

Influences of Disturbance and Vegetation on Abundance of Native and Exotic Detritivores in a Southwestern Riparian Forest

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ABSTRACT Detritivores play important roles in energy and nutrient flow in riparian ecosystems. Endemic crickets (*Gryllus alogus* Rehn) and exotic isopods (*Armadillidium vulgare* Latreille and *Porcellio laevis* Latreille.) are abundant detritivores in riparian forest floors of central New Mexico. To determine how disturbance history affects the abundance of these detritivores, we installed pitfall traps in plots that had flooded, burned, or had no recent disturbance. We also measured vegetation composition to examine the relationship between plant community composition and detritivore abundance. Crickets were most abundant in the two plots that had flooded but were rare in recently burned, nonflooded plots. Isopods were most abundant in a wildfire plot with high vegetation density and mesic conditions but were also abundant in unburned plots. Isopods were rare in the plots that had recently burned or had flooded. Multiple regression model selection results suggest that cricket abundance is best explained by plot-related variables and is partly explained by recent disturbance history. Isopod abundance was best explained by disturbance history and vegetation characteristics. Cricket abundance was positively associated with flooding while isopod abundance was positively associated with vegetation density and fire and negatively associated with flooding and exotic saltcedar. These results show that flooding can lessen the negative impact of wildfire on native detritivores and reduce the abundance of exotic species.

KEY WORDS detritivores, flood, Middle Rio Grande, riparian vegetation, wildfire

Detritivores perform important ecosystem functions that include removal of dead plant and animal matter and transfer of energy and nutrients into the detrital food web (Polis and Strong 1996). In the southwestern United States, detritivores are a diverse and abundant component of riparian forest floor arthropod communities (Cartron et al. 2003, Sabo et al. 2005). In these forests, disturbances such as flood and fire have immediate and long-term effects on detritivore populations (Ellis et al. 1999, Bess et al. 2002). These disturbances have been shown to alter the organization of riparian forest floor detritivore communities and certain detritivore species can serve as indicators of disturbance regimens (Bess et al. 2002, Cartron et al. 2003).

Riparian vegetation can regulate detritivore populations through the production of litter, which provides food and shelter for detritivore communities (Sabo et al. 2005). The litter produced by different riparian plants varies in physical structure and chemical composition (Ellis et al. 1999, Simons and Seastedt 1999); therefore, plant community composition should influence the abundance of detritivorous species. Despite the clear importance of disturbance and

vegetation to detritivores, specific mechanisms that determine abundance of individual detritivore species remain unclear.

Southwestern riparian forests provide habitat for a variety of wildlife species, most notably birds (Carothers et al. 1974, Strong and Bock 1990). The majority of riparian-nesting birds are insectivorous (Knopf et al. 1988), as are many species of reptiles, amphibians, and small mammals found in riparian forests (Degenhardt et al. 1996, Sabo et al. 2005). The vegetation structure of riparian forests has been altered from its native state by a variety of human-caused disturbances, which include xerification, introduction of exotic species, and wildfire (Howe and Knopf 1991, Busch 1995, Shafroth et al. 2002). Moreover, the frequency of natural disturbances such as flooding has been reduced by the construction of dams and other hydrologic projects (Molles et al. 1998). An understanding of the effects of these disturbances on arthropod populations is therefore vital to the conservation of many riparian wildlife species.

The riparian forests of the Middle Rio Grande Valley in New Mexico provide a unique opportunity to observe effects of different disturbance types and vegetation composition on native and exotic arthropods. We trapped native crickets and exotic isopods to estimate their abundance in several locations along the Middle Rio Grande. We used an information-theoretic model selection framework to distinguish the

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Table 1. Recent disturbance history, land managers (Middle Rio Grande Conservancy District [MRGCD] or Bosque Del Apache National Wildlife Refuge [BDNWR]), and no. trapping stations in unburned (UB) and wildfire (WF) plots where pitfall traps were installed in 2004

Plot	Disturbance history	Land manager	Pitfall stations
Rio Grande Complex UB	No flood or fire	MRGCD	13
Rio Grande Complex WF	Burned in 2000	MRGCD	13
Chavez UB	No flood or fire	MRGCD	13
Chavez WF	Burned in 2000	MRGCD	12
San Francisco UB	No flood or fire	MRGCD	10
San Francisco WF	Burned in 2003	MRGCD	10
San Pedro UB	Flooded in 2004	BDNWR	9
San Pedro WF	Burned in 1996, flooded in 2004	BDNWR	14

influences of disturbance, vegetation, and other variables on abundance of these detritivores.

