

FIRE GENERATES SPATIAL GRADIENTS IN HERBIVORY: AN EXAMPLE FROM A FLORIDA SANDHILL ECOSYSTEM

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Abstract. Disturbance can directly affect the interactions among species at different trophic levels. Because disturbances are typically localized, and many consumers are constrained in their mobility, disturbances can generate spatial variability in trophic interactions. Here, we consider how fire alters plant–insect interactions in a longleaf pine ecosystem in central Florida, USA. We hypothesized that fire in the short term would directly depress herbivore abundance, and that the rate of re-colonization by herbivores would depend upon distance from the edge of the recently burned area. Thus, fire should generate spatially varying herbivory. Orthopterans are dominant insect consumers in our system, and many species are flightless, either as juveniles or adults; these species are particularly likely to show constrained post-fire mobility. We quantified insect abundance and herbivory levels on eight common understory plants in the edge and interior of three recently burned sites. As predicted, insect abundance at the edge of burned areas was much higher than in the interior. In addition, all plant species experienced at least twice the level of herbivory in the edge than in the interior of burned sites. This demonstrates that disturbance can create strong spatial variation in the magnitude of trophic interactions. We suggest that larger burns may aid in plant management by reducing herbivory, whereas the presence of unburned refugia may be critical to insect conservation.

Key words: disturbance ecology; fire; Florida (USA) pine ecosystem; herbivory; Orthoptera; prescribed burn; sandhill ecosystem; spatial gradient; trophic interactions.

INTRODUCTION

Disturbances influence the structure and function of many communities (Petraitis et al. 1989, Shea et al. 2004). Indeed, disturbances are often defined as discrete events that disrupt ecosystem, community, or population structure and change resource, substrate availability, or the physical environment (sensu White and Pickett 1985). Because disturbances are almost always spatially localized in extent and intensity (Turner et al. 2001), they create spatial structure in a landscape; areas disturbed by some event are typically adjacent to areas less disturbed by that same event. Moreover, disturbances may differentially affect the abundance of species in different trophic levels (Power et al. 1996, Wootton 1998, Moore et al. 2004), and can therefore alter the intensity of trophic interactions and alter spatial patterns of species diversity and composition through disturbance-induced edge-effects (Fagan et al. 1999, Cantrell et al. 2001).

Disturbances that are large in spatial extent may have qualitatively different effects on species abundances than smaller disturbances (Romme et al. 1998). For example, gaps created by a single treefall are generally filled by understory trees present before the distur-

bance, whereas gaps created by multiple treefalls provide adequate light to allow recruitment of new individuals from seed (e.g., Lorimer 1989). Here we suggest that large disturbances may also allow for edge effects, since displaced organisms recolonize the edge first, and then the interior. For example, if predators are displaced by disturbance and then recolonize, prey will experience higher levels of predation near the edge than near the interior of the disturbed site. This would create spatial heterogeneity in trophic interactions, the duration of which will depend on both the size of the disturbance and the dispersal ability of the displaced species.

In this study we examine how fire influences the spatial pattern of trophic interactions between herbivorous insects and plants in a longleaf pine ecosystem, which was historically maintained by periodic fires (Platt et al. 1988). Effects of fire on plant diversity and community composition are well documented, as are the effects of temporal burn patterns (e.g., Menges and Hawkes 1998). However, less is known about how fire influences other trophic levels, such as herbivorous insects (Swengel 2001). Even less is known about how trophic interactions vary spatially within burned sites (but see Vickery 2002).

Fire may directly and indirectly affect the abundance and diversity of herbivorous insects (Swengel 2001). In the short term, fire negatively affects insect numbers; many are killed by fire, or die of starvation before their host plants reemerge or germinate post-fire. Less mo-

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PLATE 1. (Top left) Sandhill Ecosystem at the Ordway Preserve. This photograph was taken a few months after a growing season burn. Photo credit: Stephen Coates. (Top right) *Melanoplus rotundipennis*, a common grasshopper at the Ordway Preserve that is flightless throughout its life. Photo credit: Jon Chase. (Bottom left) Typical *Tephrosia virginiana* individual in the interior of a recently burned sandhill at the Ordway Preserve, where the incidence of herbivory is low. Photo credit: T. Knight. (Bottom right) Typical *Tephrosia virginiana* individual in the edge of a recently burned sandhill at the Ordway Preserve, where the incidence of herbivory is high. Photo credit: T. Knight.

