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Complexity and variation in the effects of low-severity fires on forest biota

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COMPLEXITY AND VARIATION IN THE EFFECTS OF LOW-SEVERITY FIRES ON FOREST BIOTA

by

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B.Sc. University of Arizona, USA, 1996

Presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

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ABSTRACT

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Complexity and variation in the effects of low-severity fires on forest biota. (206 pp.)

Advisor: Richard L. Hutto

The ecological effects of fire are varied and complex, yet the effects of even the most commonly applied fire treatments in the United States have been documented in ways that necessarily mask complexity and hide much of the variation effected by nominally similar burns. Reliance upon information gleaned from case studies of a narrow range of fire effects within a limited focal area to develop fire-management strategies for a wide domain of interest is especially evident in the American Southwest. Despite ardent speculation on both the acute and chronic influences of prescribed burning on populations of southwestern forest biota, including birds and arthropods, actual responses have seldom been quantified, and have never been quantified in ways that convey reliability.

Here, I provide the first estimates of short-term responses of a wide range of arthropods to low-severity, fall burns in southwestern ponderosa pine forests. I characterize these effects functionally, by grouping all insects, arachnids, and myriapods according to their general ecological roles within the forest community, and quasi-experimentally, by capitalizing on three nominally similar prescribed fires set within widely separated stands of comparable forest. I show that arthropods of southwestern ponderosa pine forest are keenly sensitive to even the most outwardly benign fire treatments, and that similar fires can effect disparate responses from a number of taxa.

Birds that depend heavily on the forest understory for food, cover, or both, are commonly assumed to be sensitive to prescribed burns. I show that the reproductive success of a ground-nesting, ground-foraging, insectivorous bird - the Yellow-eyed Junco - can indeed be compromised by low-severity, autumn fire in southwestern ponderosa pine forest. I attribute this effect to changes in availability of preferred nesting microhabitat. If all fires were to affect junco demography in a similar fashion, the chronic influence (i.e., historic recurrence) of disturbance alone could set bounds to populations of these birds. I show, however, that different prescribed burns can affect key resources in different ways, such that fire's influence on junco populations may differ considerably among treatments.

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In the fall of 1996 my interest in fire ecology was piqued as I watched the woods burn in Saguaro National Park. I was a seasonal Biological Science Technician, hired by the park to conduct breeding bird surveys, but assisting at the time with a prescribed burn in ponderosa pine forest atop Mica Mountain. This experience spurred my initial ideas for this research, work that would capitalize upon prescribed burns to further our understanding of the ecological role of fire in Southwestern ponderosa pine forests. It was also work that, from the outset, I knew would not be possible without tremendous logistical assistance from the park. For their unwavering support over the many years that followed, I am so very grateful to past and present staff at Saguaro National Park including Natasha Kline, Meg Weesner, Kathy Schon, Rick Anderson, Rob Martin, Pat Haddad, Chuck Scott, Paula Natsiatka, Don Swann, Bob Lineback, Doug Morris, Frank Walker, Bill Dabney, Jim Williams, Todd Nelson, and Denise Jupinko.

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PREFACE

The ecological effects of fire are incredibly varied and can be extremely complex. The response of any given plant or animal population to burning, for example, depends not only on the characteristics of the fire (e.g., timing, intensity, duration, extent), the nature of the affected organisms (e.g., vital attributes *sensu* Noble and Slatyer 1980), and the post-fire weather, but also on any fire-caused changes in the activity or density of biota — from microbes to vertebrates — with which the target individuals reliably interact (Whelan 1995). The potential for broad differences in fire characteristics and the vulnerabilities of organisms to effect varied outcomes of burning has long been emphasized in fire-effects literature (e.g., Ahlgren and Ahlgren 1960, Whelan 1995, Miller 2000). Hence we expect, for example, disparities in the responses of the same forest biota to crown versus understory fires and in the responses of different plants or animals to either type of burn. Yet because (1) no two fires ever behave in precisely the same way (Johnson and Miyanishi 1995, Whelan 1995), (2) no two patches of land are ever exactly alike in terms of the biota they support or, moreover, the abiotic influences (i.e., weather) to which they are subject (Gleason 1926, Downes et al. 2000, Hansson 2003), and (3) all but the immediate, or first-order, influences of burning are underlain further still by a snarl of contingencies and complex interactions (e.g., Bailey and Whitham 2002; reviewed in Whelan 1995), even nominally similar fires are liable to effect very different latent changes in population vital rates, and community structure, and ecosystem processes within a given habitat. In other words, it is probably a safe bet that *any two fires* will differ in the direction or magnitude of many key ecological effects, including those of prime management interest.

The potential for marked disparities in the ecological effects of nominally similar fires should have a strong bearing on the ways in which fires are studied, fire-effects information is interpreted, and fire management decisions are made. As no single study can ever characterize fully the range of potential outcomes effected by fires set or allowed to burn under particular conditions within a region of interest, explanations and expectations of *typical* changes must be tempered continually to reflect new revelations from investigations repeated in space and time (Whelan 1995, Aquiliani et al. 2000, Van Mantgem et al. 2001, Johnson 2002). Such is the crux of adaptive fire management (Walters 1986, Arno and Allison-Bunnell 2002). Recent qualitative reviews of the way in which fire-effects research has been conducted in the U.S. over the past half century or so suggest, however, that fire-effects information has been amassed largely with a blind eye toward the complexity of and variation in latent (i.e., indirect) ecological responses to burning (McMahon and deCalesta 1990, Robbins and Meyers 1992, Engstrom et al. 1996, Lyon and Smith 2000, Tiedemann et al. 2000, van Mantgem et al. 2001). These critics contend that much research has been focused and designed in ways that compromise both the internal and external validity of causal inferences drawn from individual studies and preclude meaningful synthesis of findings from independent investigations conducted within management domains. Hence, as Van Mantgem et al. (2001) explain, while "the literature is rife with conflicting reports for very basic fire effects," the degree to which this variation reflects "unique fire-mediated responses of the organisms and resources under study" as opposed to "the difficulty in assessing impacts of fire using traditional statistical approaches" (i.e., via the study of truly replicated fire treatments) is unclear.

In chapter 1, I show, via the first quantitative review of this topic, that the ecological effects of even the most commonly applied fire treatments in the United States have indeed been documented in ways that necessarily mask complexity and hide more of the true variation effected by nominally similar treatments than they reveal. In particular, I show that (1) case studies of single fire events within (often much broader) domains of interest have been a primary source of fire-effects information, (2) studies of the short-term effects of burning on vegetation dominate the literature, and (3) despite opportunities for experimentation afforded by prescribed burning (Whelan 1995, Van Mantgem et al. 2001), strong causal inferences can be drawn from few investigations. Consequently, for at least a half century, decisions of whether, when, and how to burn within the most fire-prone vegetation types in the U.S. have often been (1) heavily influenced by observations from a single fire within the region of interest, (2) made against a background of little or no information on the effects of fire (or a fire regime) on a range of biota and hence with little appreciation of the potential for complex fire-stimulated interactions to influence the outcome(s) of interest, and (3) based on necessarily weak inferences drawn from inadequately designed research. In sum, fire-effects studies have seldom been conducted in ways that allow us to gauge the reliability of or to develop a more sophisticated understanding of the often complicated indirect effects of replicated fire treatments and to adapt our management practices accordingly.

