INSECT HERBIVORES DRIVE IMPORTANT INDIRECT EFFECTS OF EXOTIC PLANTS ON NATIVE COMMUNITIES

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Abstract. Exotic plant species can affect native plant species both directly via competition and indirectly by modifying native species' interactions with other organisms in the community. Both direct and indirect effects can have strong fitness impacts on the native species and can result in cascading effects throughout the invaded community. Many exotic plant species escape from the herbivores with which they co-evolved, but in our study system, the exotic Egyptian alfalfa weevil (*Hypera brunneipennis*) has been introduced to California and is able to feed both on the exotic plant *Medicago polymorpha* and on the California native *Lotus wrangelianus*. Because these two plant species share this common herbivore, the possibility of strong herbivore-mediated indirect interactions between these introduced and native plant species is plausible.

We used observational studies and manipulative field experiments to determine whether exotic *Medicago* affects herbivory on the native *Lotus* and whether *Medicago* reduces the fitness of *Lotus* through direct competitive effects and/or herbivore-mediated indirect effects. Both observational and experimental data indicate that *Medicago* increases weevil herbivory on the native *Lotus*. Additionally, *Medicago* reduced *Lotus* fitness through direct as well as indirect mechanisms. In 2002, *Medicago* reduced *Lotus* fitness even when herbivores were experimentally reduced, suggesting direct competitive effects of *Medicago* on the native *Lotus*. In contrast, in 2003, *Medicago* reduced *Lotus* fitness only in the presence of herbivores, indicating that the fitness effects in that year were largely indirect and mediated by herbivores. Our results demonstrate that the net fitness consequences of indirect and direct effects of exotic plant species on native plants can vary temporally, depending on the abundance of members of the herbivore community. Also, rather than limiting the success of exotics, introduced herbivores that feed on exotic plants may provide additional, indirect avenues through which exotic plants can reduce the fitness of native species.

Key words: *apparent competition; associational susceptibility; biological invasion;* Hypera brunneipennis; *indirect effect;* Lotus wrangelianus; Medicago polymorpha; *plant–insect interaction.*

INTRODUCTION

While the direct effect of exotic plants on native vegetation via competition has been well documented (e.g., Walker and Vitousek 1991, Dunbar and Facelli 1999), less obvious indirect effects of exotics on native species may go undetected (but see Callaway et al. 1999, Grosholz et al. 2000, Brown and Mitchell 2001, Chittka and Schurkens 2001, Irwin et al. 2001, Brown et al. 2002, Suarez and Case 2002, Callaway et al. 2004, Rand and Louda 2004). Indirect effects are strictly defined as the effects of one species on another that are mediated by a third species (Wootton 1994). Important indirect effects of exotic plants on native plant species could be mediated by herbivores (Callaway et al. 1999, Sessions and Kelly 2002, Rand and Louda 2004), pollinators (Brown and Mitchell 2001, Chittka and Schurkens 2001, Brown et al. 2002), mychorrhizal fungi (Marler et al. 1999), endophytic fungi (Clay and Holah

1999, Clay 2001), or parasites (Irwin et al. 2001). Such indirect effects can take many forms (e.g., indirect mutualism, apparent competition) and can influence population growth (Power 1990, Wootton 1993), community structure, and species coexistence (Holt 1977, Menge 1995, Schmitz 1998, 2003). While some indirect effects are predictable functions of the products of direct effects among species, other indirect effects can only be detected experimentally and are not inherently predictable (Wooton 1994). Thus, if exotic species commonly exert strong indirect effects, the community consequences of biological invasions may be difficult to predict and detect.

If exotic herbivores invade with exotic plants or if exotic plants are fed upon by generalist herbivores already present in the community, then exotic plants may indirectly affect co-occurring native plant species via these natural enemies (Holt and Lawton 1994, Louda et al. 1997, Rand and Louda 2004). Similar indirect effects mediated by shared predators have been documented between native and exotic avifauna and a shared disease (van Riper et al. 1986) and between exotic and native phytophagous insects and shared par-

asitoids (Settle and Wilson 1990). In the plant–herbivore literature, these kinds of indirect effects have been termed associational resistance (Tahvanainen and Root 1972) and associational susceptibility (Brown and Ewel 1987). Herbivore-mediated indirect effects, such as associational susceptibility and resistance, may have strong evolutionary and demographic consequences for native plant species and may even cascade through interaction webs to influence the native species' interactions with other herbivores in the community. These other community members may exacerbate or ameliorate the effects of the invasion, resulting in complex ecological patterns that may vary both spatially and temporally, depending on the abundance of members of the herbivore community.