bile species (e.g., flightless grasshoppers [Bock and Bock 1991]) and life stages (e.g., eggs and pupae in the soil) are particularly vulnerable. Insect populations can recover after a fire by in situ survival of individuals and by recolonization from adjacent unburned (refugia) areas (Harper et al. 2000, Panzer 2003). Insect species less adept at flight may take months to years before they can completely recolonize a large burned area (Pippin and Nichols 1996, Swengel 2001). Therefore, we hypothesize that in the burned area shortly after a fire, herbivorous insects should be most abundant near edges adjacent to unburned refugia and lowest in the interior of the recently burned area. If these herbivores can inflict significant damage on plants, this spatial pattern in herbivore abundance should lead to spatial heterogeneity in the intensity of herbivory.

METHODS

Our study sites were in the sandhill ecosystem of North-Central Florida, which occurs on hilltops with well-drained sands (Myers 1990; see Plate 1). The overstory of this community is dominated by longleaf pine (*Pinus palustris*). Ground cover is typically dense, dominated by wiregrass (*Aristida stricta*), juvenile longleaf pine, turkey oak (*Quercus laevis*), shrubs (e.g., Florida rosemary, *Ceratiola ericoides*), and a wide variety of perennial herbs. Sandhill vegetation once covered >28 million hectares in the southeast United States, while today only <2 million hectares remain (Noss 1989). The natural fire frequency in sandhills is 1–10 years (Myers 1990, Frost 1998, Menges and Hawkes 1998). When fire is suppressed, the system succeeds toward a hardwood forest community (Myers

1990), and thus prescribed burning is a critical tool for managing these endangered habitats (Platt et al. 1988).

We chose three sites that had large prescribed fires in early spring 2003: two at the Katharine Ordway Preserve-Swisher Memorial Sanctuary (University of Florida; Melrose, Florida, USA) and the third at Goldhead Branch State Park (Keystone Heights, Florida, USA; 15 km from Ordway). At the Ordway sites, fires occurred on 15 February (site 1) and 26 March (site 2); each covered 1.9 km² and were separated by 300 m. One km² of the third site was burned on 13 February. Prior to 2003, it had been >10 years since these sites had been burned. Understory plants appeared 2–3 weeks after the fire at all sites. All fires were low in intensity (did not kill canopy or understory trees) and were separated from unburned areas by narrow dirt roads. Fires were ignited using backing and strip-head techniques and were spread by south-southwest winds. The north lines were blackened first with a back fire (9 m flame lengths), and then burned with multiple flank fires that traveled from north to south through the management units (flame lengths ranged from 0.5 to 2 m). These fires left little understory unburned (low level of patchiness within each burned site).

At each site, one edge was chosen for censuses. The chosen edge was adjacent to areas not burned within the past two years and had all eight of our focal plant species at sufficient densities for sampling. At each site, we chose three sampling locations at different distances into the burn (hereafter “location”): (1) 10 m just outside the burn (“unburned edge”), (2) 10 m just inside the burn (“burned edge”), and (3) 500 m inside the burn (“burned interior”). At each location and site we sampled herbivorous insect diversity and abundance. In two locations (burned edge and burned interior) we also estimated insect herbivory. Plants in these locations presumably experienced the same intensity of fire and post-fire soil nutrient conditions, and occurred at similar densities. Therefore, differences in herbivory levels should be due to differences in the abundances of herbivores at these locations. We did not sample herbivory in the unburned edge, because such a comparison would provide limited information. Differences in herbivory between burned and unburned sites could be due to differences in the abundances of herbivores, the nutritional quality of the leaves, or the density of the focal plant species. At each site and location, we sampled insects and plant damage twice—during the peak of the growing season (17–30 May 2003), and near the end (16–19 August 2003). By sampling twice we could assess whether any spatial patterns in herbivore abundance and plant damage occurred and whether they attenuated throughout the season.

