount by which the total prey population was reduced). As an added measure of the indirect effects of plant architecture on the prey of *D. coloradensis*, I also examined the number of *U. affinis* larvae produced per seed head in each arena. This allowed me to assess whether the reduction in adult *U. affinis* numbers was sufficient to affect *U. affinis* recruitment. It also provided a measurement of *U. affinis* attack on *C. maculosa*. I used the same model as above to test for treatment effects, except that arena was added as a random factor to account for the multiple seed heads produced in each arena. To evaluate the indirect effects of plant architecture on *C. maculosa* host plants (the secondary receiver species), I examined the number of seeds produced per *C. maculosa* seed head in each arena, employing the same model used to assess *U. affinis* larvae. All dependent variables were positively skewed. To meet assumptions of normality and homoscedasticity, the adult *U. affinis* data were square-root transformed and the *U. affinis* larvae and seed data were inverse transformed (Tabachnick and Fidell 1989). Data presented in figures are back-transformed least squares means, and the variances are back-transformed upper or lower limits (Haase et al. 2008). I calculated web area

from web length and width on the basis of the geometry of a triangle (Jackson 1978; Pearson 2009).

Results

Treatments were effective and represented natural conditions reasonably well (fig. 3). Mean web area on small substrates was nearly identical to field measurements of webs built on *Achillea millefolium* (fig. 3A). Mean web area on large substrates was comparable to that of webs built on *Centaurea maculosa* in the field (95% confidence interval of experimental mean included mean field estimate). In the high-density treatment, about half ($\bar{x} = 7.7$) of the *Dictyna coloradensis* individuals introduced into experimental arenas

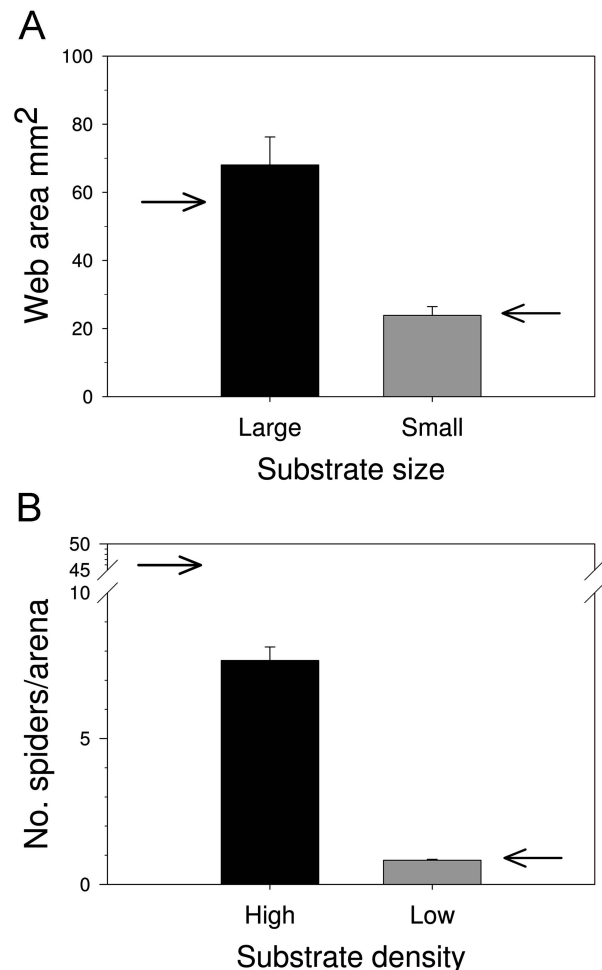


Figure 3: Treatment effect size (mean \pm SE) for (A) trait effects (web size on large vs. small substrates) and (B) density effects (number of spiders or active webs in arenas with high vs. low substrate density). Arrows indicate mean estimates for equivalent parameters obtained from field data for comparison (based on Pearson 2009).

remained on the substrates. For low-density treatments, spiders that abandoned were replaced with established spiders to ensure that the minimum density was met. Thus, the effective difference between low- and high-density treatments (a ratio of 1 : 8) was quite conservative relative to natural conditions (a ratio of 1 : 47; fig. 3B).