We used a combination of observations and manipulative experiments to address three questions concerning the direct and herbivore-mediated indirect effects of the exotic plant *Medicago polymorpha* on the co-occurring native plant *Lotus wrangelianus*: (1) Does the exotic plant *M. polymorpha* affect herbivory on the native *L. wrangelianus*? (2) Does *M. polymorpha* affect *L. wrangelianus* fitness directly via competition and/or indirectly via shared herbivores? (3) What are the *net* fitness consequences of direct versus indirect effects in this system?

MATERIALS AND METHODS

Study system

Lotus wrangelianus (native, Fabaceae) and *Medicago polymorpha* (exotic, Fabaceae) commonly co-occur in open grasslands throughout much of the McLaughlin Reserve in Napa County, California, USA. Both plants are small winter annuals that germinate with the first rains in November and flower in the late spring as the rains cease and soil moisture is depleted. *M. polymorpha* is native to the Mediterranean region and has likely been in California since the late 1800s (De Haan and Barnes 1998).

Several types of herbivores feed on the native *L. wrangelianus* (hereafter referred to as *Lotus*) and introduced *M. polymorpha* (hereafter, *Medicago*). Both plants are attacked by a folivore (*Hypera brunneipennis*, the Egyptian alfalfa weevil) and a hymenopteran seed predator (*Bruchophagus* sp.). *H. brunneipennis* is an exotic species that likely spread to Northern California from North Africa in the 1960s (van den Bosch and Marble 1971, Madubunyi and Koehler 1974). *H. brunneipennis* inflicts high levels of damage on both *Lotus* and *Medicago*, but appears to prefer *Medicago* (J. Lau, *personal observation*). A weevil (*Apion* sp.) also forms galls on the buds of *Lotus*. Several other legume species (e.g., *Lupinus* spp. and *Trifolium* spp.) occur in the study sites, but they are rarely fed upon by any herbivores that are abundant on *Lotus* and *Medicago*. Legume specialists inflicted the vast majority of herbivore damage experienced by *Lotus* and *Medicago*.

Observational study: Does natural Medicago invasion affect herbivory on, or fitness of, Lotus?

We censused *Lotus* patches on the McLaughlin Reserve over three years (2001 and 2002 [$N = 13$ patches], 2003 [$N = 16$]). Approximately half of the patches were naturally invaded by *Medicago*, while the other half were uninvaded. Patches were relatively close together with a minimum distance of ~250 m between them. Two 25-m transects were established in each patch, and we sampled *Lotus* individuals at 1-m intervals along each transect. *Lotus* plants were censused for foliar damage in each year of the study, for bud-galling damage in 2002 and 2003, and for seed predation in 2003. Foliar, bud-galling, and seed predation damage were estimated as the proportion of leaflets, buds, or seeds (respectively) that had been damaged per plant. Fitness data (seed number and seed mass) were collected in 2003. Densities of *Lotus* and *Medicago* in each patch were estimated in 2002 and 2003 by counting the number of individuals in 0.625-m² grids at 5-m intervals along each transect. In 2002, densities of *H. brunneipennis* were estimated by counting the number of larvae observed within each sampling grid.

To determine whether invaded and uninvaded patches differed in levels of herbivory on *Lotus*, we used the MANOVA option in PROC GLM (SAS Institute 2000) to analyze the 2003 census data. Response variables were average weevil folivory, bud-galling, and seed predation per patch. Invasion status of each patch was included as a fixed factor, and *Lotus* and *Medicago* densities were initially included as covariates. Covariates with $P > 0.2$ (*Medicago* density) were dropped from subsequent analyses. The assumption of homogeneous slopes was met for the remaining covariate. We used angular transformations to improve normality, and performed all analyses on patch means. Subsequent univariate analyses (protected ANOVAs) were performed to test for effects in the individual response variables for those terms that were significant in the initial MANOVA. Univariate models of the same structure were performed on weevil folivory damage levels for 2001 and 2002. Similar univariate models were also used to test for effects of *Medicago* invasion on mean *Lotus* seed production (log-transformed) per patch and mean seed mass per patch in 2003. We also tested for correlations between *Medicago* density, *Lotus* density, and *H. brunneipennis* abundance (PROC CORR; SAS Institute 2000).