Materials and Methods

Study Area

We installed arthropod trapping stations in riparian forests along the Middle Rio Grande in Valencia and Socorro Counties, NM. Along the Middle Rio Grande, riparian vegetation is largely confined between the river channel and levees on either side of the river. Rio Grande cottonwood [*Populus deltoides* spp. *wislizenii* (S. Watson) Eckenwalder] is the dominant canopy species, and Gooding's willow (*Salix goodingii* Ball.) is also found in the canopy. Native understory shrubs, exotic saltcedar (*Tamarix ramosissima* Loureiro), and exotic Russian olive (*Elaeagnus angustifolia* L.) are found in throughout the understory.

The Middle Rio Grande riparian forests are one of the most extensive cottonwood gallery forests in the southwestern United States (Howe and Knopf 1991). Historically, regular flood events resulted in a mosaic of riparian vegetation throughout the valley floor (Whitney 1996). Because of construction of dams and other water management, substantial flooding has not occurred outside the levees for 60 yr, and flooding rarely occurs within much of remaining riparian forest (Molles et al. 1998). Frequency and intensity of wildfire has recently increased within the forest because of increased human activity, drought conditions, accumulation of woody debris, and spread of exotic, flammable species (Stuever et al. 1995).

We sampled arthropods at four sites, described below. Each site contained a wildfire plot and an adjacent unburned plot. Wildfires burned during different years (Table 1), consumed most understory vegetation and litter, and top-killed most of the large cottonwood trees and understory shrubs. At each wildfire plot, cottonwoods resprouted from their roots, as did understory shrubs, to form a dense, shrub-like stand. Composition of native and exotic resprouts varied among wildfire plots (Smith et al. 2007). Unburned plots were adjacent to wildfire plots, and we assumed that their vegetation composition closely resembled that of wildfire plots before burning. All sites located on the western bank of the river channel and bordered on the west by agricultural fields, which were separated from the forest by levees and conveyance canals.

San Pedro Site. The San Pedro site is the southernmost site located at the Bosque Del Apache National Wildlife Refuge south of San Antonio, NM. The wildfire plot burned in 1996 and includes a section along the river channel and a section removed from the river channel by a low flow conveyance canal. Several floods occurring between 2001 and 2004 scoured the litter from the forest floor in both wildfire and unburned plots. Unburned and wildfire plots had a cottonwood canopy and an understory dominated by saltcedar, with coyote willow (*Salix exigua* Nutt.), New Mexico olive (*Forestiera neomexicana* Nutt.), seepwillow (*Baccharis glutinosa* Pers.), and Russian olive also abundant in the understory

Los Lunas Site. The Los Lunas site is the northernmost site and is located in Los Lunas, NM, on land managed by the Middle Rio Grande Conservancy district. The wildfire plot burned in 2000. To our knowledge, no overbank flooding occurred in the 5 yr before arthropod sampling, but occasional groundwater seepage and shallow depth to groundwater create Mesic conditions. Unburned and wildfire plots had a canopy dominated by cottonwood and an understory dominated by coyote willow. Some saltcedar and Russian olive were present in the understory, and the exotic trees Siberian elm (*Ulmus pumila* L.) and white mulberry (*Morus alba* L.) were present the canopy.

Chavez and Bernardo Sites. The Chavez and Bernardo sites were centrally located between the other sites, south of Belen, NM. These sites were relatively close to each other and had similar vegetative compositions. To our knowledge, neither site flooded in the 5 yr before our sampling. The Chavez wildfire occurred in 2002, and the Bernardo fire occurred in 2003. Both sites had a canopy dominated by cottonwood and an understory dominated by saltcedar. Gooding's willow was also present in the canopy, and Russian olive, coyote willow, wolfberry (*Lycium torreyi* Gray), and false indigo (*Amorpha fruticosa* L.) were abundant in the understory.

Arthropod Sampling

Study Species. We analyzed the abundance of the cricket *Gryllus alogus* (Rehn) and the isopods *Armadillidium vulgare* and *Porcellio laevis* (Latreille, hereafter collectively referred to as isopods). We focused on these species because they are the most abundant

detrivore species at these sites (Ellis et al. 2001) and occupy similar foraging niches, but differ in their natural ranges. *G. alogus* is endemic to the Middle Rio Grande valley, where it feeds mainly on decomposing leaves in the riparian floodplain (Ellis et al. 2001). Isopods were introduced from Europe, occupy a variety of habitats, and feed mainly on dead plant matter (Paris 1963).