Both density-mediated ($F_{1,51} = 110.75$, $P < .01$; fig. 4A) and trait-mediated ($F_{1,51} = 6.23$, $P = .02$) indirect effects of plant architecture significantly reduced adult *Urophora affinis* abundance, and there was no significant trait-by-

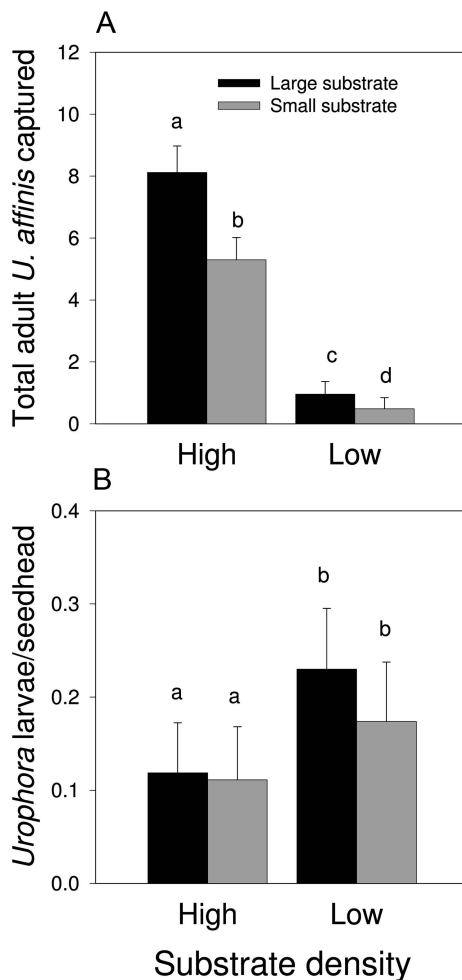


Figure 4: Density- and trait-mediated indirect effects of plant architecture on (A) adult *Urophora affinis* fly abundance and (B) *U. affinis* larvae production as transmitted by *Dictyna coloradensis* spider predation. Results are based on 8-day trials in experimental arenas where plant architecture was represented by large or small substrates (inducing trait-mediated responses in the transmitter species) and high or low substrate density (inducing density-mediated responses in the transmitter species) in a full-factorial design. Different letters over bars indicate significant differences at the $P = .05$ level. Means and variance are back transformed (see “Material and Methods”).

density interaction ($F_{1,51} = 1.39$, $P = .24$), indicating that the combined effect would be additive. The density-mediated indirect effects of plant architecture on adult *U. affinis* were strong enough to reduce the number of *U. affinis* larvae produced per seed head by nearly 50% ($F_{1,43} = 4.58$, $P = .04$; fig. 4B), but trait-mediated indirect effects alone did not significantly reduce *U. affinis* larval densities ($F_{1,43} = 0.52$, $P = .47$), nor was there a significant interaction between density- and trait-mediated effects on *U. affinis* larval densities ($F_{1,43} = 0.27$, $P = .60$). For the secondary receiver species, *C. maculosa*, density-mediated indirect effects of plant architecture significantly reduced seed production ($F_{1,34} = 8.36$, $P = .01$; fig. 5), but trait-mediated indirect effects did not ($F_{1,34} = 0.21$, $P = .65$), and there was no significant density-by-trait interaction ($F_{1,34} = 2.32$, $P = .14$). The presence of *U. affinis* larvae negatively correlated with number of seeds in *C. maculosa* seed heads ($r = -0.37$, $P < .01$).

Discussion

Prior field studies in western Montana have shown that changes in vegetation architecture due to autogenic ecosystem engineering by the exotic invasive plant *Centaurea maculosa* have increased rates of predation on insects ≥ 90 -fold by increasing the abundance and intensifying predatory behavior of native *Dictyna* spiders (Pearson 2009). These field studies suggest that plants, as autogenic engineers, may contribute substantively to community assembly via direct nontrophic influences on predators that can transmit through both DMIs and TMIs to other species. Using microcosms to isolate and quantify density and trait effects, I show here that the direct effects of autogenic engineering by *C. maculosa*, which increased the abundance and per capita capture rates of *Dictyna coloradensis* spiders, significantly reduced populations of their prey, *Urophora affinis*, via both DMIs and TMIs, with no significant density-by-trait interactions. TMIs were strong enough to reduce adult *U. affinis* populations but not strong enough to reduce *U. affinis* recruitment rates, and so they did not affect recruitment of its host plant, the secondary receiver species. In contrast, the stronger DMIs impacted *U. affinis* populations sufficiently to reduce their recruitment, which translated to reduced seed production in their host plant. The observed reductions in seed production were negatively correlated with number of *U. affinis* larvae in the *C. maculosa* seed heads, consistent with the well-documented ability of *U. affinis* to suppress *C. maculosa* seed production (Maddox 1982; Story et al. 1989). Overall, the effects of the DMIs were 4.3 times stronger than those of the TMIs on the primary receiver species, *U. affinis*. This difference in the strength of DMIs versus TMIs is consistent with (though substantially weaker in magnitude than) the difference es-