Experimental removals of Medicago and herbivores

Comparisons of naturally invaded and uninvaded patches may be confounded by other environmental differences that are correlated with invasion status. Therefore, we used a two-by-two factorial experimental design in which we manipulated both *Medicago* presence and insect presence to ascertain the effect of *Med-*

icago on *Lotus* herbivory rates, the direct competitive fitness effect of *Medicago* on *Lotus*, and the herbivore-mediated indirect fitness effect of *Medicago* on *Lotus*. This experiment consisted of four treatments: (1) *Medicago* present, insects present; (2) *Medicago* present, insects removed; (3) *Medicago* removed, insects present; and (4) *Medicago* removed, insects removed. In the absence of insects, we attribute any effects of *Medicago* on *Lotus* fitness to direct competitive effects. In contrast, in the presence of insects, both direct and herbivore-mediated indirect effects of *Medicago* are present.

Plot design.—The experiment was repeated over two years (2002 [$N = 6$ replicates] and 2003 [$N = 11$ replicates]). Treatments were imposed on 3×3m plots established in four invaded patches in 2002 and in three invaded patches in 2003.

Herbivore treatment.—We manipulated herbivore presence by spraying plots with the generalist insecticide Sevin (concentration = 5.2 mL/L; Bayer CropScience, RTP, North Carolina, USA) or an equal amount of water as a control. Insecticide treatments were applied every two to four weeks from February to April, the period of most intense weevil folivory. To ensure that the generalist insecticide Sevin did not directly affect *Lotus* fitness, we conducted a growth chamber experiment (for methods see Appendix A). Insecticide treatments did not directly affect plant growth (with Sevin, 81.91 ± 3.71 leaves; controls, 88.06 ± 3.70 leaves [mean ± SE]; $F_{1, 101} = 1.53$, $P = 0.22$). Because leaf number and seed production are correlated in this annual species ($R = 0.57$, $P < 0.0001$) and because the mean leaf number of plants receiving Sevin was less than that of controls, any direct effects of Sevin on *Lotus* fitness would likely make our tests for indirect effects conservative.

Medicago treatment.—We manipulated *Medicago* presence by removing all *Medicago* seedlings from each *Medicago*-removal plot. Between 1023 and 19 700 seedlings were removed from each *Medicago*-removal plot (5020 ± 1057 seedlings). Initial removals were performed in December and early January immediately after the first bout of germination. A second round of removal was performed in late January and early February to remove later germinating individuals. While some individuals were missed, our *Medicago*-removal treatments were very effective in reducing aboveground biomass of *Medicago* (*Medicago* removal, 2.21 ± 7.05 g/m²; control 54.72 ± 31.57 g/m²). Although we removed large numbers of *Medicago* seedlings, they were tiny (0.02 g; cotyledon or first true leaf stage), and we did not notice that their removal caused significant soil disturbances. Nonetheless, in 2002 we also included a third removal treatment as a control, where we paired *Medicago*-removal plots with removal control plots in which we removed an equal number of "other" (not *Medicago* or *Lotus*) seedlings. Because there were never significant differences between the

removal control plots and the unweeded control plots in MANOVAs including herbivory measures ($F_{3,8} = 1.10$, $P = 0.40$) or fitness measures ($F_{2,9} = 1.72$ $P = 0.23$), nor in any univariate tests on individual response variables, this labor-intensive treatment was discontinued in 2003 to allow for increased replication of the *Medicago* removal and control treatments.

