INDIRECT FACILITATION: EVIDENCE AND PREDICTIONS FROM A RIPARIAN COMMUNITY

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Abstract. Indirect facilitation occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect. Although theory predicts that these interactions may be common in assemblages of three or more competitors, experimental studies of this process are rare. Here, I report a study of a northern California riparian community, where I tested the hypothesis that the sedge *Carex nudata* had direct competitive effects on other plant species, as well as indirect facilitative effects, by suppressing a second competitor, the common monkey-flower *Mimulus guttatus.* Results of a field experiment, in which I manipulated the presence of *Carex* and *M. guttatus* in a factorial design, uncovered three qualitatively different interactions between *Carex* and three target species. I found evidence of indirect facilitation for the liverwort *Conocephalum conicum,* such that *Carex* ''facilitated'' *Conocephalum* in the presence of *M. guttatus,* while *Carex* competed with *Conocephalum* in the absence of *M. guttatus.* Plant distribution patterns supported the widespread occurrence of this interaction. *Carex* also had an indirect positive effect on the scarlet monkey-flower *M. cardinalis,* though the magnitude of this effect was similar to direct *Carex* competition. Lastly, *Carex* had no influence on the moss *Brachythecium frigidum.* The mechanisms underlying the plant interactions in this study are discussed and incorporated into a general hypothesis that indirect facilitation among competitors is most important in assemblages of species that vary in competitive mechanism.

Key words: Carex; *competition and facilitation; facilitation in plant communities; indirect effects;* Mimulus; *plant competition; riparian plant communities; species diversity.*

INTRODUCTION

While the influence of biotic interactions on species diversity is well appreciated (Huston 1994, Rosenzweig 1995), the converse, how diversity influences biotic interactions is only beginning to be explored. Understanding these community-level consequences of diversity is required for differentiating the ecological forces that structure diverse vs. species-poor communities and predicting the impact of species invasion or loss. Models of diffuse competition, or ''competition by a constellation of species'' (sensu MacArthur 1972), provide rare insights into how the intensity of species interactions changes as the number of species in a community varies (MacArthur 1972, Pianka 1974, Lawlor 1979, Bender et al. 1984, Case 1991, Stone and Roberts 1991). While the original models suggested that increased species number led to more intense competition (MacArthur 1972, Pianka 1974), these studies did not incorporate the numerous indirect interactions that emerge when species are added. Later modeling efforts, accounting for indirect interactions, concluded that increased species number could reduce the intensity of competition, or even lead to facilitation (Levins 1975, Levine 1976, Lawlor 1979, Davidson 1980, Yodzis

1988, Vandermeer 1990, Case 1991, Stone and Roberts 1991).

One of the most influential examinations of how community processes are modified by species addition or loss was provided by the three-species model of Stephen Levine (1976). Levine explored how the addition of a third competitor to a system of two competing species could alter the interaction between these species from competition to facilitation. The model suggested that three species not only compete, but also indirectly facilitate one another via suppressing a shared competitor (Fig. 1a). Levine pointed out that, when the direct competitive effect of one species on another was weaker than the indirect positive effect, a net facilitative interaction resulted from a system composed entirely of competitors. Other indirect facilitations can be mediated by shared consumers or pathogens or by competing prey (Levine 1976, Vandermeer et al. 1985). I will use ''apparent facilitation'' (sensu Davidson 1980) to refer specifically to interactions mediated by a shared competitor. Obtaining empirical support for apparent facilitation has proven challenging because of the difficulty in separating out direct and indirect effects that oppose one another (Brown et al. 1986). Probably for this reason, few studies have explicitly examined these interactions in the field (Davidson 1980, 1985, Culver 1982, Miller 1994).