Reliance upon information gleaned from case studies of a narrow range of fire effects within a limited focal area to develop fire-management strategies for a wide domain of interest is especially heavy in the American Southwest (see Chapter 1). Low-severity fires are commonly prescribed throughout the region's low-elevation, dry forests as part of ecological restoration programs developed largely according to the responses of vegetation to fires set within stands of ponderosa pine forest near Flagstaff, Arizona. These fires are set outside the historic fire season in southwestern ponderosa pine forests and therefore, strictly speaking, cannot restore fire's historic ecological role in these ecosystems. Nonetheless, these treatments are touted to reduce hazard levels of fine fuels, "revitalize" vegetation, and stimulate "natural regeneration," thereby providing for "better forest health" throughout the region (Sackett et al. 1996). Whether fall burning on a regular basis throughout the region will, in time and on average, effect such outcomes remains to be seen. To be sure, many short-term changes in fuel loadings and stand structure that are known prerequisites for desired long-term responses (i.e., periodic exposure of mineral soil, liberation of nutrients, and thinning of understory) can probably be effected reliably by the treatments (Sackett et al. 1996, Wan et al. 2001, Kopper et al. 2002). That is not to say, however, that any given fire, or suite of fires, will effect desirable changes in forest communities. Despite ardent speculation on both the acute and chronic influences of prescribed burning on populations of a wide range of forest biota, including birds and arthropods, actual responses have seldom, if ever, been quantified (Finch et al. 1997, Short and Negron 2003) and never in ways that convey reliability. It is therefore impossible even to begin to tailor burning programs to suit many local and present-day land management needs.

In Chapter 2, I provide the first estimates of the acute responses of a wide range of arthropods to low-severity, fall burns in southwestern ponderosa pine forests. Although the focus of astonishingly little research to date, these animals play key roles (e.g., as decomposers, herbivores, pollinators, predators, parasites, prey) within these communities, interacting heavily with all other forest biota both before and after burning. Because the forest floor and understory are likely to house 90% of forest arthropod species for at least part of their life cycle (Klein 1988), and the fires invariably affect these strata, these prime movers and shakers of forest communities should be vulnerable to both the direct and indirect effects of these treatments. Here, I characterize these effects functionally, by grouping all insects, arachnids, and myriapods according to their general ecological roles within the forest community, and quasi-experimentally, by capitalizing on three nominally similar prescribed fires set within widely separated stands of comparable forest. I show that arthropods of southwestern ponderosa pine forest are keenly sensitive to even the most outwardly benign fire treatments, and that similar fires can effect disparate responses from a number of taxa. Because these animals heavily influence so many key ecosystem processes, fire-caused changes in the arthropod community are surely responsible at some level for what we perceive as indirect effects of burning on other forest components, including plants and vertebrates. Research to further detail the ecological roles of a wide range of arthropods should aid the development of robust models of fire effects on any forest attributes of interest within any locale.

Whereas changes in activity or density of invertebrates may be caused directly or indirectly by fall burns in southwestern ponderosa pine forests, these treatments should affect vertebrate populations largely indirectly, via changes in the availability of food and cover. As changes in resources effected by these fires can differ considerably among replicated treatments, our ability to predict consequences of prescribed burning for these wildlife should rest squarely upon our understanding of the mechanisms that translate often-disparate resource responses into changes in demographic parameters of target vertebrate populations (Marzluff et al. 2000). For example, birds that depend heavily on the forest understory for food, cover, or both, are commonly assumed to be sensitive to prescribed burns in ponderosa pine forests, because the treatments are sure influence the availability of these key resources at multiple scales (Finch et al. 1997, Arno and Allison-Bunnell 2002). Yet there are no reports of how these animals have, in fact, been affected by any given treatments. In chapter 3, I show that the reproductive success of a ground-nesting, ground-foraging, insectivorous bird — the Yellow-eyed Junco — can indeed be acutely compromised by low-severity, autumn fire in southwestern ponderosa pine forest. I attribute this effect solely to changes in availability of preferred nesting microhabitat, as there was no evidence of a fire-caused depression in the density of active arthropod prey. If all fires were to affect junco demography in a similar fashion, the chronic influence (i.e., historic recurrence) of disturbance alone could set bounds to populations of these birds. I show, however, that different prescribed burns can affect key resources in different ways, such that fire's influence on junco populations may vary widely among treatments. This case study simply demonstrates "how possibly" the fires used to manage southwestern ponderosa pine forests can affect wildlife deemed sensitive the practice (*sensu* Hargrove and Pickering 1992). Only via synthesis of findings from similar quasi-experiments conducted repeatedly in conjunction with prescribed fires might explanations and expectations of *typical* responses and population consequences at multiple scales of interest ever emerge (Whelan 1995, Aquiliani et al. 2000, Van Mantgem et al. 2001, Johnson 2002). To this end, the data presented provide a solid foundation upon which to build.

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—CHAPTER 1—

CHALLENGES AND OPPORTUNITIES IN THE STUDY OF PRESCRIBED FIRES: AN EVALUATION OF FIRE EXPERIMENTS IN THE CONTERMINOUS U.S., 1950-2002

INTRODUCTION

Fire has long influenced the distribution and abundance of plants and animals and the evolution of their life histories (Naveh 1975, Gill 1975, Bazzaz 1984, Sousa 1984, Whelan 1995). Over the past few centuries, humans have increasingly swayed the influence of this potent ecological force on the world's biota (Anderson 1956; Stewart 1956; Pyne 1982, 1995, 1997). Today, deliberate and accidental firings of forest and rangeland largely set the pattern and tempo of ignitions in many locales, while activities such as road building, livestock grazing, timber harvest, and direct suppression efforts often dictate the behavior and first-order effects of fire (Pyne 1997b, Leenhouts 1998, Saab et al. *in prep.*). Under unprecedented human control, contemporary fire regimes often bear little resemblance to those that shaped natural communities for millennia (Agee 1990; Pyne 1982, 1995, 1997; Andersen et al. 1998).