Pitfall Trapping. We installed 9–14 pitfall stations at unburned and wildfire plots (Table 1). Trap stations consisted of cross-shaped arrays of four traps within 0.04-ha circles that were established as part of another study (Smith et al. 2007). Stations were systematically located in the riparian forests at least 50 m apart at randomly selected distances from the river. Trap stations were installed between the levees at all sites except for San Pedro, where some traps were located in the wildfire section west of the conveyance canal. Traps consisted of a 16-oz plastic cup buried so that the surface was flush with the ground. We filled each trap with propylene glycol to kill and preserve arthropods. In 2004, each trap was open for 6 d early in the season (10 May to 15 June) and 6 d late in the season (15 June to 10 August). We collected the contents of traps every 3 or 6 d and stored the contents in ethanol until they were sorted and counted. We sorted all individuals by order and separated and counted the study species. Other individuals were later counted for an additional study. We counted all individuals that were 5 mm or greater in length. We did not count individuals <5 mm because they were difficult to identify to species.

Vegetation Measurement. We measured the vegetative structure and composition in all 0.04-ha pitfall stations in 2004. After adjusted Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al. 1997), we identified trees and shrubs and counted the number of each species in various size classes within each plot. Totals of the most common woody species (cottonwood and saltcedar) were used in the data analysis because their relative abundance has the greatest effect on forest structure. We measured ground cover by estimating the number of forb stems and percent litter cover in trapping station quadrants. For each quadrant, we assigned a class designating density of forb stems (1 = 0–10, 2 = 10–50, 3 = 50–100, 4 = 100+) and calculated mean class number for each station.

Data Analysis. We estimated abundance of crickets and isopods by calculating number captured per trap per day at each pitfall station and mean number captured per trap per day in each plot. Because we could not randomly select sites and apply fire treatments, we did not use frequentist statistical methods and associated *P* values to compare means between unburned and wildfire plots (Johnson 1999). Instead, we calculated effect sizes that reflect the magnitude of differences between paired unburned and wildfire plots. We used Cohen's *d* to estimate effects size, which we calculated as

$$d = (U - W) / \sigma$$

where *U* is the unburned mean, *W* is the wildfire mean, and σ is the pooled SD. Cohen (1988) suggests a *d* value near 1 represents little probability of overlapping means. We therefore regarded $d \geq 1$ as indicating substantial separation of means.

We used information-theoretic model selection to determine if variation in arthropod abundance was associated with disturbance, vegetation characteristics, or site-related variables we failed to measure. We constructed multiple regression models with trap station as the experimental unit (so each trap station is separate). These models had number of crickets or isopods per trap per day as the response variable and various combinations of explanatory variables. Explanatory variables included disturbance history, trapping plot, and vegetation measurements described above for both cricket and isopod models. Linear regression models assumed a normal distribution. Data were log-transformed to meet this assumption (PROC GENMOD; SAS Institute 1999). Model fit was tested by dividing the scaled χ^2 by degrees of freedom from the most parameterized (global) model (Burnham and Anderson 2002).

To evaluate these models, we used information-theoretic model selection and parameter estimation (Burnham and Anderson 2002) that has been useful in identifying environmental factors that limit the abundance of organisms (Welch and MacMahon 2005). We used Akaike's information criterion (AIC), corrected for overdispersion and sample size (QAIC_C), to select the most parsimonious models in a given set. AIC was calculated using the log likelihood output from PROC GENMOD and adjusted to QAIC_C (Burnham and Anderson 2002). The resulting value is a measure of the each model's ability to fit the data while minimizing number of parameters. We compared models using relative QAIC_C values, with the lowest values belonging to the best-fit models (Burnham and Anderson 2002). We calculated ΔQAIC_C for each model by subtracting its QAIC_C value from the lowest QAIC_C value in the model set. This subtraction gives the best fit model a ΔQAIC_C value of 0 and every other model a value >0. We designated models with ΔQAIC_C value ≤ 2.0 as well supported by the data and models with ΔQAIC_C value ≤ 4.0 as somewhat supported by the data (Burnham and Anderson 2002). We used ΔQAIC_C to calculate Akaike weights (w_i), which estimate the probability of each model in our set being the best explanation of detritivore abundance (Burnham and Anderson 2002).