Insects were sampled in two ways: quadrats and sweep netting. All sampling was conducted between 09:00 and 11:00 hours, during peak insect activity times. First, two parallel rows of 10 0.1-m² quadrats were laid out, separated by 10 m; within rows, quadrats

were separated by at least 5 m (bare areas of ground were not sampled). We sampled quadrats by gently stirring the area with a 1.5-m stick and counting the number of insects of each type that emerged. This method is particularly useful for sampling grasshopper density (Onsager and Henry 1977). Second, two sweep samples were taken at each site and location to improve sampling of less mobile insects (e.g., larval lepidopterans), and to supplement our jumping-insect samples. Sweeps were separated by at least 10 m, but were within 20 m of the quadrats. Each sweep sample consisted of 10 full sweeps, each over a separate 1-m² area of vegetated ground, using a 38-cm-diameter sweep net. All insects were identified into broad taxonomic units (at least to the family level), and all orthopterans were identified to species using illustrated field guides (Capinera et al. 2001).

While we hypothesize that post-fire spatial distributions of herbivorous insects are caused by dispersal limitation, we cannot rule out other hypotheses that may generate the predicted spatial pattern, such as greater insect predation in burned interior or attraction of insects to edges. However, the small dirt roads that define the burned sites should have minimal effects on the spatial distribution of predatory species (e.g., birds, lizards) at these sites. It did seem plausible that insect abundance could be influenced by edges in general. To examine the potential of a generic edge effect, we sampled herbivorous insects (as above) at 100-m intervals from the edge into the burned (six locations: 0–500 m) and adjacent unburned areas (four locations: 0–300 m) at Ordway site 1 on 29 March 2003.

At each site and location, we estimated the amount of foliar herbivory on eight common sandhill plant species, spanning a wide variety of life-forms and plant families: tree seedlings of *Diospyros virginiana* (Ebenaceae, common persimmon) and *Quercus laevis* (Fagaceae, turkey oak); the shrubs *Asimina incarna* (Annonaceae, flag paw paw) and *Licania michauxii* (Chrysobalanaceae, gopher apple); and the perennial herbs *Croton argyranthemus* (Euphorbiaceae, silver croton), *Eriogonum tomentosum* (Polygonaceae, wild buckwheat), *Rhynchosia reniformis* (Fabaceae, dollar weed), and *Tephrosia virginiana* (Fabaceae, goat's rue). There were no significant differences in plant density or individual size between the burned edge and interior locations for these species (T. M. Knight and R. D. Holt, unpublished data). At each location and site, we censused plant damage on 10 individuals per species. Some species are capable of extensive clonal growth; for these, measurements were taken on individual ramets. For both clonal and nonclonal species, we censused individuals separated by at least 5 m to reduce the likelihood of spatial autocorrelation in herbivory. For each individual or ramet, the percentage of leaf tissue leaf lost to herbivores was visually estimated on a haphazardly chosen sample of leaves for each plant (at least 30% of the total number of leaves present were

measured). Although visual estimates may be less precise than other more destructive methods, the same individual estimated all plant damage, which should eliminate any systematic bias among locations. We categorized the type of damage into two broad categories, leaf chewing and leaf mining.

Statistical analyses

We used ANOVA to determine whether insect abundance varied with location (unburned edge, burned edge, and burned interior), time (May, August) or their interaction. Insect abundance is the sum of orthoptera seen in all sweep nets and quadrats at each location. Both location and time were considered fixed variables, and insect abundance values were log transformed prior to analyses. Following a significant location effect, we used Tukey's HSD to detect pairwise differences. For each plant species, we used ANOVA to determine whether herbivore damage varied with location (burned edge, burned interior), time (May, August) or their interaction. Measurements of damage at each location and time were averaged, and this value served as the unit of replication. We arcsine-transformed damage values prior to ANOVA to correct for any skews in distribution due to the fact that the percentage of herbivory data is constrained between 0 and 100%. Because the same plants were not sampled in each time period, repeated-measures analyses were not appropriate. Each prescribed burn was a separate replicate in this study, and therefore our replication was necessarily low, increasing the risk of a type II error.

RESULTS

Orthopterans of the families Acrididae (short-horned grasshoppers) were by far the most abundant group of herbivorous insects (by biomass) at our study sites, comprising >85% of total herbivorous insect biomass (see Plate 1). Further, this group of herbivores was observed consuming all of the study plant species except *Croton argyranthemus*. Other herbivorous groups of insects, including Coleopterans (beetles), Homopterans (leaf-hoppers and aphids) and larval Lepidopterans (moth and butterfly caterpillars) comprised <5% each of the overall biomass of herbivorous insects. In the remainder of this paper, we focus on spatial patterns in orthopterans, because meaningful statistics could be conducted on this group.