Concerns that dramatic departures from historic fire regimes could endanger native plants and wildlife have prompted efforts to restore some semblance of historic fire occurrence to natural areas worldwide via prescribed burning (Moore 1987, Van Wilgen et al. 1990, Pyne 1997, Fernandes et al 2000, Carle 2002). Yet, due to incomplete knowledge of past regimes and limitations of fire control, contemporary fire treatments may have little historic precedent with regard to their typical size, season, frequency, severity, or configuration (Whelan and Muston 1991, Harrington 1993, Haines et al. 2001). Indeed, many of the fires that we now set or allow to burn may be far from restorative (Andersen et al. 1998, Fiedler et al. 1998, Lyon and Smith 2000, Gill 2001). With only a rudimentary understanding of the ecological consequences of these increasingly applied treatments, we are beholden to careful study of prescribed burning to ensure its effectiveness as a resource conservation tool (Norris 1990, Bennett and Kunzmann 1992, Harrington 1993, Johnson and Miyanishi 1995, Whelan 1995, Andersen et al. 1998, Fernandes et al. 2000, USDI 2001).

In the United States, the contemporary ascendancy of fire as a management tool is rooted in the mid 1900s. Over the past half century, tens of millions of acres of forest and rangeland have been deliberately burned in the conterminous U.S. (Leenhouts 1998), and fire-effects information gleaned from research conducted in conjunction with these treatments has had the potential to hone and strengthen state and federal fire-use policies and programs (Norris 1990). However, recent narrative reviews lament that research to date has produced few reliable data describing the effects of these managed fires on populations of most plants or animals in any given vegetation type (McMahon and deCalesta 1990, Robbins and Meyers 1992, Engstrom et al. 1996, Lyon and Smith 2000, Tiedemann et al. 2000, van Mantgem et al. 2001). These critics contend that much research has been focused and designed in ways that compromise both the internal and external validity of causal inferences drawn from individual studies and preclude meaningful synthesis of findings from independent investigations conducted within a domain of management interest. In particular, they identify narrow taxonomic focus, lack of treatment replication, and lack of baseline or reference data necessary to isolate treatment effects as common impediments to the timely revelation of patterns reliably effected by prescribed burning within any given domain.

In this paper, I provide the first quantitative review of this topic. I provide an extensive summary of experimental approaches to the study of prescribed fires within the contiguous U.S. from 1950-2002. After fleshing out our purported reliance on case studies by examining the level of replication typical of this body of work and nominating exemplary studies that rigorously examine the effects of both well-replicated and well-described fire treatments, I group papers according to treatments and response variables within vegetation types to identify "hotbeds" of research and promising areas for future syntheses. I review studies by taxon — separating plants, arthropods, and birds — to identify any differences in research approaches among the groups. I conclude with a discussion of promising directions for future research with an eye toward the inherent complexity of and variation in the ecological effects of fire.

METHODS

I reviewed studies published in refereed scientific journals and USDA Forest Service publications (e.g., General Technical Reports, Research Papers, Research Notes). I included quantitative reports that: 1) were published between 1950 and 2002, and 2) addressed the effects of human-ignited, prescribed fires on plant, arthropod, or bird populations. I restricted my review to research conducted within the contiguous U.S. to facilitate location and mapping of studies in relation to lands historically characterized by frequent (<35 year) fire return intervals as delineated (solely within the conterminous states) as by Hardy et al. (1999: Fire Regimes I and II). These "key short-return interval ecosystems" collectively form a high-priority zone for management with prescribed fire (Haines et al. 1998); both opportunities and need for fire-effects research in this region are especially great (Agee 2000). For all taxa, I excluded studies in which fire was not the sole manipulative treatment (e.g., fire plus logging in Kilgore 1971). If effects from the same long-term study of prescribed burning were reported at different stages by different researchers (e.g., Lewis and Harshbarger 1976, Waldrop et al. 1987), I included only the most recent report to avoid evaluating the same research protocol multiple times. For the same reason, if effects of the same fire treatments on different aspects of vegetation were published in separate reports (e.g.., Waldrop et al. 1987, Waldrop and Thomas 1991), I randomly selected one of the papers for inclusion in this review.

In addition to the date, source, target taxon, and number of replicated fire treatments in each paper, I noted the following to evaluate the strength and scope of causal inference: (1) number of years (growing seasons) that data were collected before and after burning; (2) whether data were collected from both treated and untreated (control) units; (3), if replicated, whether treatments were randomly applied to experimental units; (4) whether experimental units were randomly sampled from a target population; (5) scale of treatment replication (local [experimental units <5 km apart] versus regional [units generally >10 km apart]). To identify heavily studied topics in hotbeds of research and to evaluate the potential for meaningful and effective categorization of fire treatments for review, I noted (1) location (place name, latitude, longitude) of study site(s) and plotted the locations of each study on a map modified from Hardy et al. (1999), (2) major vegetation type (following Barbour and Billings 1988) within the study area; (3) dependent variable used (e.g., abundance, biomass, rates of survival or reproduction, species richness or diversity of study organisms); (4) independent variable used (i.e., one or more types of fire treatment); (5) size of each burn treatment; and (6) whether each treatment was described well enough to facilitate classification by fire behavior and burning conditions in future syntheses. Fire spread direction (i.e., heading vs. backing fire), rate of fire spread, and weather conditions can have a striking effect on heat release (fire intensity) and, consequently, fire severity (van Wagner 1973, 1977; Barnes et al. 1998; Sackett and Haase 1998). Because all are somewhat interrelated, I considered the fire(s) well-described if at least two of the following were specified: fire spread direction, burning conditions (e.g., temperature, relative humidity, wind speed), or fire behavior (e.g., average flame length, rate of spread).

I generated descriptive statistics of studies by taxon or for all reports combined via SPSS 10.0.7. I used $P \leq 0.05$ as my criterion for statistical significance. Because there was no comprehensive list of fire-effects research to randomly sample for this review, I assume that the papers I was able to locate well represent this target population and assume that my statistics characterize published fire-effects studies in general (Rubin 1974). Because the purpose of this review is not to question the validity of any particular study, I have chosen to nominate individual papers in the following sections only when possible to do so in a positive light or without judgment. A complete list of articles included in this review are available upon request.

RESULTS

Studies of vegetation dominate the literature

Papers describing the effects of prescribed burning on vegetation were far easier to locate than either arthropod or bird studies. I found and reviewed 229 published articles, dating from 1950 to 2002, detailing responses of plants (140 papers), arthropods (52), or birds (37) to planned burns. I found accounts of fire effects on vegetation that were published in all years during this period except 1950, 1952, 1954, 1959, 1968, 1970, 1973, and 1979. In contrast, all studies of arthropods and birds located for this review were published in or after 1970 and 1966, respectively, with several years unrepresented prior to 1986 and 1994, respectively (Figure 1.01). For all three taxa, the number of studies increased significantly over the past half century (correlation between number of studies located and publishing date by 4-year period for plants: $\tau = 0.676$, $n = 13$, $P = 0.002$; for arthropods: $\tau = 0.801$, $n = 13$, $P < 0.001$; and for birds $\tau = 0.725$, $n = 13$, $P = 0.001$). For example, the number of papers describing fire effects on vegetation rose from two published between 1950 and 1953 to 27 published from 1998 to 2001 (Figure 1.01).