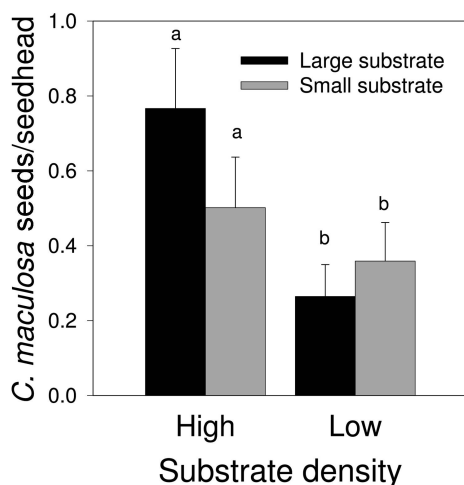


Figure 5: Density- and trait-mediated indirect effects of plant architecture on a secondary receiver species, *Centaurea maculosa*, as measured by seeds produced per seed head while under attack by the primary receiver species, *Urophora affinis*. Different letters over bars indicate significant differences at the $P = .05$ level. Means and variance are back transformed (see “Material and Methods”).

timated in field studies, which suggested that the density-mediated pathway was ≥ 23 times stronger than the trait-mediated pathway and also indicated no significant density-by-trait interactions (Pearson 2009). The difference in the relative strength of DMII and TMII between the microcosm and the field studies is attributable to the fact that density effects in microcosms were conservative relative to those of field densities due to space constraints in arenas. Actual differences between DMII and TMII are likely much stronger in nature. Regardless, the conclusions that DMII were substantially stronger than TMII and there were no significant interactions are consistent between field studies and controlled experiments.

This study demonstrates that the TMII/DMII concept can apply beyond predator \rightarrow consumer \rightarrow plant linkages to a broader range of interaction pathways, with two important general conclusions. First, expanding the concept requires certain caveats regarding its new application and interpretation. Second, expanding an established concept can generate new insights, even for prior applications, by providing novel perspectives. For example, indirect-effects studies have focused on quantifying the relative importance of TMII and DMII in contributing to net interaction outcomes. Studies examining predator \rightarrow consumer \rightarrow producer pathways have concluded that TMII are generally as strong as or stronger than DMII (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005). In this system, I found that DMII were substantially stronger than TMII. This occurred because the high natural densities achieved by the

initiator species overrode its weak per capita density effects. Per capita effects of *C. maculosa* on *Dictyna* density were low relative to trait effects (per capita density effect = 0.5, trait effect = 2.8). However, natural stem densities resulting from *C. maculosa* invasion can average 47 times higher than those in the native system (D. E. Pearson, Y. K. Ortega, and S. Sears, unpublished data). Emulating this effect in the experiment, even conservatively (only an eightfold treatment effect), resulted in very strong DMII because the initiator’s density drove the overall indirect effect. In other words, per capita density effects were relatively weak but cumulative density effects, the overall DMII, were strong relative to the overall TMII because the invasive autogenic engineer achieves “unnaturally” high densities relative to that of the natives. This result highlights the fact that autogenic architectural engineering will tend to cause DMII that are driven by initiator density (or size). This requires manipulation of initiator density to examine receiver responses, something that is rarely done in experiments of predator-initiated pathways. This result also highlights an important concept applicable to all indirect-interaction pathways. In nature, weak per capita effects can be overcome via naturally high organism densities to generate strong net indirect effects (sensu Jones et al. 1994). Net indirect-interaction outcomes likely commonly involve the integration of per capita effects across varying initiator densities, even in predator- and consumer-initiated systems. For example, predators commonly aggregate in response to resource pulses with important community-level ramifications (Holling 1959). Such responses may strongly influence net indirect effect outcomes in nature, but they have not been incorporated into TMII/DMII studies.