Treatment effects on the plant assemblage.—To determine whether treatments influenced the biomass of other plant species in the experimental plots, we collected three biomass samples per plot in April 2003 by removing all aboveground biomass of plants in an 11 cm diameter circle. Samples were sorted into rough functional groups: *Medicago*, *Lotus*, other legumes, forbs, and grasses, and dried at 60°C. We used the MANOVA option in PROC GLM (SAS Institute 2000) to determine whether our *Medicago* removal and insecticide treatments differed in biomass of nontarget plant species. Response variables included legume (excluding *Medicago* and *Lotus*), forb, and grass dry masses. *Medicago* removal and insecticide treatments were included as fixed factors, and patch and all interactions with patch were included as random factors. Additional univariate analyses were performed on *Medicago*, *Lotus*, and total biomass dry masses. *Medicago* and *Lotus* dry masses were log-transformed to improve normality.

Treatment effects on Lotus.—Thirty *Lotus* plants occurring in or near the center square meter of each plot were marked at the seedling stage. These plants were censused for folivory, bud-galling, and disease incidence (2003 only). All seeds from each experimental plant were collected after maturity so that seed predation and lifetime fertility could be estimated. Foliar, bud-galling, and seed predation damage were estimated as the proportion of leaflets, buds, or seeds (respectively) that had been damaged per plant. Disease incidence was scored as present/absent based on symptomatic spotting on leaflets, and the proportion of plants per plot exhibiting symptoms was our response variable in all analyses. Fitness variables included the number of undamaged seeds produced and mean seed mass. Flowering date was also recorded.

Data were analyzed with two MANOVAs using PROC GLM (SAS Institute 2000). The first model tested for treatment effects on damage from natural enemies; response variables were average folivory, bud-galling, seed predation, and disease incidence (2003 data only) per plot. A second MANOVA tested for treatment effects on *Lotus* fitness with mean seed number and mean seed mass per plot as response variables. *Medicago* removal and insecticide treatments were included as fixed factors, and patch and all interactions with patch were included as random factors using the random statement and the /TEST option (SAS Institute 2000). Folivory, bud-galling, and seed predation were all angular-transformed, and disease incidence and seed number were log-transformed to improve normality and reduce heterogeneity of variances. All analyses
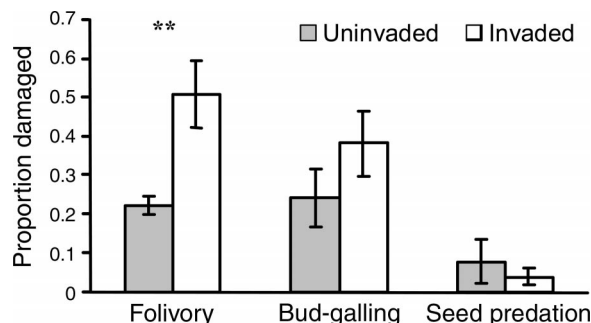
FIG. 1. Herbivore damage to *Lotus* plants growing in patches naturally invaded (open bars) or uninvaded (solid bars) by *Medicago* in 2003. Bars indicate mean ± SE. Significant differences in univariate tests are indicated as follows: **$P < 0.01$.

were performed on plot means because the frequent zero values for individual plant subsamples caused large deviations from normality when nested analyses on individual plants were used. If significant effects were observed in the MANOVAs, subsequent univariate ANOVAs were conducted for each response variable. Despite transformations, some variables deviated from normality and/or exhibited heterogeneous variances; however, analyses on ranks were not qualitatively different from the analyses performed on transformed variables, so only the transformed results are presented here. Results for both years of the *Medicago*-removal experiment are presented independently because initial models that included year as a factor revealed significant interactions with year. Additionally, in 2002, disease incidence data were not collected, and small sample sizes prevented analysis of higher order interactions with patch. Initial analyses of the 2003 data also included covariates from the vegetation biomass samples (see *Treatment effects on the plant assemblage* for more detail): total dry mass, forb dry mass, grass dry mass, and legume dry mass. For the natural enemies MANOVA, no covariates were significant ($P > 0.2$), and all covariates were dropped from the model to increase power. For the fitness MANOVA, only total plant biomass was marginally significant ($P = 0.069$) and met the assumption of homogeneous slopes, and, therefore, was included in the MANOVA and in subsequent univariate analyses of seed mass and seed number.