We constructed and analyzed sets of models using a hierarchical approach. We began by analyzing a set of four general models for each species that represented four general hypothesis explaining abundance (Table 2). The hypotheses were (1) abundance was best explained by disturbance only, (2) abundance was explained by disturbance and vegetation features, (3) abundance was best explained by vegetation features only, and (4) abundance was best explained by unmeasured, plot-related variables. General model 1 contained wildfire and flooding history as explanatory variables, general model 2 contained all disturbance

Table 2. Descriptions of general regression models used to explain variation in abundance of crickets and isopods

Model	Hypothesis modeled	Variables included
Disturbance	Abundance of crickets or isopods is associated with disturbance history of the trap station	Flood, wildfire
Disturbance and vegetation	Abundance is associated with disturbance history and vegetative composition of the trap station	Flood, wildfire, cottonwood density, forb cover, litter cover, saltcedar density
Vegetation	Abundance is associated with vegetative composition of the trap station	Cottonwood density, forb cover, litter cover, saltcedar density
Plot	Abundance is associated with unmeasured variables differing between plots	Plot

and vegetation measurements as explanatory variables, general model 3 contained all vegetation measurements as explanatory variables, and general model 4 had trapping plot as the only explanatory variable (Table 2).

For each species, we first compared QAICc values of the four general models. We identified which models were at least somewhat supported by the data ($\Delta\text{QAIC}_C \leq 4.0$). If general models 1 through 3 received some support, we added more specific models containing various combinations of variables from the supported general models to the model set to evaluate individual variables. If the unknown plot effect model (number 4) received support, however, we could not construct more specific models based on that model because it only contained one variable. After specific models were added to the set, we analyzed their ΔQAIC_C values to determine their support among the entire model set.

To reduce bias in parameter estimation and incorporate model selection uncertainty, we calculated model averaged parameter estimates, which reflect the effect of continuous variables (β) on abundance. These estimates incorporated Akaike weights across all the models in which the estimated parameters were used (Burnham and Anderson 2002). We used Akaike weights to calculate unconditional variances of the parameter estimates, which were used to construct 95% CIs (Burnham and Anderson 2002). Parameter estimates and variance were calculated for all explan-

atory variables that were included in models with at least some support from the data. With this model selection framework, we were able to identify variables that had important effects on abundance (using model selection) and determine the positive or negative direction of their effects (using model-averaged parameter estimates of β).

Results

We captured crickets and isopods at all plots. Overall, there were more crickets captured in unburned plots than wildfire plots, but the effect size of the difference was very small ($d = 0.09$). There were more crickets captured in unburned plots than in paired wildfire plots at the Bernardo site ($d = 1.22$), Chavez site ($d = 1.12$), and Los Lunas site ($d = 1.05$). The San Pedro site had the largest amounts of crickets captured of all sites (Fig. 1). More crickets were captured at the San Pedro plot than the unburned plot, but the effect size was small ($d = 0.67$).

There were similar numbers of isopods captured at pooled unburned and wildfire plots ($d = 0.11$). We captured more isopods at the Rio Grande Complex site than at the other three sites (Fig. 2). Number of isopods captured did not differ much between the unburned and wildfire plots at the Bernardo site ($d = 0.03$) or San Pedro site ($d = 0.22$). There were fewer isopods captured at the Chavez wildfire plot than its paired unburned site ($d = 1.07$). There were more

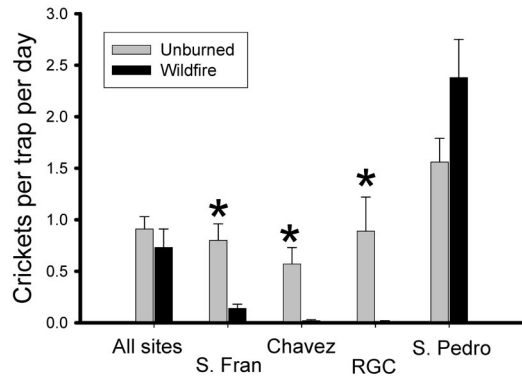


Fig. 1. Mean number of crickets captured in unburned and wildfire plots at four trapping sites in 2004. Comparisons labeled with asterisks indicate a large effect size of wildfire (Cohen's $d \geq 1$). Bars represent SE.

