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Disturbance-mediated trophic interactions and plant performance

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Abstract Disturbances, such as flooding, play important roles in determining community structure. Most studies of disturbances focus on the direct effects and, hence, the indirect effects of disturbances are poorly understood. Within terrestrial riparian areas, annual flooding leads to differences in the arthropod community as compared to non-flooded areas. In turn, these differences are likely to alter the survival, growth, and reproduction of plant species via an indirect effect of flooding (i.e., changes in herbivory patterns). To test for such effects, an experiment was conducted wherein arthropod predators and herbivores were excluded from plots in flooded and non-flooded areas and the impact on a common riparian plant, *Mimulus guttatus* was examined. In general, the direct effect of flooding on *M. guttatus* was positive. The indirect effects, however, significantly decreased plant survival for both years of the experiment, regardless of predator presence, because of an increased exposure to grasshoppers, the most abundant herbivore in the non-flooded sites. Leafhoppers, which were more abundant in the flooded sites, had much weaker and varying effects. During 2000, when the leafhopper herbivory was high, arthropod predators did not significantly reduce damage to plants. In 2001, the mean herbivory damage was lower and predators were able to significantly reduce overall leafhopper damage. The effects of predators on leafhoppers, however, did not increase plant survival, final weight, or the reproduction potential and, thus, did not initiate a species-level trophic cascade. Overall, it

was the differences in the herbivore community that led to a significant decrease in plant survival. While flooding certainly alters riparian plant survival through direct abiotic effects, it also indirectly affects riparian plants by changing the arthropod community, in particular herbivores, and hence trophic interactions.

Keywords Disturbance · Flooding · Lycosidae
Mimulus guttatus DC · Trophic interactions

Introduction

It is a commonly recognized fact that disturbances help maintain community composition across a wide variety of ecosystems (Paine and Levin 1981; White and Pickett 1985; Hobbs and Mooney 1991; Wootton et al. 1996). In many of these systems, simply increasing or decreasing the frequency of disturbance can result in drastic changes in the overall community structure (Sousa 1979; Collins 2000; Shafroth et al. 2002). Most previous work has, however, focused on the direct effects of these disturbances on community structure (Canales et al. 1994; Pascarella and Horvitz 1998) without considering the potential indirect effects of disturbances (but see Elderd 2003; Knight and Holt 2005). For instance, disturbances can alter the dynamics or composition of the herbivore community, which can have dramatic impacts on both plant populations and plant communities (Rand 2002; Knight and Holt 2005). However, these studies compare disturbed and non-disturbed areas and do not manipulate arthropod communities in order to quantify their effect. This article presents the results of an experiment designed to disentangle the indirect effects of disturbances on plant population dynamics by experimentally excluding herbivores and predators in flooded and non-flooded environments.

Similar to disturbances, herbivore pressure can also vary across spatial and temporal scales (Olf and Ritchie 1998). The degree to which herbivores can alter plant survival and, thus, plant community composition, differs

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both within and across community types (Huntly 1991). Within particular systems, herbivores can have both strong and weak effects on plant communities (Root and Cappuccino 1992; Lenssen and de Kroon 2005), depending upon the spatial gradients, temporal scales, and the control of herbivores by predators (Schmitz et al. 1997; Carson and Root 2000; Rand 2002; Knight and Holt 2005). The overall variability in herbivore pressure across these gradients can have important consequences for determining species-specific survival and the plant community structure (Louda 1982; Carson and Root 2000; Fine et al. 2004).

Floodplains represent an ideal system for studying the indirect effects of disturbances brought about by changes in herbivore pressure since floodplains consist of a spatial and temporal mosaic of terrestrial arthropod and plant communities (Day et al. 1988; Milford 1999; Silvertown et al. 1999; Townsend 2001; Lenssen and de Kroon 2005). The effects of flooding in altering arthropod species composition are particularly evident when comparing flooded and non-flooded areas. The primary predatory arthropods of riparian floodplains are wolf spiders (Family: Lycosidae) (Framenau et al. 2002), while ants (Family: Formicidae) are a more dominant component of non-flooded areas (Lude et al. 1999; Milford 1999). Paralleling these differences are changes in herbivorous insects. While the grasshopper species (Order: Orthoptera) may become established in the floodplains (Reich 1991), most species are negatively affected by the anoxic soil conditions created by flood waters, which reduce the viability of both ground-deposited eggs and nymph survival (Dempster 1963; Hewitt 1979, 1985). In contrast, most leafhoppers (Family: Cicadellidae) insert their eggs within the leaf epidermis of host plants (DeLong 1971) and are able to survive the impact of flood waters. Thus, flooding creates a spatial mosaic of arthropod community types within flooded and non-flooded areas such that herbivore pressure or the ability of the predator community to keep herbivore populations in check may vary across this gradient.

The experiments conducted in this article were carried out in a naturally flooded riparian system. By taking advantage of a natural flooding regime, an already differentiated herbivore and predator community, occurring across flooded and non-flooded areas, was manipulated. In general, it would be difficult to experimentally set up these differentiated arthropod communities because of the time period needed for their establishment. Additionally, since the flooding occurred annually due to stream overflow and the inundation of sites by snowmelt fed seeps, the flooding is repeated and uniform across experimental treatments. However, a well-known disadvantage of natural experiments is that they do not permit direct control over variation between replicates (Underwood 1990). Yet, they also provide greater generality at the larger scales involved in flooded systems and support for potential future experiments (Diamond 1986). In general, due to the uniform scale of

flooding and its predictability, experimental manipulations of the study created strong treatment effects, which will be shown, that were detectable across replicates.

Methods

To investigate differences in trophic interactions between flooded and non-flooded systems, not only was the presence of herbivores and predators in field enclosures manipulated, but also how changes in the interactions between members of the arthropod community affected plant performance determined. Instead of taking the more common approach of using plant community biomass as a metric for overall plant performance, the study focused on a single species for two reasons. First, the grass and forb species composition of areas with and without annual flooding events can be dramatically different (Elder 2003). As a result, any potentially observed differences in overall community biomass might not be due to changes in arthropod community, but to differences in plant community. Second, differences in overall arthropod community structure may elucidate mechanisms behind the successful colonization and growth of riparian plant species within the floodplain, which would be obscured by a general biomass assay. For this study, a focal species, *Mimulus guttatus*, was chosen, which is ubiquitous in floodplain systems throughout California (Caicco 1998; Elder 2003) and whose presence or absence is likely to be an indication of community-level changes in plant species composition.