We found a significant location effect (ANOVA; $df = 2$, $F = 17.06$, $P < 0.001$), but no significant time effect (ANOVA; $df = 1$, $F = 0.01$, $P = 0.937$) or time \times location interaction (ANOVA; $df = 2$, $F = 3.21$, $P = 0.076$) on [log] orthopteran abundance (Fig. 1A). In May (7–13 weeks after the fires), the significant location effect was due to lower density of orthopterans in the burned interior (Tukey's HSD; $P < 0.01$) relative to the burned and unburned edges, which were not significantly different from each other (Tukey's HSD; $P > 0.3$). In August (20–26 weeks after the fires), the

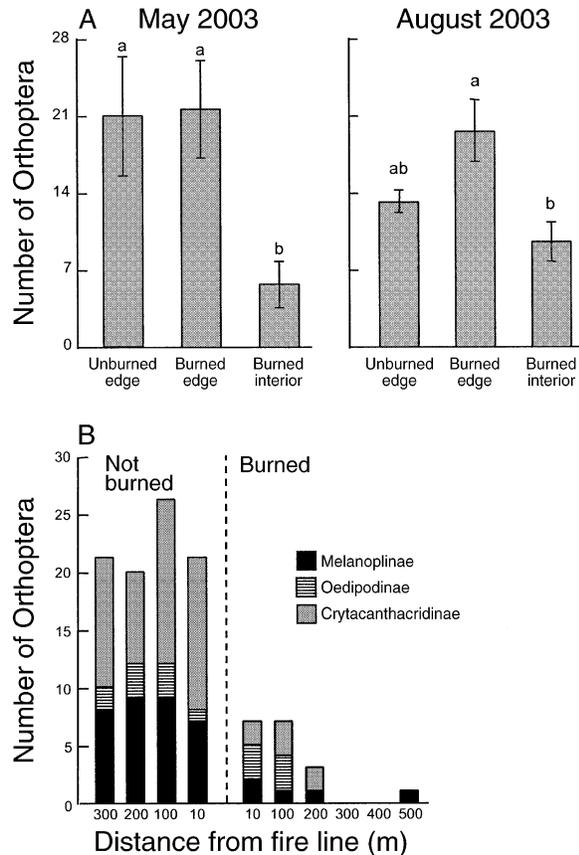


FIG. 1. Abundance of Orthoptera after fire at sites in a sandhill ecosystem, north-central Florida, USA. (A) Number of Orthoptera from three recently burned sites in May and August at three locations: unburned edge (10 m just outside the burn), burned edge (10 m just inside the burn), and burned interior (500 m inside the burn). Data are numbers of Orthoptera from twenty 0.1-m² quadrats and two sweep net samples (means \pm 1 SE across all three sites). Bars with the same lowercase letter are not significantly different between locations within the sampling date (Tukey's hsd, $P < 0.05$). (B) Number of Orthoptera in a recently burned site (Ordway 1) and unburned adjacent area at different distances from the fire edge. Bars represent numbers of Orthoptera from twenty 0.1-m² quadrats and two sweep net samples. Fill types distinguish individuals in subfamilies within the family Acrididae (Melanoplineae, Oedipodinae, Crytacanthacridinae).

highest density of orthopterans was in the burned edge (Tukey's HSD; $P < 0.03$), and numbers were equal both in the unburned edge and the burned interior (Tukey's HSD; $P > 0.2$). The marginally significant location \times time interaction indicates that more orthopterans were in the interior for the later sampling date, suggesting that the pattern might be slowly diminishing through time (Fig. 1A), which is expected if recolonization is ongoing but dispersal back into burned areas is limited in distance. We were concerned that perhaps insects were responding to edges in general, rather than the particular edge effect that we were interested in (fire), but found no evidence for such a generic edge