One of the biggest challenges in evaluating TMII and DMII in predator-driven systems has been fully partitioning density and trait effects to quantify their individual and synergistic contributions (Werner and Peacor 2003; Griffin and Thaler 2006; Abrams 2008). This is extremely challenging, because predator cues can be so closely linked to predation that it requires creative experimental approaches like gluing the predator’s mouth parts (Schmitz 1998) or complicated study designs to fully partition trait and density effects (Trussell et al. 2004; Griffin and Thaler 2006; Abrams 2008). In this system, TMII and DMII were fully partitioned by a standard full-factorial experiment manipulating initiator morphology and density, because DMII were linked solely to the initiator’s density and TMII were linked solely to its morphology. However, in other cases of autogenic engineering, trait and density effects may be closely linked. For example, the orb weaver *Aculepeira packardii* uses multiple *C. maculosa* stems to construct its webs in this system (*Dictyna* build webs within stems). Thus, density and morphology of the engineer likely simultaneously influence the abundance and behavior of *A. packardii*, and

teasing apart trait and density effects would be difficult. Given the variety of ways that plants can affect other species (Ohgushi et al. 2007; Karban 2008), density and trait effects may commonly be closely linked in plant-initiated pathways, creating challenges for partitioning effects closely paralleling those in predator → consumer → producer pathways.

This study also addresses several information gaps regarding ecosystem engineering related to engineering feedbacks, engineers in biological invasions, and efforts to merge engineering with trophic ecology (Jones et al. 1994; Crooks 2002; Wright and Jones 2006). Since the inception of the ecosystem-engineering concept, it has been recognized that any engineering effect that feeds back on the engineer could have broad system-level ramifications (Jones et al. 1994). The particular species combination used here illustrates how feedbacks could be important for autogenic engineering. *Centaurea maculosa*'s engineering effects could potentially result in increasing its own populations by reducing natural enemy attacks. My results suggest that *Dictyna* spp. can reduce *Urophora* enough via indirect interactions to actually diminish their impacts on *C. maculosa* seed production and, potentially, recruitment. Whether autogenic engineering in this particular system actually results in *C. maculosa*'s release from natural enemies through these indirect effects is unclear, because while some studies suggest that *C. maculosa* is not seed limited and is unaffected by *Urophora* (Harris 1980; Maddox 1982; Myers et al. 1988), more recent work suggests that *Urophora* suppresses *C. maculosa* populations (Story et al. 2008). Nonetheless, this system illustrates how such interactions could play out in nature and that autogenic engineers may exert feedbacks that are strong enough to affect their own populations despite the fact that, as noted by Jones et al. (1994), engineering feedbacks are likely to be complex.

Exotic invasive species may commonly impact native systems through ecosystem engineering (Crooks 2002). Crooks (2002) explored the potential for predicting invasive engineering impacts by examining how vegetation complexity affects species richness but with mixed results. In this system, autogenic engineering by *C. maculosa* may increase *Dictyna* predation sufficiently to reduce some natural prey populations and possibly increase certain prey resources. These results illustrate the strength and complexity of invasive autogenic engineering effects. They also emphasize the importance of functional roles in predicting outcomes (Duffy 2002). The community response to invasive engineers will depend on the degree to which the invader's functional roles differ from those of the natives. *Centaurea maculosa* and other exotic forbs invading western Montana differ architecturally (and in other attributes) from the natives (D. E. Pearson, Y. K. Ortega, and S. Sears, unpublished data). Thus, the populations of *Dictyna* spp. and other web spiders have predictably increased in response to these in-

vasions (Pearson 2009). In general, if the invader differs functionally from the natives, a strong response may be expected from those natives sensitive to its unique attributes (positively or negatively). However, it is important to note that exotic ecosystem engineers can also have extensive non-engineering effects. For example, *C. maculosa* dramatically reduces native plant abundance via competition, which indirectly affects herbivores and predators through trophic interactions (Ortega and Pearson 2005; Ortega et al. 2006). Accounting for nonengineering effects of invasive engineers greatly complicates the prediction of their impacts.