Empirical studies of indirect effects among plants

FIG. 1. (a) General interaction diagram for three competing species, showing all possible direct competitive interactions, and the indirect facilitative effect of A on B, mediated by the suppression of C. Direct interactions are indicated by solid lines and indirect interactions by dashed lines. (b) Diagram of plant interactions examined in this study. This diagram does not show the direct positive effects of *Carex* by providing habitat for all of these plants. See *Methods* for details.
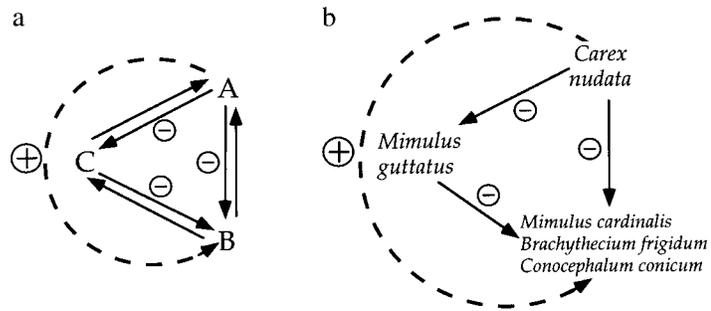
are particularly rare (Miller 1994, Callaway and Pennings 1998). This may be attributed to the prevalence of strong direct interactions among plants (Goldberg and Barton 1992), yet it is precisely these potent direct interactions that lead to strong indirect effects among competitors (Davidson 1985). Furthermore, plants undoubtedly influence one another via their effects on herbivores, parasites, pathogens, and decomposers; and, while, models of these trophically mediated interactions (particularly, apparent competition) are well recognized, empirical studies are few (Clay 1990, Connell 1990, Goldberg 1990). For this reason, our understanding of when indirect interactions between plants can or cannot be ignored is largely undeveloped, though the importance of these interactions in communities is potentially large.

Here, I report the results of a field experiment designed to examine the strength of indirect facilitation among plant species in a riparian community. In particular, I explore the hypothesis that the torrent sedge *Carex nudata* modifies the competitive effects of the common monkey-flower *Mimulus guttatus* on three other common plant species along a northern California river (Fig. 1b). I evaluate indirect facilitation in a simple field experiment where I vary the abundance of *Carex* and *M. guttatus* in a factorial design, thus allowing me to compare the effects of *Carex* on three target species, with and without *M. guttatus.*

METHODS

Study system

Large, discrete, tussocks formed by the torrent sedge *Carex nudata* W. Boott line the channels of many northern California streams. Along the South Fork Eel river in northern California, USA (39°44′ N, 123°39′ W), *Carex* tussocks average 30 cm in diameter, are densely covered with stems from late spring to fall, and occupy nearly one-third of the stream channel exposed by midsummer (J. Levine, *unpublished data*). *Carex* appears to have direct positive effects on other plant species. Of the >60 plant species occurring in this habitat, most are found growing almost exclusively on *Carex* tussocks, rooting into the accumulated sediment. By growing on tussocks, these small perennials obtain a stable refuge from scouring winter floods (J. Levine, *unpub-*

lished data). This direct positive effect of *Carex* is clearly important, but here I examine the indirect facilitative effects of *Carex,* mediated by its competitive interactions. These competitive effects arise because the associated species grow within the dense *Carex* root mat and thick vegetation.

The common monkey-flower, *Mimulus guttatus* DC, the scarlet monkey-flower, *M. cardinalis* Benth., the liverwort *Conocephalum conicum* (L.) Dum., and the moss *Brachythecium frigidum* (C Mull.) Besch. are among the most common species rooting into tussocks, with >90% of their individuals in this habitat found on *Carex* tussocks (J. Levine, *unpublished data*). In this system, *M. guttatus* grows rapidly and primarily prostrate, and its dense stoloniferous growth is known to cover areas nearly a square meter in three to four months (Vickery 1978, Ritland and Ritland 1989). I observed that these dense, stoloniferous *M. guttatus* clones only developed on tussocks where *Carex* stems were sparse, and that these tussocks were typically devoid of other plant species.

This observation lead to the hypothesis, that *Carex,* although directly competing with three other species, *M. cardinalis, Brachythecium,* and *Conocephalum,* could also have a strong indirect positive effect on these species, by suppressing the more potent competitor, *M. guttatus* (Fig 1b). This hypothesis was evaluated in an experiment where I transplanted *M. cardinalis, Brachythecium,* and *Conocephalum* into *Carex* tussocks of several experimental densities, with and without *M. guttatus* in a factorial design.