Study system and species

All work was conducted at the University of California Natural Reserve System's Sagehen Creek Field Station (lat. 39°25'N, long. 120°14'W) located 14 km north of Truckee, CA, at an elevation of 1,920 m. Sagehen receives most of its precipitation as snow in the winter months which, during the spring, melts and translates directly into increased stream flow. Additionally, many of the meadows surrounding Sagehen Creek are flooded annually by snowmelt fed seeps (Savage 1973). Thus, during the late spring and early summer, areas surrounding Sagehen Creek are consistently inundated with water. By mid-summer, the water levels have receded and the riparian areas are again above the water line.

The focal species for this study, *M. guttatus* or the common monkeyflower, occurs throughout the Western United States from Alaska to Baja California and from the Pacific Coast to the Rocky Mountains (Vickery 1978). *M. guttatus* can be a facultative annual or perennial, depending upon water availability (Hickman 1993). Within Sagehen Basin, *M. guttatus* is a perennial species (B.D. Elder, personal observation). Populations of *M. guttatus* occur in widely scattered clumps in moist meadows and along streams (Grant 1924; Lindsay 1964). It is a colonizing plant that often invades recently

disturbed habitats (Vickery 1978) and is extremely common in riparian areas throughout California (Cai-cco 1998; Hickman 1993), making it an appropriate species for studying the effects of changes in arthropod communities on floodplain flora.

Experimental design and insect surveys

During September of 1999 and 2000, seed capsules were collected from 7 distinct populations of *M. guttatus*, throughout the Truckee and Lake Tahoe basins. The capsules were stored for a week at 0°C to kill any herbivore larvae. Seeds were separated from the individual capsules and pooled within each population. An equal number of seeds from each population was then randomly selected and combined to create a yearly seed pool representing all populations. The following spring, the seeds were germinated and grown under greenhouse conditions at the University of California at Santa Cruz for 2 weeks before being transferred to Sagehen Creek Field Station. The seedlings were maintained in plug trays at Sagehen for 3 weeks before planting to assure acclimatization.

Due to the large-scale manipulation needed to directly test for the impacts of flooding across numerous sites, the author chose to investigate this factor using a natural experiment. Within Sagehen Basin, three 5 m×5 m naturally flooded sites, which were inundated on an annual basis, and three 5 m×5 m naturally non-flooded sites, were randomly chosen prior to the 2000 field season. The flooded sites were at least 200 m apart and contained standing water at the beginning of the field season. The non-flooded sites were located at least 100 m apart and were far enough from the creek and the basin's seeps so that they contained no standing water during the spring and the beginning of the field season. The flooded and non-flooded sites differed in initial vegetation composition mainly due to a shift in the graminoid species, from *Carex* spp. in flooded areas to *Poa* spp. in non-flooded areas, and not due to a change in the overall cover (B.D. Elder, unpublished data).

Within each site, a grid of nine 1-m² plots, separated by a 1-m buffer from adjacent plots, was established and three *M. guttatus* seedlings were transplanted into each plot. The seedlings were spaced 50 cm apart within each plot. Each plot randomly received one of three manipulations: the exclusion of non-flying predators, mostly wolf spiders and ants; the exclusion of both non-flying predators and herbivores; or, an unmanipulated control. To exclude non-flying predators, the plots were surrounded with a 10-cm tall tanglefoot covered (The Tanglefoot Company, Grand Rapids, MI) aluminum barrier and all predators found inside the barrier were removed with a modified leaf vacuum on a weekly basis. In general, few predators made it past these barriers. All plots were swept to control for the impacts of vacuuming on the overall arthropod community (i.e. predators and herbivores), with arthropods being able to re-colonize during the

following week. To exclude herbivores, a 1.25 g/l solution of Orthene (Valent USA, Walnut Creek, CA) was applied weekly to individual *M. guttatus* plants. Orthene protects plants from a wide spectrum of herbivores (Doak 1992) and does not affect *M. guttatus* growth (B.D. Elder, unpublished data). All plots that did not receive the Orthene treatment received a water control treatment. Since the non-flooded sites were more water-limited than the sites that experienced annual flooding, each plant was also watered daily during the experiment, in an attempt to eliminate this potential confounding factor. In 2001, the experiment was expanded and a set of cage controls was added to each existing experimental site, in order to determine the effect of the exclusion barrier on herbivore damage and plant performance. These cage controls consisted of an aluminum barrier open at all four corners with 10 cm gaps along two sides. The experiments were initiated on June 26–27, 2000 and June 28, 2001 and conducted for 7 weeks.

To assess whether the predator exclusion barriers were able to exclude non-flying predators, pitfall traps were placed in the center of a single set of treatments within each site on a weekly basis. These pitfall traps consisted of a 40-ml test tube placed in a PVC sleeve. After 48 h, all traps were collected and all wolf spider and ant species counted and identified (Table 1).

To determine whether or not there were differences in the naturally occurring arthropod communities between the flooded and the non-flooded areas, a series of pitfall trap transects, survey transects, and sticky traps were established near the experimental sites. Three pitfall trap transects were established in 2000, each consisting of four pitfall traps arranged linearly from the flooded areas to the non-flooded areas. Due to differences in the extent of the flooded/non-flooded areas, the pitfall traps were not evenly placed along each transect. The average distance between the pitfall traps was 25 m with a range of 19–39 m. During the 2000 and 2001 field seasons, these traps were opened for 48 h each week and all wolf spiders and ant species collected were counted and identified (Table 1). In 2001, 10-m grasshopper survey transects were established adjacent to each experimental site. These transects were walked on a weekly basis and all grasshoppers that moved within a 1-m belt were tallied by visual observation. To assess the abundance of leafhoppers per site, a sticky trap was placed adjacent to each experimental site for 48 h each week in 2001. These traps consisted of two 3 cm×5 cm index cards covered with tanglefoot and placed 10 cm above ground level. The author also separately collected the most common grasshopper and leafhopper species in the basin and identified them (Table 1).