The articles were published in a variety of periodicals. The top five sources of data describing responses of vegetation to prescribed burning were USDA Forest Service documents (source of 12% of all plant papers), *Journal of Range Management* (11%), *American Midland Naturalist* (9%), *Forest Ecology and Management* (7%), and *Ecology* (6%). The top five sources for arthropod research were *Environmental Entomology* (12%), *American Midland Naturalist* (10%), *Journal of Medical Entomology*, *Journal of Range Management*, and *Natural Areas Journal* (8% each). *The Transactions of the North American Wildlife and Natural Resources Conference, Wildlife Society Bulletin* (11% each), *American Midland Naturalist*, *Prairie Naturalist*, and *Wilson Bulletin* (8% each) were the top five sources of papers detailing the effects of prescribed burning on birds.

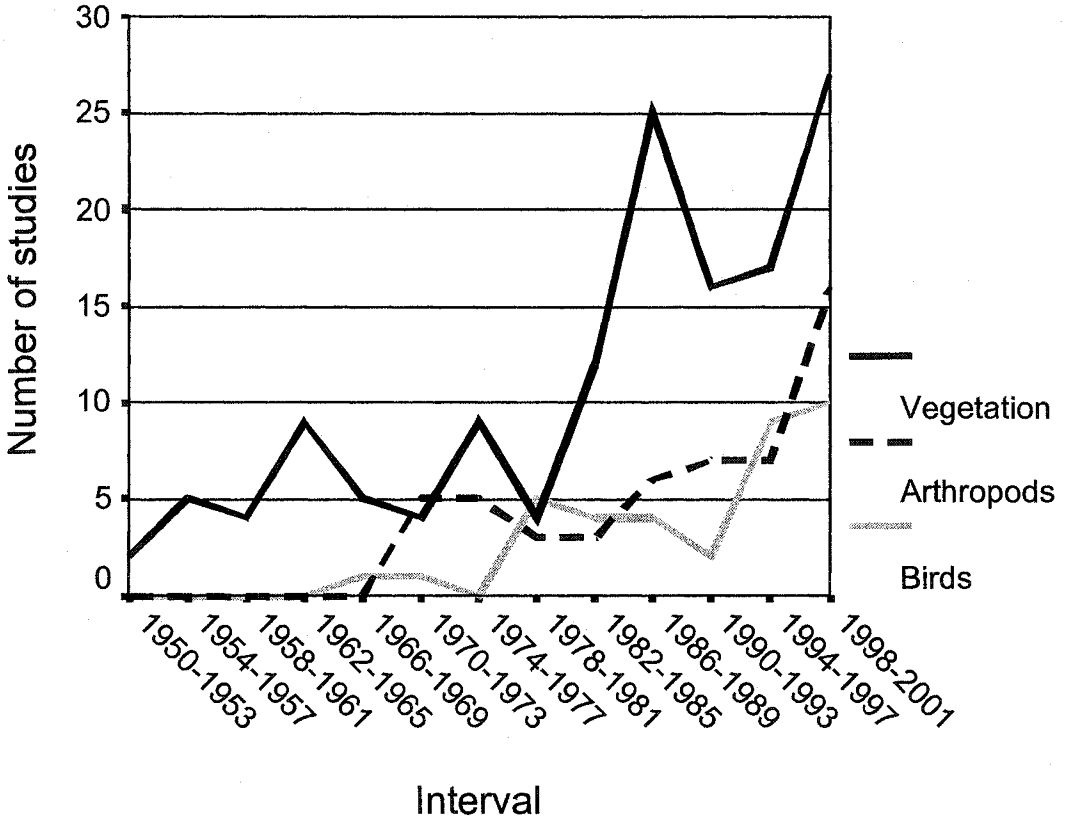

Figure 1.01. Number of studies describing the effects of prescribed burning on vegetation, arthropods, and birds published within each four-year interval from 1950 to 2001.

Case studies of single fire treatments are pervasive

Of the studies in which the degree of treatment replication was evident (94% plants, 92% arthropods, 89% birds), disproportionately large numbers in each group only included a single replicate per treatment (Figure 1.02; plants: 40%; arthropods: 42%; birds: 33%). Median number of replicates per treatment was 3 in plant and arthropod studies, and 3.5 in bird studies. The proportion of studies in which treatments were unreplicated (case studies) decreased significantly since the mid 1980s (correlation between proportion of case studies and publishing date by 4-year period for plants: $\tau = -1.000$, $n = 5$, $P = 0.014$; Figure 1.03). Even so, 22% of studies published from 1998 to 2001 and included in this review had no treatment replication; 74% averaged three or fewer replicates per treatment.

Only weak causal inferences can be drawn from many investigations

Of the 229 studies that I reviewed, twenty-two (10%) inferred fire effects based solely upon data collected on burned units after fire treatments were applied. Thirty-four (15%) of the studies that I reviewed inferred fire effects from before-after (BA) comparisons. With sufficient pre-fire data from treated sites, one can model stochastic processes that are assumed to continue operating after burning and thereby isolate the fire's effects without data from physically distinct control units (Stewart-Oaten et al. 1986, Carpenter et al. 1989). Yet, none of the BA studies in this review used this approach to estimate responses to burning; of 108 studies (regardless of taxon) in which data were collected both before and after at least one fire and in which the length of the pre-treatment sampling period was evident, 86% had pre-fire data from no more than one