Field experiment

In late April 1997, I randomly located 174 *Carex* tussocks spaced over four sites along a 1.5-km stretch of the South Fork Eel. Half of the selected tussocks were thinned to 10 stems/100 cm². Some regrowth occurred, so stem densities were maintained bimonthly. I quantified *Carex* stem density in one quarter of each of the treatments on 26 September. In addition, between the hours of 1130 and 1430 on 27 August, a clear day, I measured light availability in randomly selected full ($n = 20$) and thinned ($n = 24$) tussocks, using a hand-held LI-COR PAR meter (LI-COR, Lincoln, Nebraska). On 14 May, into a randomly selected subset of the
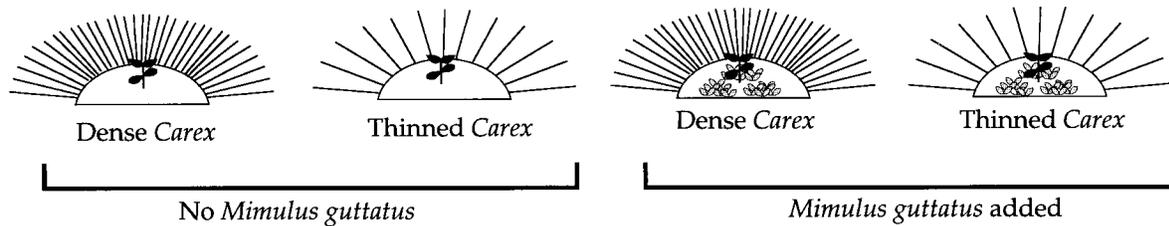
FIG. 2. Design of the experiment used to evaluate the direct and indirect effects of *Carex* on *Conocephalum conicum*, *Mimulus cardinalis*, and *Brachythecium frigidum*. The dark colored plant on each tussock symbolizes a *M. cardinalis* transplant, but the same basic design was used for the other two target species. See *Methods* for details.

thinned ($n = 28$) and dense ($n = 28$) tussocks, I transplanted a background of *M. guttatus* (Fig. 2). Three *M. guttatus* clones of five to six ramets each, collected from a common site were planted onto each tussock positioned such that each transplant was at the corner of an equilateral triangle with sides of 10 cm. All *M. guttatus* backgrounds and other transplanted species were placed on the downstream side of the tussock close to its upper surface, away from other plants. Three of these *M. guttatus* backgrounds in thinned *Carex* vegetation were completely defoliated by larvae of the buckeye *Junonia coenia,* so these tussocks were excluded from further analysis in this study. In fact, the original design included a treatment with complete *Carex* vegetation removal, but it was impossible to *establish M. guttatus* backgrounds in this treatment, due to intense herbivory by *Junonia. Junonia,* however, did not eat any of the other species in this experiment.

I randomly assigned transplants of *M. cardinalis, Brachythecium,* and *Conocephalum* into the four combinations of *Carex* and *M. guttatus* (Fig. 2). All transplanting was done from 21–23 May, the start of the natural growing season for these species along the Eel. For *M. cardinalis,* I transplanted individuals into dense ($n = 13$) and thinned ($n = 13$) *Carex* with *M. guttatus* backgrounds, positioned in the center of the triangle formed by the *M. guttatus.* In addition, they were transplanted into dense ($n = 19$) and thinned ($n = 19$) *Carex* without *M. guttatus* backgrounds. I collected the *M. cardinalis* individuals by harvesting small ramets with two to four leaves from two large populations in early March and initially rearing them in a greenhouse at the University of California, Berkeley. Soil was kept inundated for the first several weeks, until rooting began. *Brachythecium* and *Conocephalum* were transplanted directly into the experiment as 3.5 cm wide × 2 cm deep plugs with 95–100% cover of the species. These two bryophytes were transplanted onto the same tussocks far enough apart to prevent contact. For these species, I modified the *M. guttatus* background such that it was two equilateral triangles sharing one corner. Both species were transplanted into dense ($n = 20$) and thinned ($n = 20$) tussocks without *M. guttatus,* and into dense ($n = 15$) and thinned ($n = 15$) tussocks with *M.*

guttatus. Transplant mortality was <10% for all species.

Forty of the 174 randomly located *Carex* tussocks were used to examine the direct effect of *Carex* density on *M. guttatus.* Onto dense ($n = 20$) and thinned ($n = 20$) *Carex* tussocks, I transplanted *M. guttatus* clones, five to six ramets in size. Over the course of the experiment, two of these plants contained a single *Junonia* larva that left or died prior to significant damage to the plant. Nine of the *M. guttatus* transplants, all in thinned *Carex* vegetation, were completely defoliated by *Junonia.* Since plots with defoliated *M. guttatus* backgrounds were not used in the analysis, neither were these nine. Current research is examining the effects of *Carex* density on the intensity of *Junonia* herbivory.