During each week of the experiment, a suite of performance measurements and the extent of herbivore damage for each plant was recorded. Herbivory was quantified as the percentage of individual leaf area damaged and classified as either due to insect chewing, largely due to grasshoppers, or pitting of the leaf, largely due to leafhoppers. Performance measurements included

Table 1 Formicidae and Lycosidae species found in pitfall traps placed in experimental treatments and Cicadellidae and Orthoptera species found at experimental sites

Taxonomic group	Species
Formicidae ^a	<i>Formica lasiodes</i>
	<i>Formica neoclara</i>
	<i>Formica neorufibarbis</i>
	<i>Formica obscuripes</i>
	<i>Myrmica discontinua</i>
	<i>Tapinoma sessile</i>
	<i>Camponotus</i> spp.
Lycosidae	<i>Pardosa sternalis</i>
	<i>Pardosa tuoba</i>
Cicadellidae	<i>Lemellus bimaculatus</i>
	<i>Pasaremus concentricus</i>
	<i>Draeculacephala noveboracensis</i>
	<i>Helochara delta</i>
Orthoptera ^b	<i>Empoasca confusa</i>
	Acridinae
	Oedipodinae

^a If species or genus could not be identified, they were classified to the nearest subfamily as either myrmicine or formicine.

^b Species were classified to nearest subfamily.

the length of the longest leaf, the number of leaves, the height, a composite measurement of clonal and sexual reproduction potential (i.e., the number of flowers plus the number of side stems), and plant survival, along with cause of mortality. Due to the high correlation between weekly measurements, only the final mean values of each plot was analyzed. At the end of the experiment, the above-ground biomass of all living plants was harvested, dried for 5 days at 50°C, and weighed. Since dry weight is significantly correlated with the longest leaf length (2000: $r=0.79$, $P<0.0001$, $n=42$; 2001: $r=0.51$, $P<0.0001$, $n=60$), number of leaves produced (2000: $r=0.76$, $P<0.0001$, $n=42$; 2001: $r=0.55$, $P<0.0001$, $n=60$), and height (2000: $r=0.82$, $P<0.0001$, $n=42$; 2001: $r=0.32$, $P=0.0105$, $n=60$); dry weight was used to quantify the impacts of treatments on *M. guttatus* growth.

Statistical analysis

To analyze whether there were differences in the counts of ants and wolf spiders along a non-flooded/flooded gradient, a repeated measures Analysis of Variance (rmANOVA) was conducted on the pitfall trap transect data. Since the untransformed data did not meet the assumptions of homogeneity the rank of the counts, which is outlined by Neter et al. (1996), was analyzed. To facilitate analysis, the pitfall traps were divided into two categories (i.e., flooded and non-flooded). Differences in ambient grasshopper and leafhopper abundance between the flooded and non-flooded areas were also analyzed with rmANOVA. The grasshopper counts were natural log transformed to meet statistical assumptions (von Ende 1993).

The effectiveness of experimental treatments to exclude predators was also analyzed by rmANOVA, using

the natural log transformed data of pooled counts of wolf spiders and ants within individual pitfall traps. Since there was only a single replicate pitfall trap within an experimental treatment, the error term for this analysis consisted of the interaction of the experimental treatments and site nested within the flooding treatment. If these differences were significant, the author analyzed whether there was a difference between the experimental treatments and controls for 2000 and 2001, and, for 2001, whether there was a difference between the cage controls and the non-cage controls.

To analyze the effects of flooding and experimental treatments on *M. guttatus*, a MANOVA was conducted using percent herbivory per leaf due to grasshoppers, percent herbivory per leaf due to leafhoppers, final dry weight, and final reproduction potential. If an individual plant did not survive until the final week of the experiment, the percent herbivory was calculated using the measurements recorded during the final week of the plant's survival and, thus, represented a conservative estimate of herbivore damage. If the MANOVA was significant for a particular effect, univariate ANOVAs were performed on each of the dependent variables (Scheiner 1993). The means of all plants within each plot were used and all dependent variable data were natural log transformed to meet the assumptions of normality. The effects of the treatments on plant survival were also analyzed. Since the percent survival was not normal, these data were ranked and analyzed (Neter et al. 1996). If the individual ANOVAs proved significant for a particular factor, individual contrasts were conducted using Tukey's honestly significant difference test, which corrects for multiple tests under pairwise comparisons, on the least-squares mean values (Neter et al. 1996).

For both experimental data and herbivore surveys, the site was nested within the flooded and non-flooded effects. For the arthropod predator surveys within experimental treatments and the mortality analysis, nested interactions were dropped from the analysis if $P>0.25$ (Underwood 1997) and the analysis re-run. For experimental analyses, the error term for the interaction between flooding and experimental treatments consisted of the interaction between the experimental treatment and site nested within flooding, unless otherwise noted.

All analyses were conducted using PROC GLM in SAS Version 8.0 (SAS Institute 1999) and all test statistics use a Type III Sum of Squares. For field experimental analyses, data was analyzed by year, since the cage controls were implemented in 2001 and combining analyses between years would have confounded both treatment and year effects.

Results

Insect surveys

The flooded meadows had significantly more wolf spiders than the non-flooded meadows ($F_{1,17}=23.70$,

$P < 0.0001$; Fig. 1a) and significantly fewer ants ($F_{1,17} = 55.41$, $P < 0.0001$; Fig. 1b) for all the weeks surveyed. There was no difference in counts between years for either wolf spiders or ants (wolf spiders: $F_{1,17} = 0.15$, $P = 0.7076$; ants: $F_{1,17} = 0.18$, $P = 0.6723$) and differences in ant counts did not vary between transects ($F_{2,17} = 1.63$, $P = 0.2222$). For wolf spiders, there was a significant effect of transect ($F_{2,17} = 8.43$, $P = 0.0029$) due to fewer wolf spiders along a single transect. Overall, wolf spiders were more prevalent in the flooded areas; whereas, ants were more prevalent in the non-flooded areas (Fig. 1).