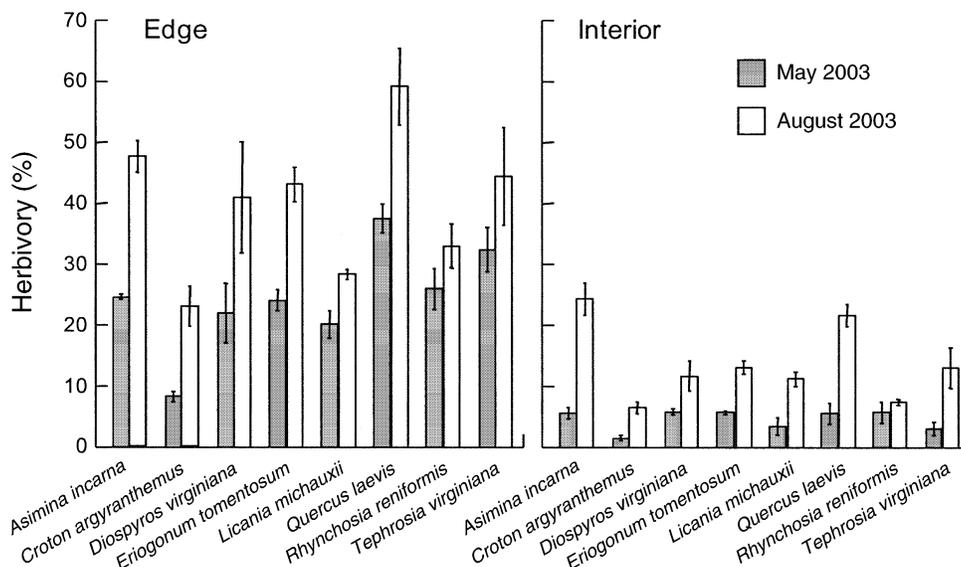


FIG. 2. Herbivory on eight plant species in the edge (10 m from the fire edge) and interior (500 m from the fire edge) of three burned sites in May and August. Data are means \pm 1 SE; the average percentage leaf herbivory was estimated from 10 plants per species at each location.

effect on abundance (Fig. 1B). In the burned, but not the unburned, areas, distance from edge had a strong effect on orthopteran abundance; this pattern is consistent with the hypothesis that these insects were directly reduced by the fire and had recolonized burned areas from unburned areas.

The effects of fire on insect abundances were paralleled by dramatic spatial variation in herbivore damage. For most plant species, leaf chewing was the most destructive damage (in terms of tissue loss), although species varied in the proportion of different types of damage they received. For example, turkey oaks (*Quercus laevis*) received a large proportion of mining damage (see also Kerstyn and Stiling 1999), whereas flag pawpaw (*Asimina incarna*) received only leaf-chewing damage. We only present data on total leaf damage, because this is the response variable most pertinent to the plants. In May, 7–13 weeks after the fires, there was at least a four-fold greater amount of damage to most of the plant species at the edge compared to the interior of the burn (a significant effect of location; Appendix, Fig. 2, Plate 1). In all but one species (*Rhynchosia reniformis*), there was a significant time effect; plants had more damage in August than in May (Appendix, Fig. 2). Four species had a significant (or nearly significant) location \times time interaction; differences between burned edge and interior were more pronounced in May than in August (Appendix, Fig. 2).

DISCUSSION

We have shown that a localized disturbance such as fire can have strong, predictable effects on the spatial pattern of trophic interactions. Interior plants may indirectly enjoy a respite from insect herbivory because

of the direct impact of the fire in reducing insect herbivore abundance, and a lag in recolonization by these taxa. This pattern is expected since the dominant herbivores in this system should be displaced by fire. Many species of sandhill grasshoppers overwinter as adults or nymphs (Squittier and Capinera 2002), including *Achurum carinatum*, the most common species in our early surveys. Because both adults and nymphs are wingless, it is unlikely they could escape early spring fires. However, other species of grasshoppers overwinter as eggs underground. For example, another common sandhill species, *Melanoplus rotundipennis*, is almost entirely in the egg stage during the February and March fire season (Squittier and Capinera 2002). We found that this species was also more abundant in the edge than in the interior of the burn. This suggests that even though prescribed fires in these sandhill ecosystems are low in intensity, they either kill underground eggs or otherwise reduce hatching success.

Even more than 20 weeks following a fire there was a strong effect of spatial location on both insect abundance and the amount of herbivory received by plants. Most grasshoppers at our sites spend a significant proportion of their lives as flightless juveniles (Squittier and Capinera 2002), which are likely ineffective at long-distance dispersal. Moreover, many species of sandhill grasshoppers, including some of the most common species in our study (*A. carinatum* and *M. rotundipennis*), are brachypterous (wingless) as adults, and are likely to experience dispersal constraints.