Transplants of all species were sampled nondestructively on 28 September, the end of the natural growing season, just prior to the first fall flood event. I recorded one or two measurements of size that varied by species: for *M. cardinalis,* node number; for *M. guttatus,* ramet number; for *Conocephalum,* area; and for *Brachythecium,* area and branch number. Biomass was estimated by means of regressions compiled by nondestructively sampling 80–100 naturally occurring nonmanipulated plants of each species and then harvesting these plants for dry mass. These natural plants were collected from the same 1.5-km stretch of river as the experiment, over the full range of light environments. *M. cardinalis* individuals are found less frequently than the others, so I harvested only 28 individuals from two of the largest populations.

Sampling of field patterns

To determine if the interaction among *Carex, M. guttatus,* and *Conocephalum,* was reflected in plant distribution patterns, I quantified the co-occurrence of these species over a 4-km stretch of the Eel River. In early fall, I sampled 581 *Carex* tussocks, recording the density of sedge stems in a randomly located 100-cm^2 subsample, and the percent of each tussock surface covered by *M. guttatus* and *Conocephalum.*

Statistical analysis

The relationships between the nondestructive measures of plant size and aboveground biomass were eval-

TABLE 1. Regression equations used to calculate species biomass in the experiment.

Species	Regression equation	r	P	N
Mimulus guttatus	Mass $= 0.0007 + 0.0060$(Ramet no.)$^{1.2}$	0.921	0.001	80
Brachythecium†	Mass $= -0.0180 + 0.0023$(Area (cm^2)) $+ 0.0026$(Branch no.)	0.931	0.001	83
Mimulus cardinalis	Mass $= -0.1800 + 0.0390$(Node no.)	0.966	0.001	28
Conocephalum	Mass $= 0.0110 + 0.0270$(Area (cm^2))	0.954	0.001	98

† A multiple regression model was used to correlate Area and Branch no. to Mass.

uated with linear regression (Table 1). For *M. guttatus,* ramet number raised to the 1.2 power produced the best fit to the data. For *Brachythecium,* I used multiple regression, since there were two nondestructive measures. Regression results indicated that the nondestructive measures of plant size were highly correlated with the biomass of each species and were used to predict biomass for each of the transplants at the end of the experiment (Table 1). These relationships also provided estimates of the initial mass of the transplants (*M. cardinalis,* 0.11 g; *Conocephalum,* 0.29 g; *Brachythecium,* 0.06 g; and *M. guttatus,* 0.07 g).

To assess the effects of the *Carex* manipulations on *Carex* stem density and light availability, I used two-way ANOVA, blocked by site, and tested for the effects of *Carex* density, *M. guttatus,* and the interaction. I used this same ANOVA to evaluate the direct and indirect effects of *Carex* and *M. guttatus* on the three target species. For untransformed data, the interaction term was of particular interest because it assessed the indirect effect (Wootton 1994). If only direct competitive effects were important (the null hypothesis), then the combined effects of *Carex* and *M. guttatus* would be additive, yielding significant main effects of *Carex* and *M. guttatus,* but a nonsignificant interaction term. If indirect effects were important, however, then the effect of *Carex* would depend on the presence of *M. guttatus,* yielding a significant interaction. Finally, I tested for the direct effects of *Carex* density on the biomass of *M. guttatus* with one-way ANOVA, blocked by site.

To evaluate field patterns, I compared *Carex* stem density, *Conocephalum* cover, and percent occurrence of *Conocephalum* on tussocks dominated by *M. guttatus* (>50% cover) to those where *M. guttatus* was present but sparse (<25% cover). The difference between *Carex* stem density on these two types of tussock was tested with a Mann–Whitney *U* test. The correlation between *Carex* density and *M. guttatus* cover, if present, was evaluated with Spearman rank correlation. A Mann–Whitney *U* test was also used to examine the effect of *M. guttatus* abundance on *Conocephalum* cover. The effect of *M. guttatus* on the percent occurrence of *Conocephalum* was evaluated with a χ^2 test. Finally, the relationship between *Carex* density and *Conocephalum* cover, in the absence of *M. guttatus,* was examined with Spearman rank correlation. All statistical analyses were performed with SYSTAT 7.0 (SPSS).