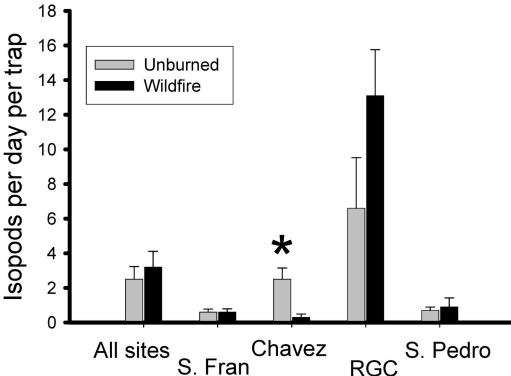


Fig. 2. Mean number of isopods captured in unburned and wildfire plots at four trapping sites in 2004. Comparisons labeled with asterisks indicate a large effect size of wildfire (Cohen's $d \geq 1$). Bars represent SE.

Table 3. ΔQAIC_c values for general and specific models explaining variation in cricket and isopod abundance

Species	General model	ΔQAIC_c	Specific model	ΔQAIC_c
Crickets	Plot	0	Fire	3.3
	Disturbance	4.4	Flood	49.9
	Disturbance and vegetation	7.2		
	Vegetation	46.1		
Isopods	Disturbance and vegetation	0	Fire saltcedar	19.5
	Plot	0.8	Fire litter	19.7
	Vegetation	8.2	Flood saltcedar	19.8
	Disturbance	38.3	Flood litter	30.8
			Flood forb	38.8
			Flood cottonwood	38.8
			Fire forb	41.7
			Fire cottonwood	41.9

isopods captured at the San Pedro wildfire plot than at the unburned plot, although the effect size was smaller (<1 ; $d = 0.70$).

Multiple regression models explaining cricket and isopod abundance fit the data well (deviance/df = 1.15). The general model representing unmeasured, plot-related variables best explained variation in cricket abundance and received considerable support among the model set ($w_i = 0.75$). The general model representing disturbance effects also received some support ($w_i = 0.08$). The remaining models received little support, having ΔQAIC_c values > 6 (Table 3). We added specific models containing fire and flood as individual explanatory variables to the model set. The model that contained a flood effect received some support, whereas the model that contained a fire effect received little support (Table 3). Model-averaged parameter estimates showed that flooding was positively associated with cricket abundance ($\beta = 1.65$, 95% CI: 1.64–1.65), and fire had a weaker, positive association with cricket abundance ($\beta = 0.16$, 95% CI: 0.11–0.21).

The general model that best explained isopod abundance contained disturbance and vegetation variables and received most of the support among the model set ($w_i = 0.56$). The model representing unmeasured plot effects also received some support ($w_i = 0.37$). We added specific models containing combinations of fire, flood, and vegetation variables to the model set. None of these models were supported by the data (Table 3). Model-averaged parameter estimates showed that wildfire ($\beta = 1.59$, 95% CI: 1.59–1.59), litter cover ($\beta = 0.05$, 95% CI: 0.05–0.05), forb cover ($\beta = 0.37$, 95% CI: 0.37–0.37), and cottonwood density ($\beta = 0.04$, 95% CI: 0.04–0.04) were positively associated with isopod abundance, whereas flooding ($\beta = -1.92$, 95% CI: -1.92 to -1.92) and saltcedar density ($\beta = -0.02$, 95% CI: -0.02 to -0.02) were negatively associated with abundance.

Discussion

Data from pitfall traps suggests that crickets were less abundant at recently burned plots than unburned plots. Crickets were most abundant at the San Pedro wildfire plot, which had burned 8 yr before trapping and subsequently flooded several times. Flooding

seems to have a positive effect on cricket abundance, whereas abundance does not seem to respond to wildfire, although abundance was reduced in recently burned sites. These results reflect the relationship of *G. alogus* and flooding found in other studies (Ellis et al. 2001, Cartron et al. 2003) and suggest that cricket numbers initially respond negatively to wildfire but can recover with time if flooding occurs.

The hypothesis identified by model selection as the best explaining cricket abundance stated that unmeasured, plot-related variables were strongly associated with cricket abundance. We therefore cannot conclude that flooding alone resulted in the high cricket abundance at the San Pedro site. In addition, the San Pedro site was the only one to flood before sampling, so we cannot rule out other variables that could result in high abundance at this site. Previous research has shown that *G. alogus* prefers habitat with moistened leaf litter (Ellis et al. 2001, Cartron et al. 2003), however, so we are confident that the presence of flooding is among the most important variables limiting the abundance of this organism. Additional sampling at plots that burned but were not subsequently flooded is needed to confirm the importance of flooding to postfire cricket recovery. Because this study is exploratory in nature, additional variables such as litter composition and decay rates should be measured or experimentally altered to fully understand variation in cricket abundance.