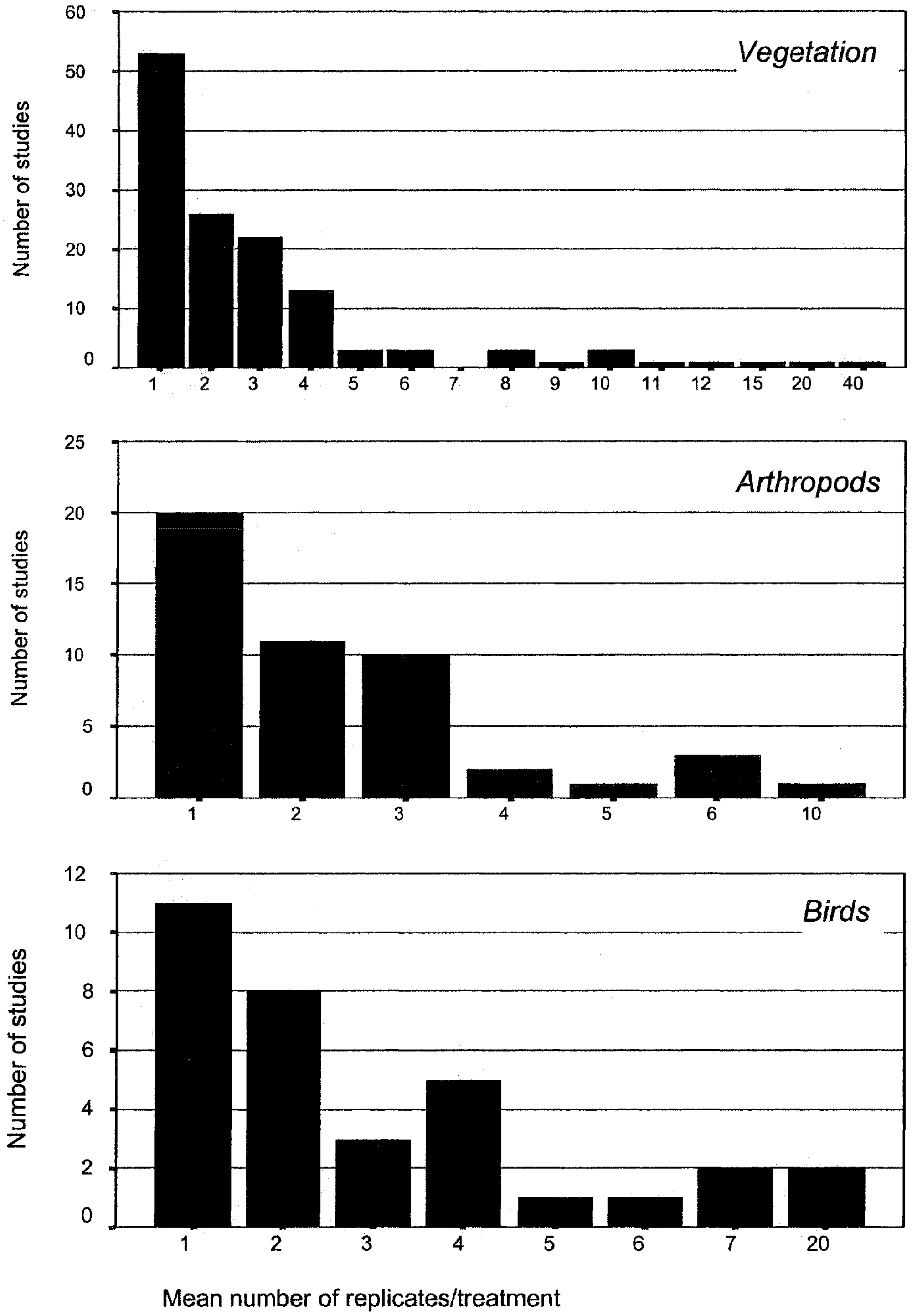

Figure 1.02. Distribution of studies describing responses of vegetation, arthropods, and birds to prescribed burning, with respect to treatment replication. The modal level of treatment replication was one.

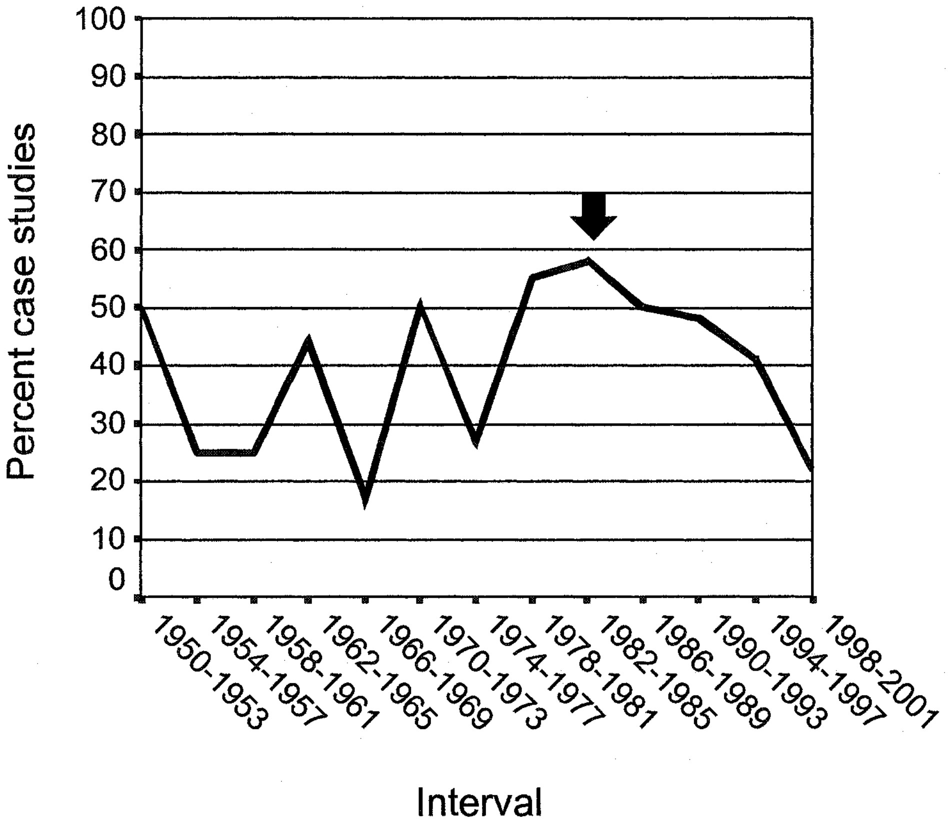

Figure 1.03. Percentage of studies, by four-year publishing interval from 1950 to 2001, in which treatments were not replicated. The arrow marks the beginning of a significant decline in the proportion of studies without treatment replication.

year.

In most studies (75%), fire effects were inferred from a comparison of one or more treated units that were spatially distinct from the treated (impact) unit(s). In 46% of studies that included control units (or 35% of all reports), data were collected only after burning (control-impact, or CI, design). The remainder (54%) collected data before and after burning on control (unburned) and impact (burned) study units (BACI design). The most common research approach differed for studies of plants and animals (Figure 1.04). More studies (46%) describing fire effects on vegetation used a BACI design than any other, whereas more studies (48% and 40%, respectively) of arthropod and bird responses inferred fire effects by comparing burned to unburned study units than any other method (Figure 1.04). Of 43 studies that used a replicated CI or BACI approach to determine fire effects, only 26% reported that treatments had been randomly assigned to experimental units. However, of 74 studies comparing the effects of fires differing in season, frequency, severity, or extent in which treatments were replicated, 60% reported that treatments had been randomly assigned to experimental units.