Treatment effects on Lotus *flowering time.*—A preliminary analysis revealed that there may be interactions between the various herbivores and that these interactions may be mediated by *Lotus* flowering time. We performed an ANOVA to determine how *Medicago* removal and insecticide treatments influenced flowering time over both years of study. *Medicago* removal and insecticide treatments were included in the model as fixed factors, and patch and all interactions with patch were included as random factors. Additionally, because we expected bud-gallers to be responsive to

flowering phenology, a regression was performed to determine the effect of flowering time on rates of bud-galling (PROC REG; SAS Institute 2000). The model included both linear and quadratic components of flowering time as predictor variables and proportion of buds galled as the response variable. The parameter estimates from this model were then used to predict how changes in flowering time might affect bud-galling rates.

RESULTS

Observational study: does natural Medicago *invasion affect herbivory on, or fitness of,* Lotus?

Medicago presence significantly affected herbivory on the native *Lotus* (MANOVA; Appendix B). Subsequent univariate analyses on folivory, bud-galling, and seed predation indicated that *Lotus* individuals in patches invaded by *Medicago* received approximately twice the foliar damage as *Lotus* in uninvaded patches (Fig. 1, Appendix B). This result was consistent across three years of observations (in 2001, uninvaded 0.16 ± 0.019, invaded 0.29 ± 0.072; in 2002 uninvaded 0.24 ± 0.025, invaded 0.37 ± 0.052; in 2003, uninvaded 0.22 ± 0.025, invaded 0.51 ± 0.086). Additionally, densities of the predominant folivore *H. brunneipennis* observed feeding on *Lotus* increased linearly with increasing *Medicago* density (Fig. 2), indicating that *Medicago* may be increasing herbivory rates on the native *Lotus* by increasing the density of this shared enemy. In contrast to the strong effect of *Medicago*, *Lotus* density had no effect on folivore density (Fig. 2). In contrast to folivory by *H. brunneipennis*, bud-galling and seed predation were not significantly different in invaded vs. uninvaded patches (Fig. 1, Appendix B). *Lotus* individuals produced significantly more (302%) seed in uninvaded vs. invaded patches, but mean seed mass did not differ with invasion status (Fig. 3).
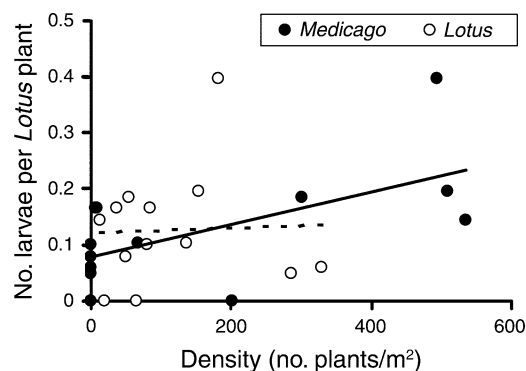

FIG. 2. Average number of *Hypera brunneipennis* larvae feeding on *Lotus* as a function of *Medicago* density (solid line) or *Lotus* density (dashed line). *Medicago* density was significantly correlated with weevil density ($R^2 = 0.37$, $P = 0.026$). Each point represents one patch.
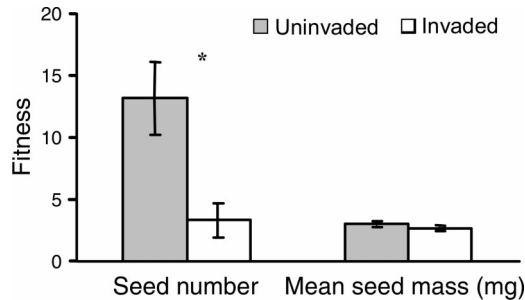
FIG. 3. Individual fitness of *Lotus* growing in patches invaded (open bars) or uninvaded (solid bars) by *Medicago*. Bars indicate mean ± SE. Significant differences in univariate tests are indicated as follows: *$P < 0.05$.