Model selection results supported the hypothesis that variation in isopod abundance is best explained by disturbance and vegetation variables. These results are consistent with previous studies showing a negative response of isopods to flooding (Ellis et al. 2001) and a positive response to density of native vegetation (Paris 1963). Isopods were most abundant at the Rio Grande Complex (RGC) site. One possible explanation for this high abundance is that the high density of native vegetation at this site, including coyote willow and forbs (Smith et al. 2007), creates conditions favorable for isopods. Isopod density has been linked with availability of dead leaves and forbs (Paris 1963), both of which are abundant at the RGC wildfire plot (Smith et al. 2007). Desiccation is a common form of isopod mortality and isopod abundance is positively associated with moisture (Paris 1963, Warburg et al.

1984). High vegetation density and mesic conditions at the RGC wildfire seem to provide abundant food and low risk of desiccation for isopods during high temperatures, resulting in high isopod abundance. Areas of the forest with high saltcedar density are often more xeric and have less litter cover than areas with more native vegetation (D.M.S., unpublished data). These shrubland-like stands of saltcedar are likely less suitable for isopods, and this may explain the negative association of isopods with saltcedar. Although crickets were captured in large numbers at the RGC unburned sites, few were captured in the RGC wildfire plot where isopods were most abundant. Conditions that result in high isopod abundance in wildfire plots could therefore be detrimental to cricket abundance. Further research is necessary to better understand conditions that result in high isopod abundance and low cricket abundance in wildfire plots.

Loss of crickets from riparian forests could have negative consequences for animals at various trophic levels. Detritivores are an important link between producers and consumers in systems such as arid environments (Polis 1991, Polis and Strong 1996). In the Middle Rio Grande, crickets are often depredated by breeding forest songbirds (D.M.S., unpublished data) and are likely preyed on by a variety of arthropod and vertebrate predators. As consumers of leaf litter, crickets play an important role in transferring energy and nutrients from riparian vegetation to higher consumer species. Terrestrial isopods, however, are thought to be unpalatable to many predator species, and little evidence exists for high levels of predation on isopods (Paris 1963, Moulder and Reichle 1972). Replacement of crickets by less palatable detritivores such as isopods could result in loss of a food resource for birds and other secondary consumers. In addition to consumers, plants and other producers are negatively affected when exotic species, such as isopods, are abundant (Crooks 2002). For reasons such as this, invasive species are one of the greatest threats to forest ecosystems, and their population growth must be controlled (USDA Forest Service 2004). In the event of wildfire in riparian forests, managers should create conditions that prevent the establishment of isopods as dominant detritivores to preserve natural ecosystem processes.

We found little evidence for strong positive effects of fire on native detritivores. Cricket abundance was high at only one wildfire plot where flooding had also occurred, so fire alone cannot be linked to high cricket abundance. Costs of fire in riparian forests include loss of native vegetation, increased densities of exotic vegetation, and changes in riparian-dependent animal communities (Busch 1995, Smith et al. 2006). For these reasons, continued occurrence of wildfire, or prescribed burns, will negatively affect native crickets and alter the composition of forest floor arthropod communities as forests recover (Bess et al. 2002). To protect native forest floor arthropods and the entire riparian ecosystem, wildfires should be prevented and prescribed fire should be used sparingly.

Numerous authors have shown that restoration of flooding in the riparian understory is essential to the persistence of native plant and animal species (Howe and Knopf 1991, Molles et al. 1998, Scott et al. 2003). The results of this study provide an example of how flooding can mitigate the impacts of unnatural disturbance on native riparian fauna. By flooding wildfire plots, managers can aid the recovery of *G. alogus*, an ecologically important native detritivore and prevent dominance of exotic isopods. Mesic, but nonflooded, conditions found in the RGC wildfire plot seem to favor isopods and not crickets. Plots with an open understory that receives occasional flooding seem to have the highest cricket density and can best recover from wildfire. Although exotic saltcedar may not directly affect native crickets, removal of saltcedar may indirectly benefit crickets by reducing wildfire danger. In this riparian system, flooding results in lower saltcedar densities, increased survival of native vegetation, and reduced isopod density (Molles et al. 1998, Ellis et al. 2001). Managed flooding will likely benefit native detritivores in burned forests, but additional research on groups such as beetles and ants is needed to generalize these findings to the entire native detritivore community.

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