The scope of statistical inference is invariably limited to sampled units

Selection of experimental units was not detailed in any of the 229 studies that I reviewed. Random sampling was never mentioned, and no target populations were defined. Therefore, in each study, the scope of statistical inference was necessarily limited to the sampled units. In order to generalize findings beyond the study units, the authors had to assume that the units (and treatments) were representative of a larger population in question. Reasonably, the more extensive the distribution of experimental

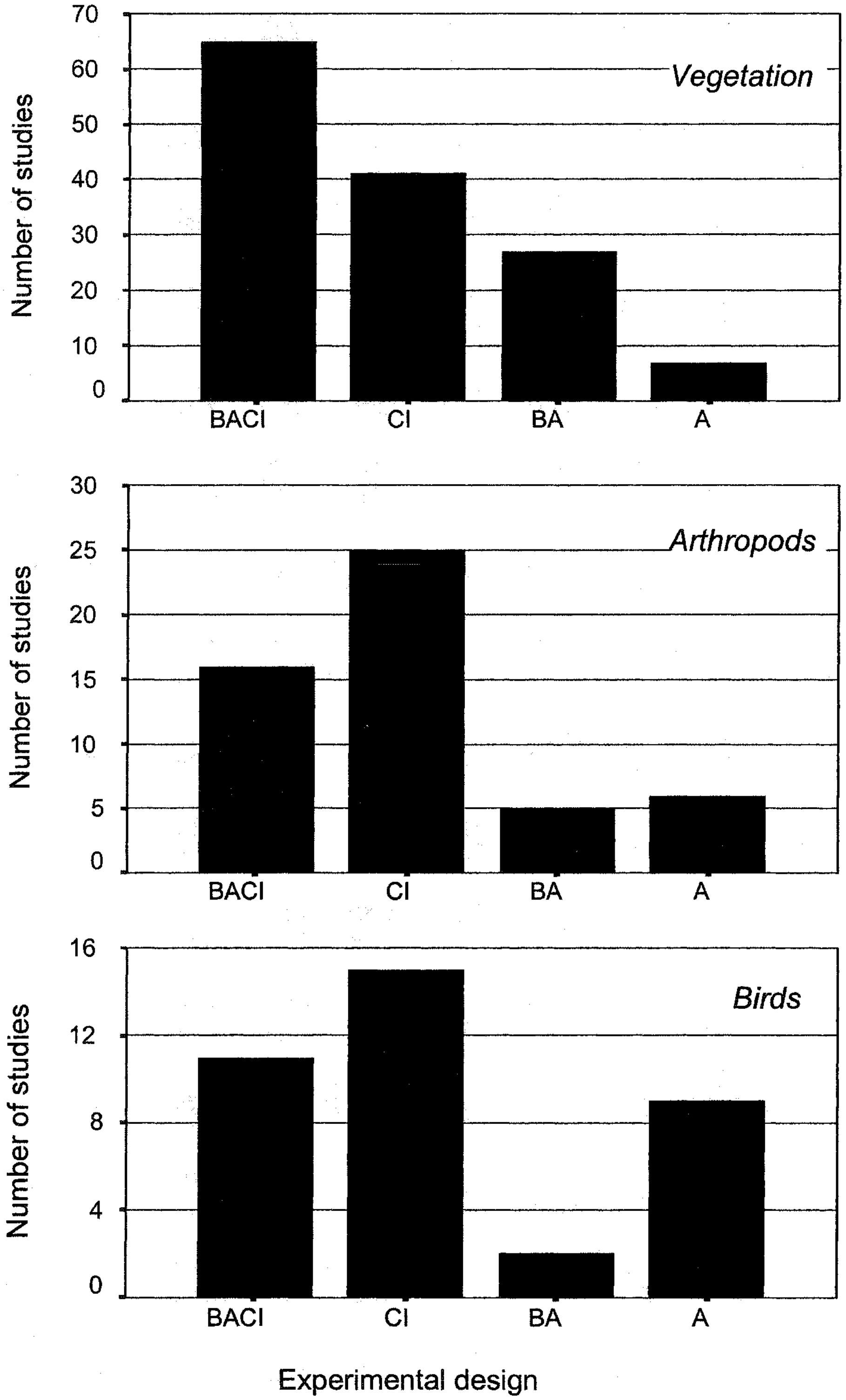

Figure 1.04. Distribution of studies describing responses of vegetation, arthropods, and birds to prescribed burning, with respect to experimental design (BACI = before-after-control-impact, CI = control-impact, BA = before-after, A = after only).

units in space, the greater the spatial scope of inference. In 21% of all studies with replicated treatments, it was not clear how the treated units were positioned with respect to one another. Of the remainder, 65% had treatments replicated only locally (within 5 km of each other).

Only four studies (2%) can be considered exemplary

Fires were seldom well described. Only 40%, 19%, and 22% of plant, arthropod, and bird studies, respectively, provided detailed descriptions of fire behavior and burning conditions. Fewer than 5% of studies included in this review used a randomized BACI approach that included both replicated and well-described fire treatments (vegetation: Gaines et al. 1958, Kaufmann and Martin 1990, Barker and Williamson 1988, Barnes and van Lear 1998, Spier and Snyder 1998, Huddle and Pallardy 1999, Pendergrass et al. 1999, Busse et al. 2000; arthropods: Brose and McCormick 1992 and Scifres et al. 1988; birds: Artman et al. 2001). Only Barker and Williamson (1988), Brose and McCormick (1992), Busse et al. (2000), and Artman et al. (2001) included more than three replicates of at least one fire treatment. I consider these latter four studies, which constitute less than 2% of the entire body of literature in this review, to be exemplary.

Influence of fire on grassland vegetation has received much attention

Most of the studies that I reviewed were conducted in grassland (32% of vegetation, 48% of arthropod, and 40% of bird studies; Figure 1.05) — usually tallgrass prairie. Research from the southeastern coastal plain and eastern deciduous forest was also relatively abundant. Collectively, studies in these three vegetation types, which