Experimental removals of Medicago *and herbivores*

Effects on natural enemies.—*Medicago* removal and insecticide treatments significantly affected attack by natural enemies (Appendix C). Univariate analyses on folivory levels revealed consistent trends towards decreased folivory on *Lotus* in the *Medicago*-removal plots over both years of the study; however, this difference was only significant in 2003 (Fig. 4A, E). Rates of bud-galling and seed predation varied substantially across the two years of the study. In 2002, both bud-galling and seed predation rates were high, and *Medicago* removal increased attack on *Lotus* from both of these herbivores (Fig. 4B, C). In contrast, in 2003, bud-galling and seed predation were low, and neither herbivore responded significantly to *Medicago* removal or insecticide treatments (Fig. 4F, G). Disease incidence (recorded in 2003 only) was reduced in both *Medicago* removal and insecticide treatments; however, these differences were not statistically significant (Appendix C).

Effects of Medicago *on* Lotus *flowering time.*—In 2002, in the presence of insects, *Lotus* individuals in the *Medicago* removal plots flowered approximately two weeks later than those in the *Medicago* presence control plots and in the surrounding population (Fig. 4D). While we can only speculate as to why this effect occurred only in the *Medicago*-removal treatment, observational evidence suggests that this shift in flowering time could be responsible for the markedly increased rates of bud-galling in these plots. Based on data relating flowering time to bud-galling, this two-week delay in flowering time would be expected to result in increased bud-galling (105% increase predicted from the equation describing the relationship between flowering time and bud-galling: percentage of buds galled = $1.27 - 0.102$(flowering date) + 0.00274 (flowering date)^2); this magnitude of effect is consistent with what we observed in the experimental plots. Thus, the delayed flowering time may explain some of the observed increase in bud-galling in the *Medicago*-removal plots relative to the control plots in 2002. In 2003, there were no significant treatment effects on flowering time and a corresponding lack of effect on

bud-galling and seed predation, providing additional evidence supporting delayed flowering time as a mechanism underlying the effects on late season herbivory in 2002 (Fig. 4H).

Effects on Lotus *fitness.*—*Medicago* removal and insecticide treatments both significantly increased *Lotus* fitness (Fig. 5, Appendix D); however, the mechanism underlying the *Medicago* removal effect varied between years. We calculated the effects of *Medicago* removal within each insecticide treatment separately by using the SLICE option in PROC GLM (SAS Institute 2002). This analysis revealed that *Medicago* removal only increased *Lotus* fitness in the absence of insects (insecticide plots) in 2002 (Fig. 5A, B). In the absence of herbivores, we attribute negative effects of *Medicago* on *Lotus* fitness to the competitive effect of *Medicago*. In contrast, in plots where insects were present, *Medicago* removal both decreased the competitive
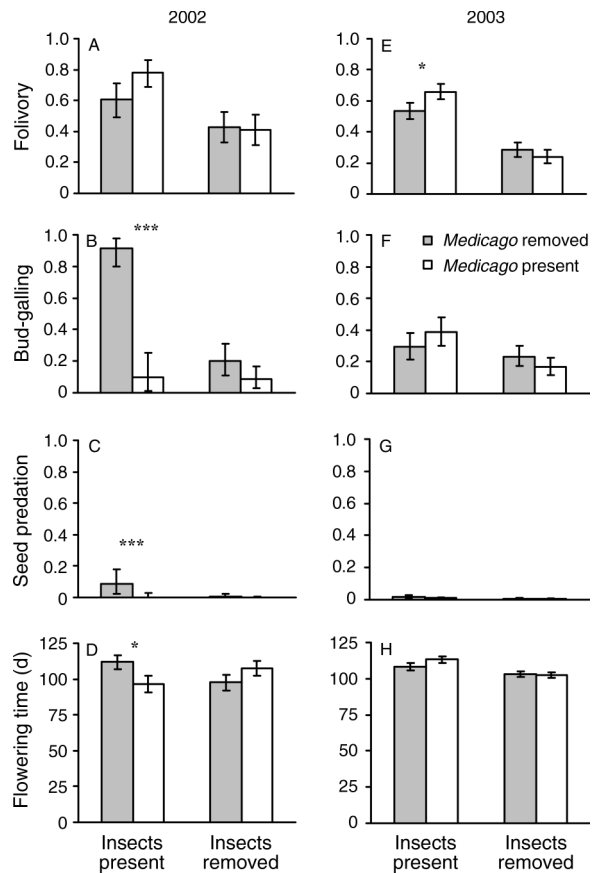