Differences in herbivorous insects between meadow types were also significant. There was significantly more leafhopper activity in the flooded meadows than in the non-flooded meadows ($F_{1,4} = 16.17$, $P = 0.0158$; Fig. 2a). There was also, consistently, more grasshopper activity in the non-flooded meadows when compared with the flooded meadows ($F_{1,4} = 14.36$, $P = 0.0193$; Fig. 2b). In general, leafhoppers were more common in the flooded meadows and grasshoppers were more common in the non-flooded meadows (Fig. 2).

Field experiments

The predator/herbivore and predator exclusion treatments effectively reduced the wolf spider and ant numbers (2000: $F_{2,8} = 12.69$, $P = 0.0033$; 2001: $F_{3,12} = 15.16$, $P = 0.0002$). This effect was significant irrespective of whether the wolf spiders and ants were pooled or analyzed independently (B.D. Elder, unpublished data). Across both years and all weeks, there were, on an average, over 7 times as many ants and 4 times as many wolf spiders in the control rather than the exclusion plots; these differences were significant for 5 and the entire 7 weeks of the experiment in 2000 and 2001, respectively. During 4 of the experiment's 7 weeks in 2001, there was no difference between the cage controls and the controls. Otherwise, there were significantly fewer predators in the cage controls when compared to the controls, indicating a potential cage effect. These

treatments, overall, successfully excluded arthropod predators from both the predator/herbivore and predator exclusion treatments.

In terms of the experimental effects on herbivory and plant performance, the MANOVA, for 2000, showed a marginally significant effect of the flooding treatment and a significant effect of experimental exclusion treatment (Table 2). For 2001, there was only a significant effect of the experimental exclusion treatment. For both years, there was also a highly significant effect due to differences across sites. The subsequent univariate analyses and individual contrasts highlight the variables that are responsible for driving these effects (Table 2). Overall, the MANOVA shows that there were strong effects of the exclusion treatments and a varying effect of flooding on herbivory and plant condition.

In terms of leafhopper herbivory, in 2000, there was significantly greater herbivory in the flooded areas than in the non-flooded areas (Fig. 3a), but no effect of the experimental treatment (Table 2; Fig. 3b). In 2001, there was close to a three-fold decrease in leafhopper herbivory in the flooded sites (Fig. 3c) relative to 2000 (Fig. 3a). Moreover, in the predator exclusion plots, there was a significantly greater percent herbivory per leaf than in any other treatments (Fig. 3d). Additionally, the cage control plots were not significantly different from the other experimental treatments. Thus, predators had a strong effect on leafhopper damage but only when overall herbivory was relatively lower.

In contrast, the effects of the experimental treatments on grasshopper herbivory were quite different. First, there was no significant effect of flooding, for either year, because of the high variation between sites (Table 2; Fig. 4a, c). Second, the grasshopper herbivory for both years was significantly reduced by the herbivore exclusion treatments (Fig. 4b, d). Third, the effects of predator manipulation varied between years. In 2000, there was no difference in percent herbivory between the predator exclusion sites and the control sites. In 2001, the percent herbivory was slightly lower in the predator exclusion and cage control plots than in the unmanipulated control plots. The lack of difference between the

Fig. 1 a Wolf spiders and b ants collected in pitfall traps in flooded (filled circle) and non-flooded meadows (open circle) during the course of the experiment in 2000 and 2001 (mean count \pm SE), analyzed using a repeated measures ANOVA. An asterisk (*) indicates a significant difference of $P < 0.05$ between meadow types.

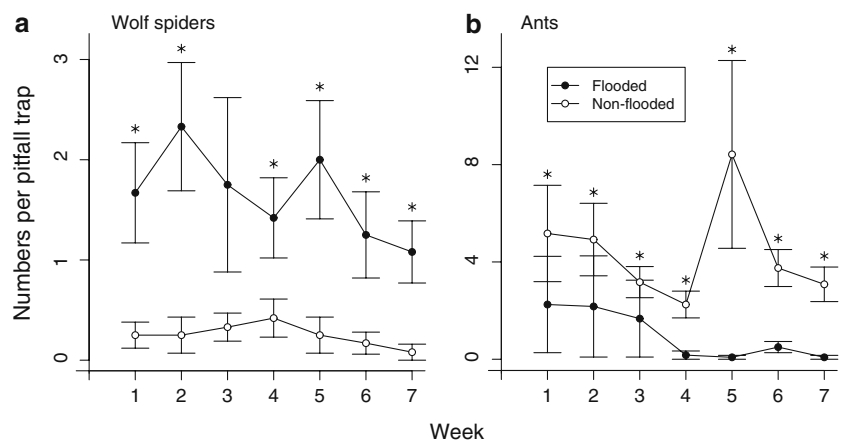


Fig. 2 a Leafhoppers collected by sticky traps and **b** grasshoppers along transect surveys in flooded (filled circle) and non-flooded (open circle) meadows adjacent to experimental sites in 2001 (least-squared mean count \pm SE), analyzed using a repeated measures ANOVA. An asterisk (*) indicates a significant difference of $P < 0.05$ between meadow types and a “†” indicates a marginally significant difference of $P < 0.1$.