RESULTS

Carex *manipulations effectively reduce* Carex *stem density and increase light availability*

Thinning *Carex* decreased stem density 60%, from a mean ± 1 SE of 25.89 ± 0.77 to 10.10 ± 0.83 stems/100 cm^2 ($F_{1,32} = 232.867$, $P = 0.001$). Thinning also increased light availability 10-fold from 50.05 ± 25.98 to 505.98 ± 28.80 µmol photons·m^{-2}·s^{-1} ($F_{1,37} = 138.056$, $P = 0.001$). Light was not measured below the *M. guttatus* canopy, so I could not detect any effects of this species on PAR. Block, *M. guttatus,* and the *Carex* × *M. guttatus* interaction effects were nonsignificant for both stem density (Block, $F_{3,32} = 0.040$, $P = 0.989$; *M. guttatus,* $F_{1,32} = 0.449$, $P = 0.508$; and *Carex* × *M. guttatus* interaction, $F_{1,32} = 0.063$, $P = 0.934$) and light availability (Block, $F_{3,37} = 1.179$, $P = 0.331$; *M. guttatus,* $F_{1,37} = 0.226$, $P = 0.637$; and *Carex* × *M. guttatus* interaction, $F_{1,37} = 0.331$, $P = 0.569$).

Evidence for indirect facilitation, varying by species

For two of the three species examined, *Carex* not only competed with, but also indirectly facilitated these plants by suppressing a shared competitor. This competitor, *M. guttatus,* had one-third the biomass when grown under dense *Carex* as compared with experimentally thinned *Carex* (Fig. 3a, Table 2). This positive indirect effect of *Carex,* combined with direct *Carex* competition, yielded three qualitatively different interactions between *Carex* and each of the three target species, *Conocephalum, M. cardinalis,* and *Brachythecium.*

The interaction between *Carex* and *Conocephalum* was an indirect facilitation, whereby dense *Carex* reduced competition by *M. guttatus. Carex* "facilitated" *Conocephalum* in the presence of *M. guttatus,* but this interaction was mediated by a reduction in *M. guttatus* competition. In the absence of *M. guttatus,* thinning *Carex* doubled liverwort biomass, but with *M. guttatus* present, thinning *Carex* halved liverwort biomass, as *M. guttatus* increased three-fold in response to thinning (Fig. 3a, b). This alteration of the interaction between *Carex* and *Conocephalum* by *M. guttatus* was reflected in the highly significant interaction term in the ANOVA (Table 2).

Carex also had an important indirect positive effect on *M. cardinalis,* but for this species, the indirect effect
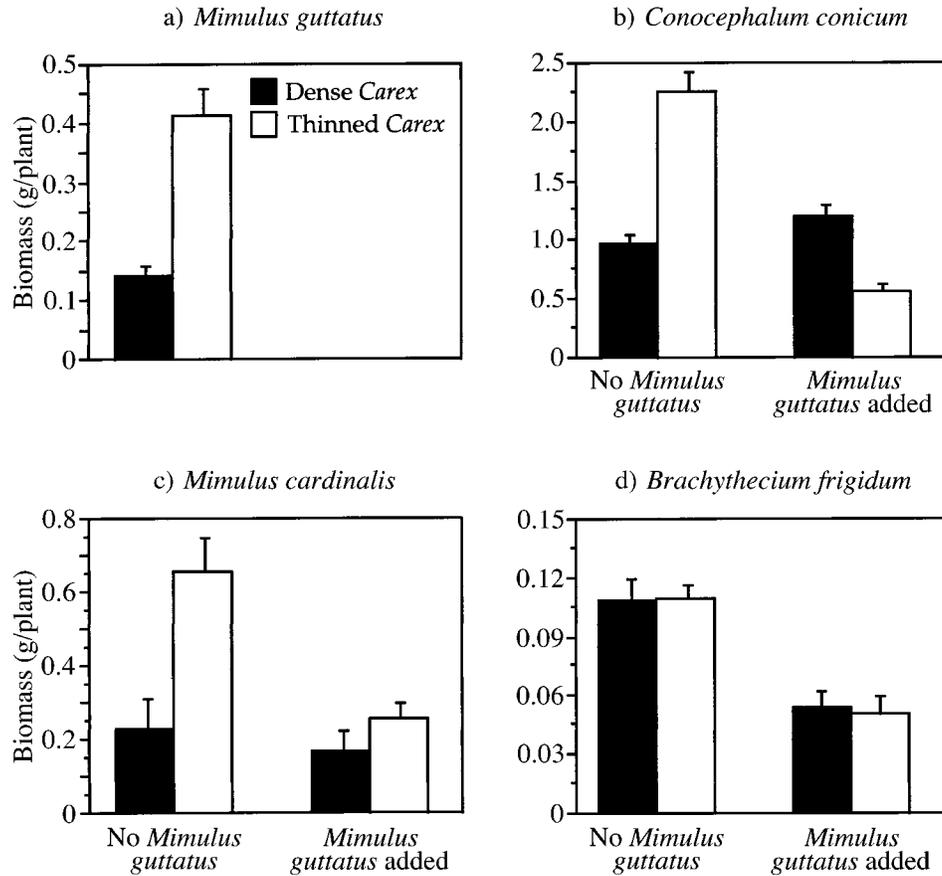
FIG. 3. (a) The effect of *Carex* on the biomass of *Mimulus guttatus*; and the effect of *Carex* on the biomass of (b) *Conocephalum conicum,* (c) *Mimulus cardinalis,* and (d) *Brachythecium frigidum,* with and without *M. guttatus* present. Bars represent means + 1 SE.