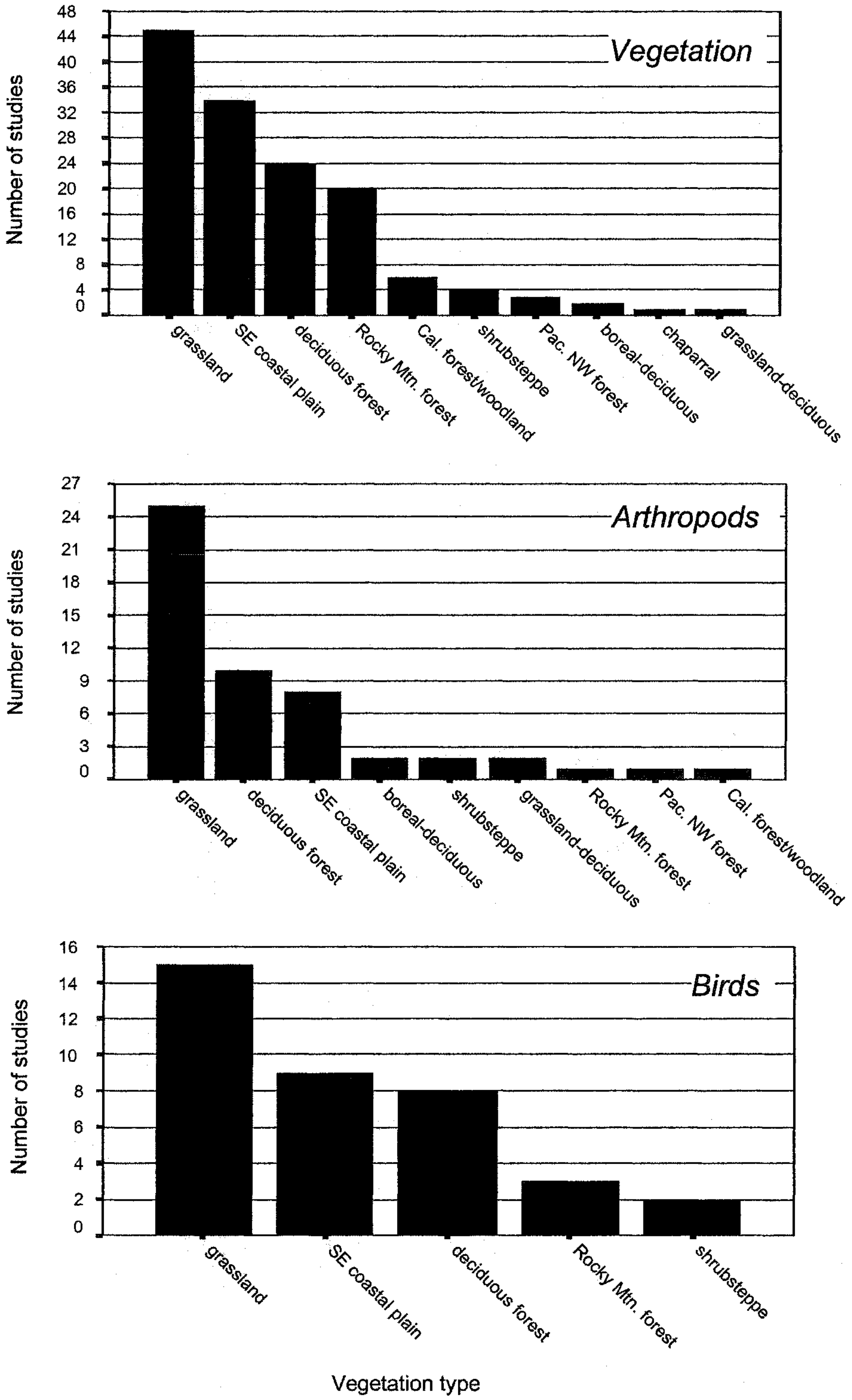

Figure 1.05. Distribution of studies that examine effects of prescribed burning on vegetation, arthropods, and birds among broad vegetation types (following Barbour and Billings 1988). Fires in grasslands, vegetation of the southeastern coastal plain, and deciduous forests have been the foci of much research.

occur mainly in the east-central U.S., accounted for 74%, 83%, and 86% of the published research on plants, arthropods, and birds, respectively. Vegetation types that occur in the western U.S., including the forests of the Rocky Mountains, are less well represented in the literature, except for a number of studies conducted in ponderosa pine forest near Flagstaff, Arizona (Figures 1.05, 1.06). I found strikingly few studies of arthropod or bird responses to burning in the fire-prone vegetation of the West that met the criteria for inclusion in this review (Figure 1.06).

Research has focused on numeric responses

The dependent variable most commonly included in fire-effects studies was a metric of the abundance of the target organism(s) (Figure 1.07). The second most common response variable was a metric of productivity for plants and a metric of species richness or diversity for the animals (Figure 1.07). Half of the plant studies included data describing survival or reproduction, whereas only 35% of bird or arthropod studies included such demographic information. Arthropod studies were most likely to report survival statistics, while studies of birds were most likely to include productivity data (Figure 1.07). Twenty-nine percent of arthropod studies also detailed fire effects on vegetation, whereas 60% of bird studies included these additional data. Five percent of bird studies also included arthropod data. Eight percent of arthropod studies and 11% of bird studies documented diet or foraging behavior. Of the studies in which the schedule of data collection was clear (79%), most reported only the acute effects of burning on their variables of interest. Most papers (36% plants, 51% arthropods, 50% birds) provided data from only the first year postfire. Only 34%, 26%, and 27% of plant,