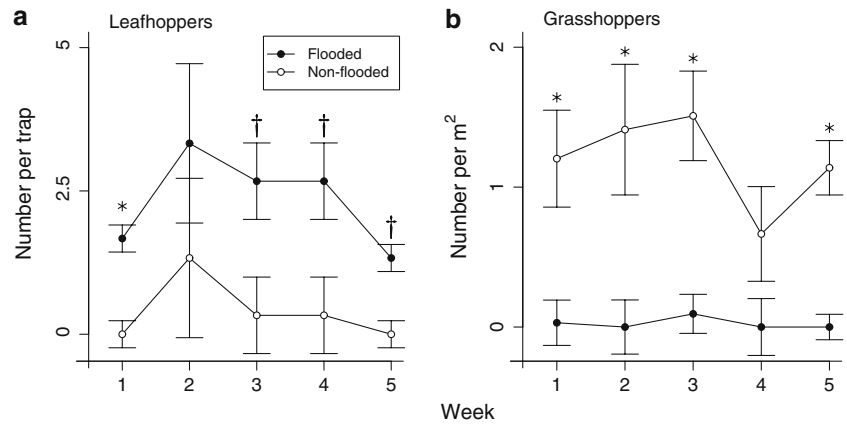


Table 2 MANOVA and subsequent ANOVA results if the MANOVA effect is significant or marginally significant. Dependent variables are percent herbivory per leaf due to grasshoppers, percent herbivory per leaf due to leafhoppers, dry weight, and reproduction potential (i.e., side stems plus the number of flowers produced)

Year	Effect	Response variable	<i>df</i>	Pillai's trace	<i>F</i>	<i>P</i>
2000	Flood ^a	Grasshopper	4,1	0.999	204.04	0.0525
		Leafhopper	1,4		2.19	0.2134
		Weight	1,4		16.59	0.0152
		Reproduction	1,4		14.63	0.0187
		Reproduction	1,4		16.97	0.0146
	Site(Flood)	Grasshopper	16,144	1.119	3.50	< 0.0001
		Leafhopper	4,36		5.36	0.0017
		Weight	4,36		1.21	0.3253
		Reproduction	4,36		6.67	0.0004
		Reproduction	4,36		2.79	0.0407
	Exclusion	Grasshopper	8,66	0.500	3.34	0.0089
		Leafhopper	1,36		9.28	0.0016
		Weight	1,36		1.27	0.2937
		Reproduction	1,36		24.64	0.0311
Reproduction		1,36		1.57	0.2228	
Flood \times Exclusion ^b		8,12	1.090	1.80	0.1739	
	Exclusion \times Site(Flood)	32,144	0.512	0.66	0.9143	
2001	Flood ^a	Grasshopper	4,1	0.919	2.83	0.4156
		Leafhopper	16,192	1.177	5.00	< 0.0001
		Weight	4,48		13.45	< 0.0001
		Reproduction	4,48		4.54	0.0034
		Reproduction	4,48		6.41	0.0003
	Exclusion	Grasshopper	4,48		15.38	< 0.0001
		Leafhopper	12,141	1.051	6.34	< 0.0001
		Weight	3,48		21.23	< 0.0001
		Reproduction	3,48		8.59	0.0001
		Reproduction	3,48		4.15	0.0108
	Flood \times Exclusion ^b		12,33	0.903	1.19	0.3332
		Exclusion \times Site(Flood)	48,192	0.903	1.17	0.2337

^a The error term for the Flood treatment was Site(Flood).

^b The error term for Flood \times Exclusion was Exclusion \times Site(Flood).

cage control plots and the predator exclusion plots indicates a cage effect on the herbivores, such that cages reduce grasshopper activity irrespective of the predator presence. It, therefore, appears that predators have no effect on grasshopper herbivory (Fig. 4). In general, when not excluded from treatments by insecticide and regardless of the presence of predators, grasshoppers consumed upwards of 5–15% of leaf tissue per leaf as compared to 1–3% of tissue damaged by leafhoppers (Figs. 3, 4).

Grasshopper herbivory was particularly intense throughout both years of the experiment, which, in turn, had significant impact on dry weight (Table 2). The exclusion treatments essentially reflected overall levels of grasshopper damage, such that treatments that excluded herbivores had significantly larger plants than the control plots for both years (Fig. 5b, d). Additionally, predator exclusion treatments were not significantly different from those that excluded herbivores and the control plots. In 2001, the cage control plots contained

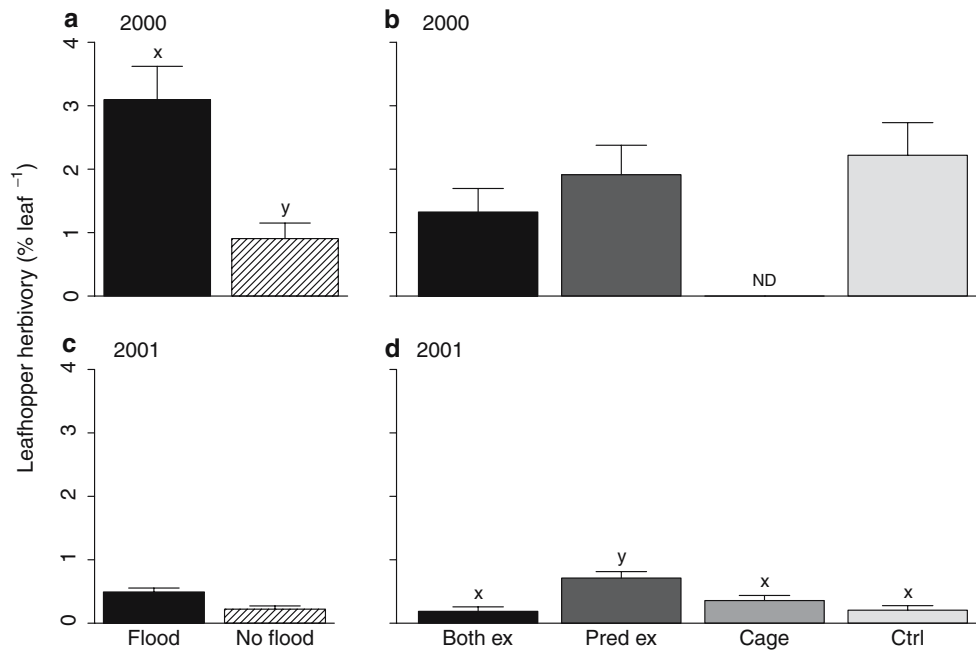


Fig. 3 Leafhopper herbivory on *Mimulus guttatus* in response to flooding (**a** and **c**) and arthropod exclusion (**b** and **d**) for 2000 and 2001, respectively (least-squared mean + SE of percent herbivory per leaf). Exclusion treatments are defined as herbivore and predator exclusion (Both ex), predator exclusion only (Pred ex), cage controls (Cage), and controls (Ctrl). Bars with different letters

indicate a significant difference ($P < 0.05$) between experimental plots with Tukey's correction for multiple tests. Contrasts for (**b**) and (**c**) were not conducted because either the MANOVA or the ANOVA term was not marginally ($P < 0.1$) or statistically ($P < 0.05$) significant. ND indicates no data available since cage control treatments were not applied in 2000.