Ecosystem engineers can produce such powerful and widespread indirect interactions that they have been compared with keystone species (e.g., Jones et al. 1994). Although most autogenic ecosystem engineers, as in this case, would not strictly qualify as keystone species (Power et al. 1996), these powerful effects emphasize the need to better incorporate ecosystem engineering into indirect-interaction frameworks. Additionally, there are many other types of nontrophic interactions, cataloged as competition, facilitation, and mutualisms, for example, that are also extremely important and need to be more fully incorporated into studies of community interactions. The current study suggests that nontrophic interactions can be better incorporated into community ecology by simply expanding current ecological concepts and frameworks. It also illustrates the underutilized potential of biological invasions for advancing community ecology and integrating ecology and evolution.

Hairston, Smith, and Slobodkin's (1960) green-world hypothesis (HSS) stimulated tremendous advances in ecology. However, it also created a predator-centric perspective that currently constrains ecological thinking (Pringle et al. 2007). Ecological concepts such as trait- and density-mediated interactions have been underutilized because of such restricted perspectives. Thus, nontrophic interactions could be more fully incorporated into ecology by simply loosening the predator-centric veil of HSS. Expanding on this, the more broadly an ecological concept is applied, the more it will contribute. All ecological concepts should be stretched to their limits, for two reasons. First, applying concepts in new contexts can provide unique insights and perspectives, as is noted by this study. Second, finding the boundaries of conceptual applications can be equally insightful. For example, the conclusion that trophic cascades were more prominent in aquatic than terrestrial environments stimulated extensive discussions about the attenuation of trophic cascades that increased knowledge of indirect interactions in both aquatic and terrestrial systems (Strong 1992). Stretching concepts with discrete origins across ecological (e.g., aquatic vs. terrestrial), taxonomic (e.g., plant vs. animal), or vocational (ecology vs. evolution) boundaries will generate new insights by offering new perspectives and defining important attributes that truly delineate conceptual boundaries.

The food-web framework also has inhibited integration of nontrophic interactions. Food webs provide the conceptual core for much ecological theory. However, food webs exclude the many nontrophic interactions known to profoundly affect community structure and function. Community interaction webs were developed to incorporate nontrophic interactions into community-assembly theory (Paine 1980), but they remain underutilized (Ohgushi 2008). Food-web complexity has been addressed by partitioning webs into subcompartments or motifs to examine the influence of different motifs on community outcomes (Rip et al. 2010). Conceptually, food webs could be expanded into interaction webs by incorporating hybrid motifs that include nontrophic interactions. Broader integration will be achieved once it is recognized that food webs are merely a class of motifs that provide the scaffolding for more complex interaction webs.

Finally, biological invasions present unique natural experiments offering novel insights for ecology and evolution. This fact has been noted (Sax et al. 2005) but is rarely fully capitalized on. A massive literature exists on biological invasions (Richardson and Pysek 2008), but most studies focus on the causes of invasion or the impacts of invaders. Very few studies actually examine invasions as natural experiments in community assembly. When a strong invader (*sensu* Ortega and Pearson 2005) enters a new system, the native community is forced to rapidly reassemble in response to the new conditions. Thus, the roles that competition, herbivory, predation, and facilitation, for example, play in structuring the community, as well as the importance of rapid evolutionary responses to these ecological changes (Cox 2004), can be observed in real time. Biological invasions represent a lucrative frontier for exploring concepts in ecology and evolution and the interface between the two that demands greater attention.

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Literature Cited

- Abrams, P., B. A. Menge, C. G. Mittelbach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 in

- G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Abrams, P. A. 2008. Measuring the impact of dynamic antipredator traits on predator-prey-resource interactions. *Ecology* 89:1640–1649.
- Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. *Ecology* 80:518–523.
- Bailey, J. K., and T. Whitham. 2006. Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology* 31:294–297.
- Callaway, R. M. 2007. *Positive interactions and interdependence in plant communities*. Springer, Dordrecht.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Cox, G. W. 2004. *Alien species and evolution: the evolutionary ecology of exotic plants, animals, microbes, and interacting native species*. Island, Washington, DC.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.
- Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* 99:201–219.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- Griffin, C. A. M., and J. S. Thaler. 2006. Insect predators affect plant resistance via density- and trait-mediated interactions. *Ecology Letters* 9:333–346.
- Haase, J., R. Brandl, S. Scheu, and M. Schädler. 2008. Above- and below-ground interactions are mediated by nutrient availability. *Ecology* 89:3072–3081.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Harris, P. 1980. Effects of *Urophora affinis* (Fröhl.) and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Compositae). *Zeitschrift für Angewandte Entomologie* 90:190–210.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Huntzinger, M., R. Karban, and J. H. Cushman. 2008. Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89:1972–1980.
- Jackson, R. R. 1978. Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae). I. Social organization and web characteristics. *Reviews of Arachnology* 1:133–164.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Karban, R. 2008. Plant behavior and communication. *Ecology Letters* 11:727–739.
- Karban, R., and I. T. Baldwin. 1997. *Induced responses to herbivory*. University of Chicago Press, Chicago.
- Krivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. *Oikos* 107:239–250.
- Kurle, C. M., D. A. Croll, and B. R. Tershy. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. *Proceedings of the National Academy of Sciences of the USA* 105:3800–3804.
- Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by cat-