Our study lasted only one season, and so it is an open question as to how long the spatial signal of the fire on orthopteran abundance and herbivory will last. Another study on small burned plots in Florida sand-

hills found that grasshoppers increased in abundance in years following a fire (Kerstyn and Stiling 1999). This is most likely because plants became more edible (the pulse of soil nutrients after a fire results in more nutrient-rich foliage, e.g., Radho-Toly et al. 2001) and grasshoppers could quickly get to the center of the small plots. However, in a much larger California grassland fire, Porter and Redak (1996) found that it took nearly two years for grasshoppers to rebound in the interior of the burn. Surprisingly, this long recovery time occurred despite the fact that the dominant species of grasshopper at the site was *Melanoplus sanguinipes*, a winged grasshopper capable of long-distance flights, and whose common name is the “migratory grasshopper.”

On average, plants in our study experienced 220% more herbivory at the edge relative to the burn interior. However, we only measured the amount of damage, and we do not know how this tissue loss will translate into plant fitness. Nevertheless, we suspect that the herbivory observed during the time frame of this study could decrease lifetime plant fitness for two reasons. First, herbivory levels at the burn edge are high; many plants lost 30–40% of their leaf tissue to herbivores. Second, the period after a burn may be important for pulses of growth and reproduction for these long-lived species capitalizing on reduced competition and a flush of nutrients (Myers 1990, Heuberger and Putz 2003). Thus, herbivory during this critical time window may influence lifetime fitness and population dynamics. If herbivory does indeed decrease plant fitness at the edge of burned sites, then we would expect to see herbivory-mediated shifts in the plant community between the edge and interior locations in the future.

Although often overlooked in the management of fire-obligate ecosystems, insect herbivores may affect the ability of the plant community to respond to fire. Vickery (2002) found that seed predation on a threatened plant species, northern blazing star (*Liatrix scariosa* var. *novae-angliae*), declined along transects from the edge to the interior of large burns in a grassland in Maine (USA). He suggested that the conservation of this rare species would require burns of a larger size. Our results suggest that a similar management strategy may benefit sandhill plant species. Larger burns would provide more “interior” area, allowing a greater proportion of plants to have a temporary release from insect herbivory.

Our study focused on the immediate negative effects of fire on insects. However, fire may have indirect positive effects on herbivorous insects in the long-term (Kerstyn and Stiling 1999, Panzer and Schwartz 2000, Swengel 2001, Panzer 2002). Fire releases nutrients into the soil, which may increase host-plant abundance and quality. Moreover, without fire, the ecosystem to which these insects are adapted would be lost. Despite these benefits of fire, entomologists have argued that small, isolated insect populations may be incapable of

surviving repeated management burns (e.g., Schlicht and Orwig 1992, Reed 1997, Dietrich et al. 1998). Insects may only be able to tolerate large burns if there are adequate unburned refugia nearby, or patchiness within the burned site itself that increases in situ survival of these species (Panzer 2003). Our results suggest that sufficiently large and heterogeneous landscapes must be protected to replicate the natural systems in which these species evolved. In such landscapes, plants can have temporal refuge from herbivorous insects after a fire and insect populations can rebound from population losses during the fire without facing the risk of local extinction.

Some theoretical and empirical work has suggested that disturbance may differentially influence the abundance of species in different trophic levels (Power et al. 1996, Wootton et al. 1996, Wootton 1998). However, the spatial consequences of disturbances on trophic interactions have been neglected both theoretically and empirically. In our study, disturbance (fire) positively affects plants and negatively affects herbivores. The spatial configuration of the system will determine the overall strength of the interaction between herbivores and plants. Both the frequency (temporal) and size (spatial) of fire determine its effect on the ecosystem. While there has been much theoretical and empirical work done elucidating effects of the temporal sequence of fires on plant persistence (e.g., Amarasekare and Possingham 2001), the spatial arrangement of fires has rarely been considered. However, even under identical temporal sequences, whether fires occur as a few large or several small fires could have profoundly different consequences for plant fitness and plant–insect interactions, because plants reemerging following small fires would be expected to experience more herbivory.

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APPENDIX

A table presenting ANOVA results for each plant species of the main effects of location, time, and their interaction on the total percentage of vegetative herbivory observed is available in ESA's Electronic Data Archive: *Ecological Archives* E086-031-A1.