heavier plants than the unmanipulated controls, again reflecting a potential cage effect on the herbivores (Fig. 5d). The dry weight, with respect to flooding treatments, was significantly greater in the flooded sites in 2000 (Fig. 5a), but there was no effect in 2001 (Fig. 5c). The final reproduction showed similar patterns to the dry weight, except for the lack of significance among exclusion treatments in 2000 (Table 2). Overall, grasshopper herbivory had a negative effect on both the final weight and the reproduction potential of *M. guttatus*.

The survival of *M. guttatus* also mirrored grasshopper herbivory damage. In 2000, there was a significant interaction between the flooding and experimental treatments, which resulted in a uniformly high survival in the flooded sites and low survivorship in the unmanipulated non-flooded control plots (Table 3; Fig. 6a). The results in 2001 were roughly similar (Table 3; Fig. 6b, c). First, there was a marginally higher survival in flooded areas. Second, survival in the control plots was significantly lower than all other treatments, although, in 2001, there was no significant interaction. In terms of the cause of mortality, 49 and 93% of the deaths in 2000 and 2001, respectively, in the non-flooded and the non-insecticided plots were attributable to grasshoppers. In 2000, the other major factor influencing survival in the non-flooded areas was frost damage, which accounted for 49% of the deaths in the non-flooded and the non-insecticided plots. In general, the dramatic negative impact of grasshoppers on survival

essentially paralleled that of their impact on both the final weight and reproduction.

Discussion

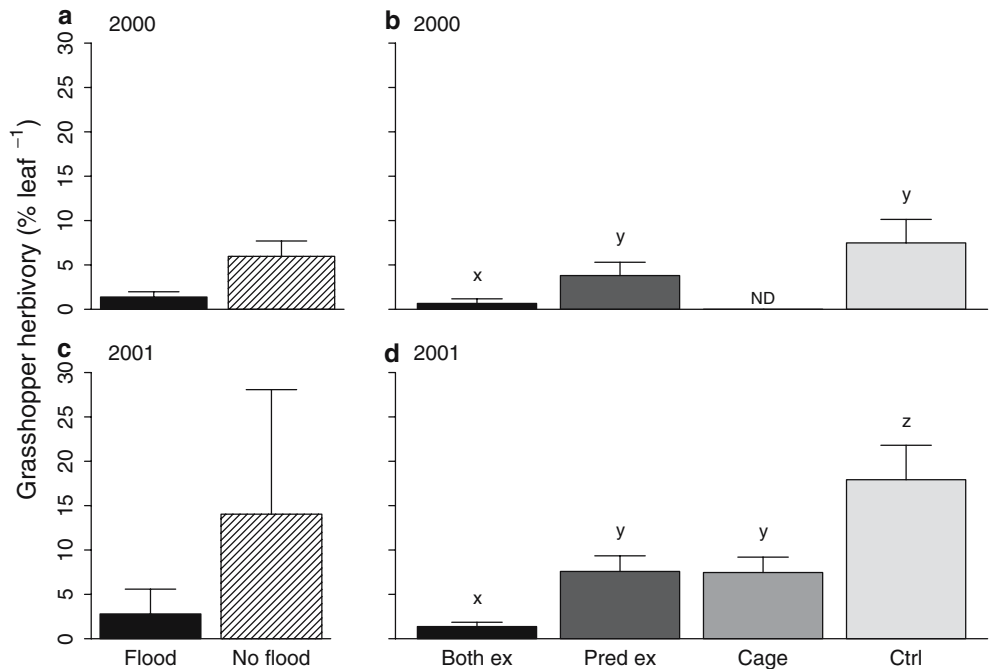
Within the riparian floodplain of Sagehen Creek, disturbances create a gradient of arthropod community types, which sets the stage for a variety of indirect interactions. Across this gradient, grasshopper and ant activity was significantly greater in the non-flooded areas; whereas, leafhopper and wolf spider activity was greater in the flooded areas. For *M. guttatus*, the ability to survive along this disturbance-created gradient was dictated by the herbivores that were active at a site. Grasshoppers had a significantly negative effect on plant

Table 3 ANOVAs for the effects of flooding and exclusion treatments on *Mimulus guttatus* survival for 2000 and 2001

Effect	2000			2001		
	df	F	P	df	F	P
Flood ^a	1	15.98	0.0162	1	6.22	0.0672
Site(Flood)	4	5.35	0.0013	4	10.31	<0.0001
Exclusion	2	14.05	<0.0001	3	6.29	0.0009
Flood × Exclusion	2	6.98	0.0023	3	1.33	0.2722
Error	44			60		

^a Site(Flood) used as error term

Fig. 4 Grasshopper herbivory on *Mimulus guttatus* in response to flooding (**a** and **c**) and arthropod exclusion (**b** and **d**) for 2000 and 2001, respectively (least-squared mean + SE of percent herbivory per leaf). Exclusion treatments are defined as herbivore and predator exclusion (Both ex), predator exclusion only (Pred ex), cage controls (Cage), and controls (Ctrl). Bars with different letters indicate a significant difference ($P < 0.05$) between experimental plots with Tukey's correction for multiple tests. Contrasts for (**a**) and (**c**) were not conducted because either the MANOVA or the ANOVA term was not marginally ($P < 0.1$) or statistically ($P < 0.05$) significant. ND indicates no data available since cage control treatments were not applied in 2000.



survival and biomass. As a result, across the flooded and non-flooded areas, it appears that grasshoppers probably play a role in limiting the distribution of *M. guttatus*. Predators also at times modified the indirect effects of disturbance by changing herbivore pressure. Specifically, the predators reduced leafhopper damage only when leafhopper damage was at its lowest. The interaction between the predators and leafhoppers, thus, fluctuated temporally. The reduction in damage, however, had no subsequent effects on plant weight, reproduction potential, or survival. In short, the potential species-level

trophic cascade, whereby predators reduce leafhopper damage and this, in turn, benefits plant survival or reproduction, trickled out (Halaj and Wise 2001; Strong 1992). In general, changes in the herbivore community, brought about by the lack of flooding, had a highly negative indirect effect on plant population demography.