- erpillars increases insect herbivore diversity on white oak. *Ecology* 84:682–690.
- Maddox, D. M. 1982. Biological control of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Sci* 30:76–82.
- Martinsen, G. D., E. M. Driebe, and T. G. Whitham. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* 79:192–200.
- Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution* 20:685–692.
- Myers, J., C. Risley, and R. Eng. 1988. The ability of plants to compensate for insect attack: why biological control of weeds with insects is so difficult. Pages 67–73 in E. Delfosse, ed. *Seventh International Symposium on Biological Control of Weeds*. Istituto Sperimentale per la Patologia Vegetale, Ministero dell'Agricoltura e delle Foreste, Rome.
- Ohgushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81–105.
- . 2008. Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facilitative interactions. *Entomologia Experimentalis et Applicata* 128: 217–229.
- Ohgushi, T., T. Craig, and P. W. Price. 2007. Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, Cambridge.
- Ortega, Y. K., and D. E. Pearson. 2005. Strong versus weak invaders of natural plant communities: distinguishing invasibility from impact. *Ecological Applications* 15:651–661.
- Ortega, Y. K., K. S. McKelvey, and D. L. Six. 2006. Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird. *Oecologia (Berlin)* 149:340–351.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- . 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667–685.
- Pearson, D. E. 2009. Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia (Berlin)* 159:549–558.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250: 811–814.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenge in the quest for keystones. *BioScience* 46:609–620.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? the effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences of the USA* 104:193–197.
- Richardson, D. M., and P. Pysek. 2008. Fifty years of invasion ecology: the legacy of Charles Elton. *Diversity and Distributions* 14:161–168.
- Rip, J. M. K., K. S. McCann, D. H. Lynn, and S. Fawcett. 2010. An experimental test of a fundamental food web motif. *Proceedings of the Royal Society B: Biological Sciences* 277:1743–1749.
- SAS Institute. 2003. *SAS/STAT user's guide*, version 8. SAS Institute, Cary, NC.
- Sax, D. F., J. J. Stachowicz, and S. D. Gaines. 2005. *Species invasions: insights into ecology, evolution and biogeography*. Sinauer, Sunderland, MA.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- . 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect effects. *Ecology Letters* 7: 153–163.
- Sheley, R. L., J. S. Jacobs, and M. F. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technology* 12:353–362.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the USA* 99:10500–10505.
- Story, J. M., K. W. Boggs, and R. M. Nowierski. 1989. Effects of two introduced seed head flies on spotted knapweed. *Montana Ag-Research* 6:14–17.
- Story, J. M., K. W. Boggs, and W. R. Good. 1992. Voltinism and phenological synchrony of *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae), two seed head flies introduced against spotted knapweed in Montana. *Environmental Entomology* 21:1052–1059.
- Story, J. M., K. W. Boggs, W. R. Good, L. J. White, and R. M. Nowierski. 1995. Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed capitula. *Environmental Entomology* 24:1467–1472.
- Story, J. M., L. Smith, J. G. Corn, and L. J. White. 2008. Influence of seed head-attacking biological control agents on spotted knapweed reproductive potential in western Montana over a 30-year period. *Environmental Entomology* 37:510–519.
- Strong, D. R. 1992. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754.
- Tabachnick, B. G., and L. S. Fidell. 1989. *Using multivariate statistics*. Harper Collins, New York.
- Trussell, G. C., P. J. Ewanchuk, M. D. Burtness, and B. R. Silliman. 2004. Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects. *Oecologia (Berlin)* 139:427–432.
- Van Zandt, P. A., and A. A. Agrawal. 2004. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology* 85:2616–2629.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* 36:419–444.
- Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience* 56:203–209.