FIG. 4. Herbivory (proportion of plant material damaged) on, and flowering times (day 1 = January 1) of, *Lotus* plants growing in the *Medicago*-removal and control plots in the presence and absence of insects in (A–D) 2002 and (E–H) 2003. Results are shown for (A, E) folivory, (B, F) bud-galling, (C, G) seed predation, and (D, H) flowering time. Bars indicate back-transformed means ± SE. Significant differences between *Medicago* removal and control plots in the presence and absence of insecticide are indicated as follows: *$P < 0.05$; ***$P < 0.001$.
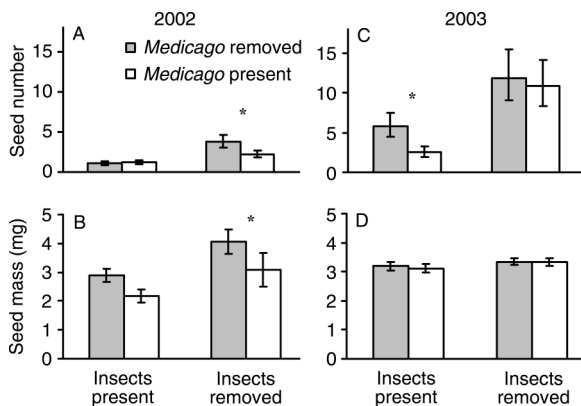
FIG. 5. Fitness of *Lotus* individuals growing in the *Medicago*-removal and control plots in the presence and absence of insects in (A, B) 2002 and (C, D) 2003. Bars indicate back-transformed means ± SE. Significant differences between *Medicago* removal and control plots in the presence and absence of insecticide are indicated as follows: *$P < 0.05$.

effect of *Medicago* and decreased folivory on *Lotus*; however, *Lotus* also exhibited delayed flowering time that caused increased rates of bud-galling and seed predation. These dual direct and indirect effects (release from competition and from folivory, but increased flower and fruit predation) resulted in the *net* effect that *Medicago* removal did not affect *Lotus* fitness in the presence of insects in 2002. Thus, in 2002, *net* fitness effects due to competition with *Medicago* were stronger than the *net* fitness consequences of herbivore-mediated indirect effects, despite the fact that herbivory rates were very high. The term "net" is used because indirect effects were strong, but they consisted of multiple effects that were opposite in direction.

In contrast, in 2003, the net fitness consequences of herbivore-mediated indirect effects exceeded the direct competitive effect. *Medicago* only significantly decreased *Lotus* fitness in the presence of herbivores (Fig. 5C, D). We interpret this result as *Medicago* decreasing *Lotus* fitness indirectly by boosting folivory rates. We note that in 2003, *Medicago* removal had no effect on *Lotus* flowering time, and there was also a corresponding lack of effect on bud-galling and seed predation (Fig. 4F, G). Furthermore, bud-galling and seed predation rates were relatively low in 2003.

Treatment effects on the plant assemblage.—The effects of the *Medicago* removal and insecticide treatments on *Lotus* herbivory and fitness likely were not due to indirect effects on *Lotus* through changes in the biomass of other plant species. Treatments did not significantly differ in forb biomass, grass biomass, legume biomass, or total biomass (Appendix E). Additionally, when these biomass variables were included as covariates, all were nonsignificant and did not qualitatively change the results. Also recall that direct effects of Sevin on *Lotus* growth were not significant, and were, if anything, suppressive.

DISCUSSION

This study provides strong evidence that the exotic plant species *Medicago polymorpha* affects the fitness of the native plant *Lotus wrangelianus* both directly and indirectly. Furthermore, the net fitness consequences of direct vs. indirect effects vary among years, reflecting temporal variation in the abundance and composition of the herbivore assemblage. In 2002, the net fitness effects of *Medicago* on the native *Lotus* were largely direct; *Medicago* presence only significantly decreased *Lotus* fitness in the absence of insects (Fig. 5A); however, this result also reflects the fact that, in 2002, multiple herbivore-mediated indirect effects were opposite in direction. *Lotus* in the *Medicago*-removal plots experienced lower rates of folivory, but much greater rates of bud-galling and seed predation. Thus, though independently strong, herbivore-mediated indirect effects had minimal net fitness consequences in this year. In contrast, in 2003, the fitness effects of *Medicago* on the native *Lotus* were entirely indirect; *Medicago* presence only decreased *Lotus* fitness in the presence of insects (Fig. 5C). The herbivore-mediated indirect effects observed in 2003 likely result because *Medicago* boosts densities of the common folivore *H. bruneipennis*, thus increasing foliar damage to the native *Lotus*, while having minimal impacts on other members of the herbivore community.