By relying on annual flooding to impose disturbance effects, the flooding levels in the study, by definition, represented natural levels. A possible disadvantage of such a nested natural experiment, however, is that

Fig. 5 *Mimulus guttatus* dry mass in response to flooding (**a** and **c**) and arthropod exclusion treatments (**b** and **d**) for 2000 and 2001, respectively (least-squared mean + SE). Exclusion treatments are defined as herbivore and predator exclusion (Both ex), predator exclusion only (Pred ex), cage controls (Cage), and controls (Ctrl). Bars with different letters indicate a significant difference ($P < 0.05$) between experimental plots with Tukey's correction for multiple tests. Contrasts for (**c**) were not conducted because the MANOVA term was not marginally ($P < 0.1$) or statistically ($P < 0.05$) significant. ND indicates no data available since cage control treatments were not applied in 2000.

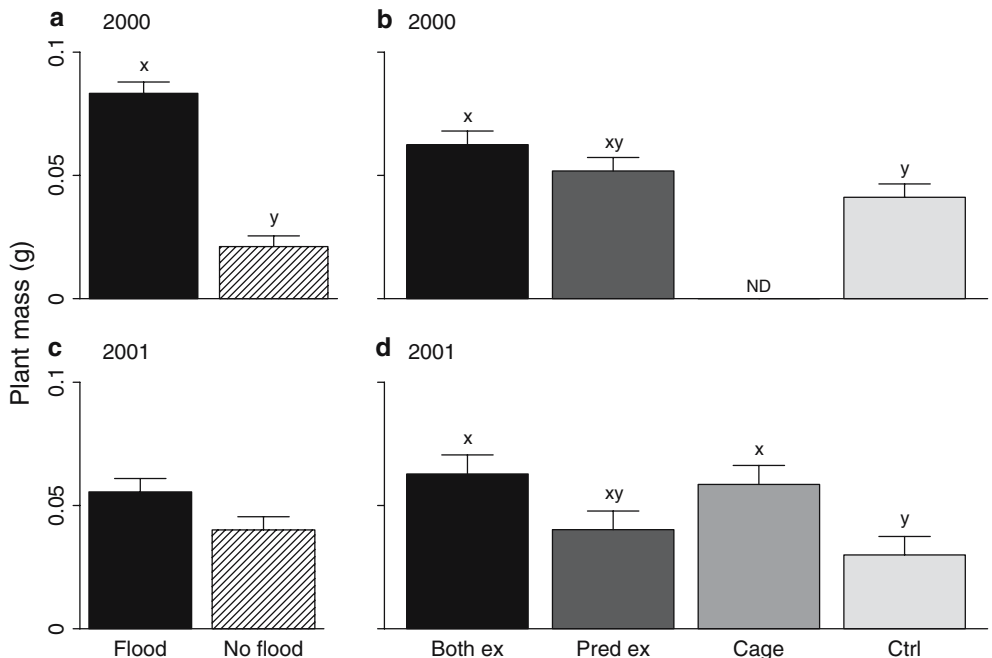
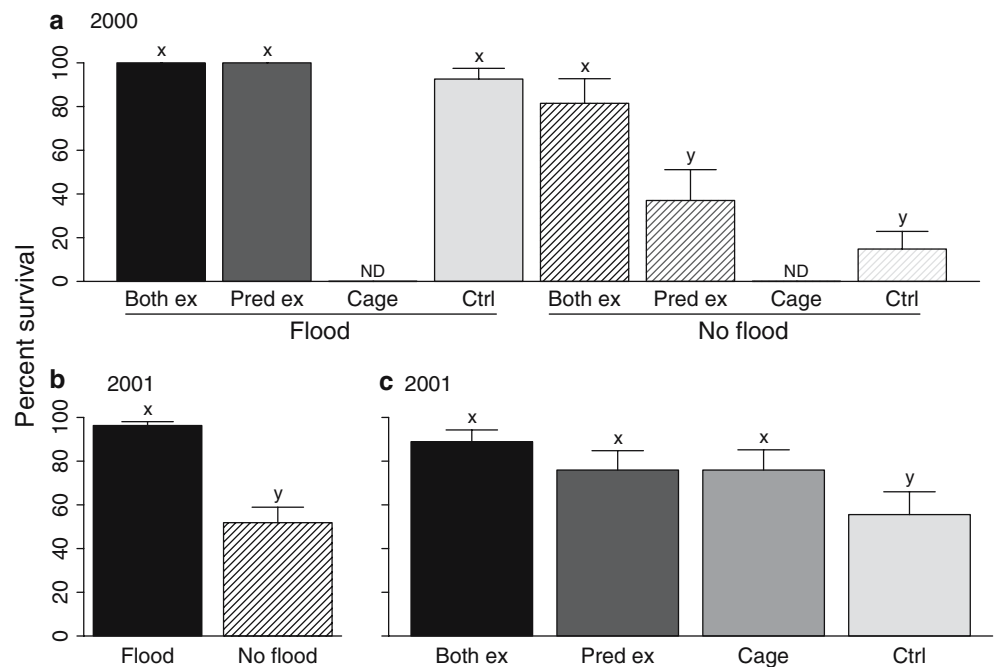


Fig. 6 *Mimulus guttatus* survival for **a** flooded (shaded bars) and non-flooded (diagonal lines) experimental treatments in 2000, **b** flooded treatments in 2001, and **c** exclusion treatments in 2001 (mean percent + SE). Exclusion treatments are defined as herbivore and predator exclusion (Both ex), predator exclusion only (Pred ex), cage controls (Cage), and controls (Ctrl). Bars with different letters indicate a significant difference ($P < 0.05$) between experimental plots with Tukey's correction for multiple tests. ND indicates no data available since cage control treatments were not applied in 2000.