was comparable in magnitude to direct competition. Thinning *Carex* tripled the biomass of *M. cardinalis* without *M. guttatus* competition, but the same manipulation had a negligible effect when *M. guttatus* was present (Fig. 3c). This weak total interaction reflects dense *Carex* competing with *M. cardinalis,* yet simultaneously decreasing competition by *M. guttatus.* The effect of *M. guttatus* on the *Carex/M. cardinalis* interaction was reflected in a significant interaction term in the ANOVA (Table 2).

Finally, *Carex* had no effect on *Brachythecium,* independent of *M. guttatus,* but *M. guttatus* competition

reduced *Brachythecium* biomass by one half (Fig. 3d). The pairwise effects of *Carex* and *M. guttatus* were additive yielding a nonsignificant interaction (Table 2).

Indirect facilitation evident in field patterns

Field patterns from the South Fork Eel also suggested indirect facilitation of *Conocephalum* by *Carex.* *M. guttatus* cover was negatively correlated with *Carex* stem density ($r_s = -0.22$, $P = 0.003$), such that *M. guttatus* dominated on tussocks containing 30% fewer *Carex* stems (no. stems/100 cm^2 = 10.36 ± 1.13; mean ± 1 SE) than tussocks where *M. guttatus* remained

TABLE 2. Summary of ANOVAs testing for effects of *Carex* on *Mimulus guttatus,* and the main and interactive effects of *Carex* and *Mimulus guttatus* on the biomass of the three target species.

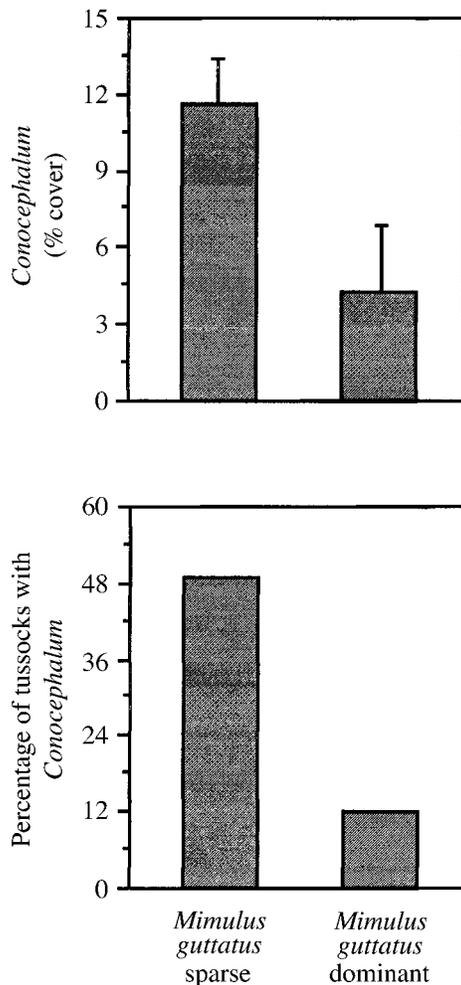| Source of variation	Mimulus guttatus			Conocephalum			Mimulus cardinalis			Brachythecium		
	df	F	P	df	F	P	df	F	P	df	F	P
Block	3	0.614	0.612	3	0.148	0.931	3	0.939	0.429	3	2.796	0.047
Carex density	1	46.014	0.001	1	6.719	0.012	1	10.084	0.003	1	0.059	0.809
Mimulus guttatus				1	33.977	0.001	1	8.210	0.006	1	60.559	0.001
Interaction (*Carex* × *M. guttatus*)				1	57.687	0.001	1	4.340	0.042	1	0.073	0.787
Error	24			54			52			62		