Flowering time appears to mediate interactions between *Lotus* and late season herbivores. In 2002, under ambient herbivory, *Lotus* flowered later when *Medicago* was removed. The delay in flowering was positively related to damage by bud-gallers, suggesting that flowering phenology may be an important mechanism driving indirect effects of *Medicago* on *Lotus*. In contrast, in 2003, *Medicago* removal had no effect on flowering time, and also no effect on bud-galling or seed predation. Thus, the only effect of *Medicago* removal on herbivores was to decrease weevil folivory rates. The increased folivory experienced by *Lotus* in the presence of *Medicago* then lacked any opposing effect from the late season herbivores and translated into observable, negative herbivore-mediated indirect effects on *Lotus* fitness.

Our results suggest that the fitness effects of apparent competition among plant species can be mediated by effects on plant phenology and by other herbivorous insects in the community. In this specific case, it appears that variation in the net fitness consequences of direct and indirect effects might be explained in part by interactions of plant phenology and early season folivory with later season herbivory rates. Such complexity makes the prediction and measurement of indirect effects extremely difficult. However, this complexity also highlights the importance of indirect effects. Strong indirect effects, like the associational susceptibility observed here, may cascade through interaction webs to affect many community members.

This study emphasizes the fact that introduced species, though often thought to have ''escaped'' their herbivores (but see Maron and Vila 2001, Louda and Rand 2002, Agrawal and Kotanen 2003, Colautti et al. 2004), can still have important herbivore-mediated indirect effects on community members. These effects occur when introduced plants are used by oligophagous or generalist native herbivores, and they can also be pronounced if, contrary to popular wisdom, introduced herbivores accompany their introduced host to the novel range. In this California system, an exotic herbivore has invaded many of the same areas as the exotic host plant. However, instead of limiting the success of *Medicago*, the insect herbivores have provided an alternative avenue for negative impacts of the invader on the native community. This situation may be analogous to the nontarget effects of introduced biocontrol agents and may result in strong demographic effects (Louda et al. 1997, Louda 2000, Rose et al. 2005), and potentially evolutionary consequences for native species (Rose et al. 2005). For example, in this system, indirect effects of introduced species on natives mediated by shared herbivores alter patterns of natural selection on plant defense traits in the native species (J. Lau, *unpublished manuscript*).

With this research, we have shown that an exotic plant species can affect a co-occurring native plant species both directly and indirectly via effects on a shared herbivore. In addition, we revealed community-wide effects of the invasion via changes in the herbivore assemblage on the native plant. Thus, while indirect effects among exotics and natives may be less obvious than many direct effects, they can have important ramifications on the ecology, and potentially the evolution, of the invaded community.

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APPENDIX A

Experimental methods (direct fitness effects of the insecticide Sevin) are available in ESA's Electronic Data Archive: *Ecological Archives* E086-163-A1.

APPENDIX B

Summary results for a MANOVA comparing herbivory on *Lotus* in patches that were or were not invaded by *Medicago* are available in ESA's Electronic Data Archive: *Ecological Archives* E086-163-A2.

APPENDIX C

A summary of results for a MANOVA testing the effects of *Medicago* removal, insecticide, and *Lotus* patch on rates of natural enemy attack on *Lotus* is available in ESA's Electronic Data Archive: *Ecological Archives* E086-163-A3.

APPENDIX D

A summary of results for a MANOVA testing the effects of *Medicago* removal, insecticide, and patch on *Lotus* fitness is available in ESA's Electronic Data Archive: *Ecological Archives* E086-163-A4.

APPENDIX E

A summary of results for a MANOVA testing the effect of *Medicago* removal and insecticide treatments on the biomass of three plant functional groups is available in ESA's Electronic Data Archive: *Ecological Archives* E086-163-A5.