variability among replicates can swamp out treatment effects. In these experiments, there were, indeed, differences among replicates, as shown by the significant effect of the site in both the MANOVA and univariate analyses. As discussed earlier, however, the average effects of flooding were nevertheless strong and statistically significant, showing that a natural experiment was, in this case, a successful choice. A related point is that, although there were differences in densities of both herbivores and predators between the flooded and non-flooded areas (Figs. 1, 2), all the species involved were easily able to cross between the flooded and non-flooded areas. It, therefore, seems likely that the differences in the insect community between the flooded and non-flooded areas were due to the effects of flooding rather than to the geographic barriers to movement. In other words, it seems likely that flooding affects the insect community, which, in turn, can have varying indirect impacts on the plant community, which has also been shown in other disturbance-driven systems (Rand 2002; Lenssen and de Kroon 2005).

As described earlier, insect abundance offers the most likely explanation for the indirect effects of flooding and could only be examined in a natural experiment, due to the time needed to establish differentiated arthropod communities. An inherent feature of a natural experiment, however, is that there may have been some other covariate besides insect abundance, which explains differences in the impact of flooding. Although, there were no obvious differences between the flooded and non-flooded areas, it is certainly true that plant fitness was generally higher in the flooded areas, suggesting that there may have been differences in factors other than the insect community. It is important to note, however, that in spite of such effects, it was nevertheless possible to

clearly disentangle the effects of herbivory from factors intrinsic to flooding. Second, and more generally, this kind of confounding is, arguably, a basic problem with any experiment that attempts to disentangle the effects of interactions among multiple species. In particular, it is certainly true that the same difficulties can arise in both artificial and natural experiments (Hairston 1989).

In the experimental exclusion treatments, changes in herbivores across the flooded and non-flooded sites dramatically affected plant survival. Within non-flooded areas, grasshoppers had a tremendous effect on *M. guttatus*'s survival during 2000, as seen by the extremely low survivorship in non-flooded non-insecticided plots and the overall lower survivorship in the control sites during 2001 (Fig. 6). The severity of the effect of grasshopper herbivory is also highlighted by the decline in the final dry weight of surviving plants in the control plots during both years (Fig. 5). This overall difference seen in survival and weight would have been even greater between non-flooded and flooded sites if the potential direct effects of water limitation, i.e. by watering each plant on a daily basis, had not been controlled for. While grasshoppers strongly affect *M. guttatus*'s performance, these effects were not influenced by top-down control from predators, due to a weak interaction between the predators and their prey. The striking effect of grasshoppers demonstrates the importance of the herbivore community for determining the *M. guttatus* population dynamics.

In previous studies, grasshopper densities have generally declined in the presence of predators (Risch and Carrol 1982; Schmitz et al. 1997). The lack of an effect of predators in these experiments was, therefore, probably due to the biology of the particular predators species present (Table 1). In an effort to understand the lack

of an effect of ants, a colleague and the author carried out an experiment in which grasshoppers were confined 1-liter mesocosms containing an individual *M. guttatus*. In these mesocosms, grasshopper mortality was much higher in the presence of ants than in the absence of ants (ant addition: 95.8%; no-ant controls: 33.3%; $G = 22.73$, $P < 0.0001$, $n = 24$ for each treatment (B.D. Elder and J. Jacobs, unpublished data)), demonstrating that ants, at least, are capable of attacking and killing grasshoppers. Since the key difference between the mesocosms and these experiments was that the grasshoppers in the mesocosms were confined, it appears that ants had little effect in the experiments simply because they could not catch the grasshoppers. Similarly, other data have shown that the two species of wolf spiders in these experiments are only capable of catching and killing first through third instar grasshoppers, but not later instars (B.D. Elder, unpublished data). It therefore appears that wolf spiders had little effect on grasshopper herbivory since they could not catch or subdue later instars. Thus, neither common arthropod predator in the system could potentially control grasshopper herbivory.

When the leafhopper herbivory was taken into account, the ability of predators to control herbivores was found to be dependent upon the year of the experiment. In 2000, a potential increase in leafhopper populations resulted in an almost three-fold increase in the leafhopper herbivory as compared to 2001. At this level of damage, the predators could not control the herbivory. It, thus, appears that increasing numbers of leafhoppers allowed the escape of the prey population from the predators (Holling 1959). In 2001, the herbivory damage dropped, most likely due to differences in the herbivore populations since there was no change in arthropod predator counts between years. Following this decline, the predators were able to reduce the herbivory, as seen by the differences between the control and the predator exclusion plots (Fig. 3). The leafhopper herbivory, however, was not of sufficient strength to affect the weight or reproduction potential of *M. guttatus*. Regardless of predator control, the leafhoppers had weak and varying effects on plant demography.

Overall, disturbances have both direct and indirect effects on plant demographics. For *M. guttatus*, a common riparian plant, flooding can directly increase plant survival, weight, and reproduction. Flooding also indirectly influences plant survival by altering the herbivore community. Specifically, grasshoppers had an overwhelmingly negative effect on plant survival. However, predators can sometimes modulate the indirect effects of increased herbivory. For instance, when the leafhopper herbivory was low, predators were able to keep this herbivore in check. This reduction in the herbivory did not have overall positive effects on plant performance and, thus, this potential species-level cascade trickled out (Halaj and Wise 2001; Strong 1992). With much higher levels of leafhopper herbivory, the predators were not able to control the herbivore pressure. Regardless of

predator control, however, the degree to which leafhoppers affected *M. guttatus* was relatively weak, which is not uncommon with respect to herbivores in other non-disturbance-driven systems (Huntly 1991; Root and Cappuccino 1992). In general, disturbance events such as flooding can create a spatial gradient by altering the composition of the herbivore guild within a community, which, in turn, affects plant population dynamics. These results suggest that it is important to consider overall changes in the arthropod community structure when examining the impact of disturbances on plant population dynamics.

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