FIG. 4. Results from sampling 581 natural *Carex* tussocks over a 4-km stretch of the Eel River. Presented are percentage *Conocephalum* cover and percentage of *Carex* tussocks with any *Conocephalum* on tussocks where *M. guttatus* dominates vs. those where *M. guttatus* is sparse. Bars represent means + 1 SE.

sparse (no. stems/100 cm^2 = 14.85 ± 0.53; U = 1258.0, Z = −3.625, P = 0.001). These thinner tussocks, dominated by *M. guttatus* had fewer than half the *Conocephalum* as tussocks where *M. guttatus* was sparse (Fig. 4; U = 1317.0, Z = −3.720, P = 0.001), and were one quarter as likely to have any *Conocephalum* at all (Fig. 4; χ^2 = 15.75, P = 0.001). The reduced *Conocephalum* on these *M. guttatus*-dominated tussocks was not a direct response to the thinner *Carex*, since *Conocephalum* cover was negatively correlated with *Carex* density when *M. guttatus* was absent (r_s = −0.12, P = 0.017).

DISCUSSION

The results of this study demonstrate important indirect facilitation among plant species in a northern California riparian community. Along the South Fork Eel, plants are found growing almost exclusively on *Carex* tussocks, directly benefiting from the stable structure provided by tussocks (J. Levine, *unpublished data*). This study shows that *Carex* also has important indirect facilitative effects on some of these species, effects that are less intuitive. Indirect facilitation by *Carex*, mediated by its suppression of a shared competitor, *M. guttatus*, qualitatively altered the interactions for two of the three species examined. This positive indirect effect of *Carex*, combined with direct *Carex* competition influenced the growth of *Conocephalum*, *M. cardinalis*, and *Brachythecium* in three qualitatively different ways (Fig. 3). The interaction between *Carex* and *Conocephalum* was an indirect facilitation, such that the indirect positive effect of *Carex*, via a reduction in *M. guttatus* competition was stronger than direct *Carex* competition. Indirect facilitation among these species was also suggested by natural plant distributions along the Eel. *Carex* also had an important indirect positive effect on *M. cardinalis*, but for this species, the indirect effect was comparable in magnitude to direct competition. Finally, *Carex* had no effect on *Brachythecium*, independent of *M. guttatus*.

The study is one of the few that has explicitly examined indirect effects among competitors, yet evidence for the importance of these interactions in communities is growing. Connell (1983) reviewed field studies of competition and found a surprising number of studies documenting facilitation, a result attributed to indirect effects. Buss and Jackson (1979) found nontransitive competitive networks (A > B, B > C, C > A) among cryptic coral reef invertebrates. These nontransitive competitive interactions lead to indirect effects among competitors, though they differ from apparent facilitation in that the latter can arise in assemblages with transitive hierarchies. Davidson (1980, 1985) found evidence for apparent facilitation in an assemblage of three Chihuahuan desert harvester ants that differed in size. Diet overlap was related to body size. Thus competition between the large and small species was minimal, while the indirect positive effect of the large species on the small, via suppression of the intermediate, was strong. Another clear example of apparent facilitation was found for subtidal marine algae (Kastendiek 1982). Miller (1994) estimated direct and indirect effects of competition among five weedy species in an old field. He found consistent indirect positive effects, though the strongest of these was of similar magnitude to direct competition. In addition, Fowler (1981) suggested that indirect effects among competitors may be prevalent in a North Carolina grassland, and Takahashi (1997) argued that these interactions control the regeneration of two subalpine conifers. Furthermore, many of the studies that compiled pairwise competitive interactions into community matrices predicted indirect facilitation among compet-

itors in a wide range of communities (Lane 1975, Lawlor 1979, Davidson 1980, Hallett 1991).

Using mechanism to predict indirect facilitation

Carex is abundant throughout northern California streams and hosts many more species than those examined in this study. Along the South Fork Eel alone, *Carex* hosts a suite of >60 species, most of which are small, perennial, herbaceous plants or bryophytes, highly similar to those examined in this study. Based on the results presented here, I hypothesize that indirect facilitation may be widespread in this habitat. However, for some species, direct competition may be of greater magnitude than indirect positive effects. Therefore, an important question is what information can be used to predict the assemblages with frequent apparent facilitation.

Apparent facilitation may be more likely to arise in assemblages where the different pairs of competitors compete for different resources, or have significantly different mechanisms to acquire resources. Given the simple network of three competitors in Fig. 1a, indirect facilitation will only arise when the direct effects of A on C, and of C on B, are stronger than the direct effects of A on B (Davidson 1985). However, this condition is less likely if all species compete for the same resource. For example, if A strongly shades out C, and C strongly shades out B, then it is unlikely that A will have any less of an effect on B than does C, and thus there will be no indirect facilitation. There may still be an indirect positive effect of A, yet it is likely to be of lesser magnitude than the direct competition. Alternatively, if the mechanism by which A outcompetes C, differs from the mechanism by which A and C outcompete B, then the constraints on the intensity of the interactions are decoupled. For example, if C is better able than A to preempt the nutrients required by B, yet A severely suppresses C by light competition, then an indirect facilitation between A and B results.

While this study did not isolate the resources involved in the indirect facilitation of *Conocephalum,* competition for multiple resources appears probable. *Carex* likely suppressed *M. guttatus* by light competition, since *M. guttatus* growth is sensitive to low light availability (Vickery 1978), and light was severely reduced by dense *Carex*. Liverworts, in contrast, are relatively shade tolerant (Glime and Vitt 1984), and *Conocephalum* frequently grows in shady regions of the river. I observed, however, that the dense web of stoloniferous growth produced by unshaded *M. guttatus* was rarely penetrated by *Conocephalum,* and thus *M. guttatus* stolons provided a physical barrier to liverwort growth. I thus hypothesize that *Carex* inhibits *M. guttatus* via shading, while *M. guttatus* physically interferes with *Conocephalum* spread.

The consequences of indirect facilitation for community organization

Recent work has found that, in many systems, both competition and facilitation operate between the same species either simultaneously, or with the strength of each varying in time or space (Bertness and Hacker 1994, Callaway et al. 1996, Callaway and King 1996). Consequently, a more synthetic perspective on the ways plants influence one another is emerging, where plant interactions are viewed as complex combinations of negative and positive components (Callaway and Walker 1997, Brooker and Callaghan 1998). This study suggests that ecologists need to focus on these various components of plant interactions rather than concentrating on net effects, the output of simple removal experiments. The interactions involving *Carex* not only comprised both negative and positive components, but the indirect positive effects were the result of a series of competitive interactions. Furthermore, only when the competitive effects of *Carex* were separated from its direct positive effect by providing habitat was the theory on indirect effects among competitors relevant. Simply regarding *Carex* as a net facilitator misses important details about the complex relationship between *Carex* and its associated species, as well as bypassing critical information for predicting the community's response to environmental perturbations.

This study shows how pairwise competitive interactions can change to net zero, or even net positive effects by incorporating interactions with a third competitor. If competitive interactions are to be predictive of community organization, ecologists must incorporate the major indirect effects that emerge when these interactions are viewed in the context of entire communities (Stone and Roberts 1991). For example, Case (1991) shows that competitively superior invading species are less likely to displace natives in more diverse assemblages due to the prevalence of indirect effects among competitors in these systems. That indirect facilitation can contribute to the coexistence of species in diverse communities can be inferred from several other theoretical studies (Lawlor 1979, Yodzis 1988, Vandermeer 1990, Stone and Roberts 1991), though determining the generality of this conclusion requires further empirical work.

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