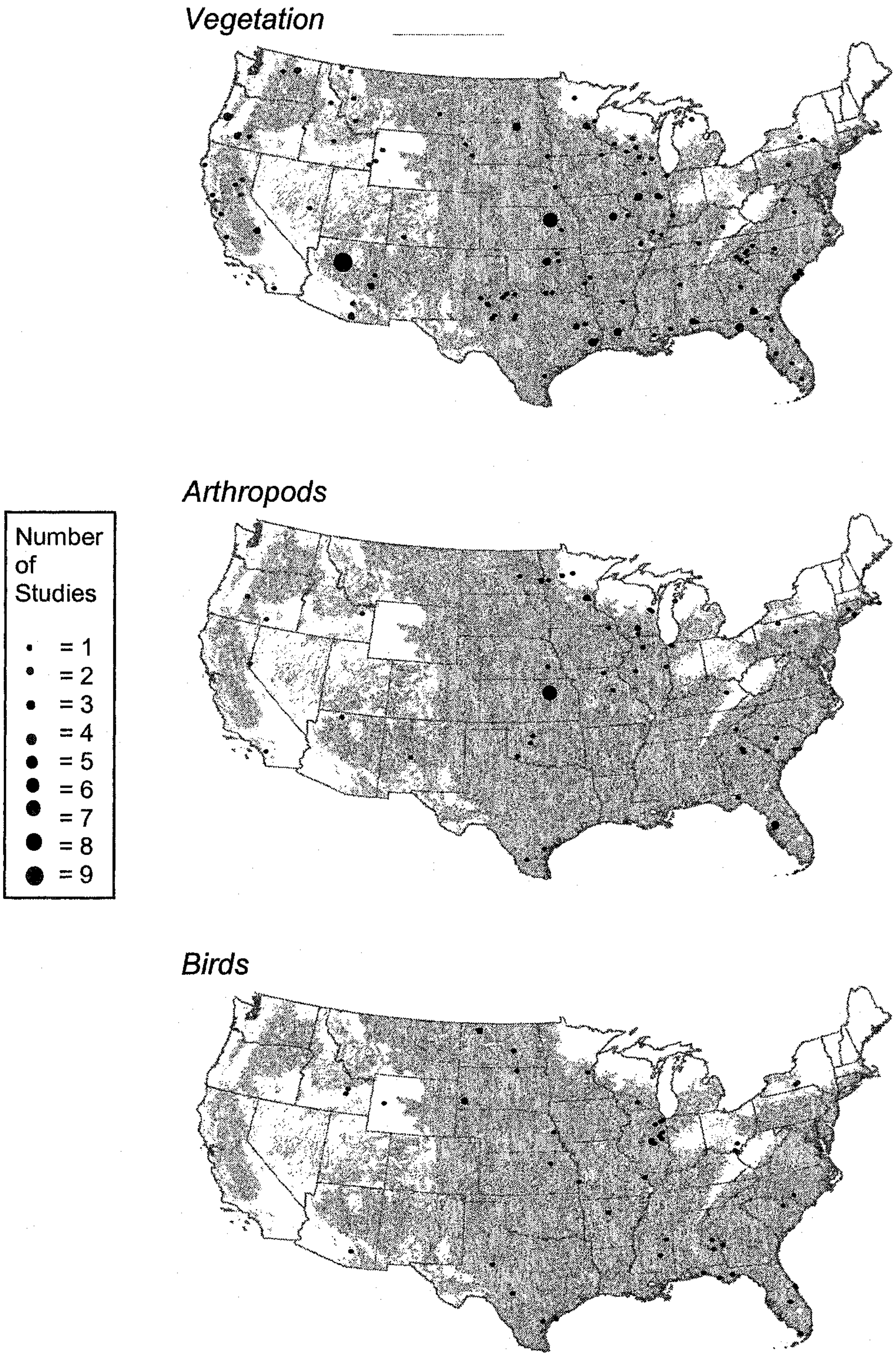

Figure 1.06. Locations of studies conducted in conjunction with prescribed burning in the contiguous United States from 1950-2002. Studies of widely-distributed treatments may be represented by more than one dot. Lands historically subject to frequent fires (<35 year mean return intervals), and therefore best suited for management via prescribed burning are shown in gray.

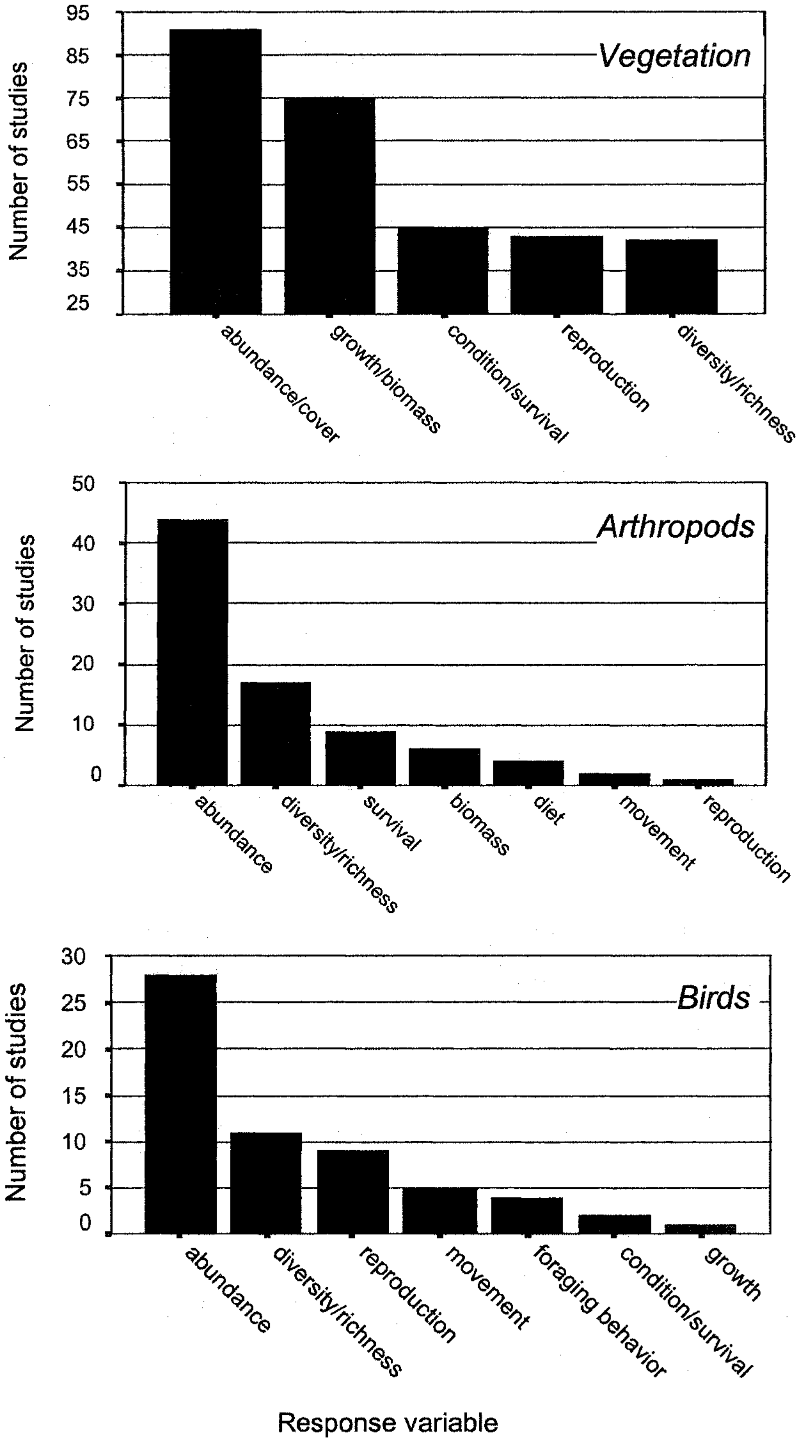

Figure 1.07. Distribution of studies that examine various demographic or behavioral responses of vegetation, arthropods, and birds to prescribed burning. Some papers included data for more than one response variable.

arthropod, and bird studies, respectively, reported data from beyond postfire year 3.

Studies have focused on one type of fire at a time

Of the plant, arthropod, and bird studies, 44%, 64%, and 70%, respectively, described the effects of a single type of fire treatment. The remainder in each category compared the effects of fires differing in frequency, season/date, severity, extent or a combination of these characteristics. Only 61%, 69%, and 60% of vegetation, arthropod, and bird research papers, respectively, reported the sizes of fire treatments. Most plant studies (71%) were conducted in conjunction with prescribed fires <10 ha in size (Figure 1.08; range: 0.0002 ha [Cheplick and Quinn 1988] to 5813 ha [Lindenmuth 1960]). Half of the arthropod studies that reported burn size were of fires smaller than 10 ha; another 39% were conducted in conjunction with at least one fire that was 10-100 ha in size (Figure 1.08; range: 0.01 ha [Lussenhop 1976] to 2200 ha [Santoro et al. 2001]). In contrast, most bird studies (54%) that reported burn size utilized at least one fire that was 100-1000 ha in size (Figure 1.08; range: 0.65 ha [Jacobson and Hurst 1979] to 5800 ha [Fischer et al. 1997]).

Few studies have been repeated

The most heavily studied organisms within the most heavily studied habitats hold the most promise for meaningful quantitative review. By grouping the relatively large number of reports of plant responses to prescribed burning within tallgrass prairie (to represent the east-central U.S.) and southwestern ponderosa pine forest (to represent the West) by fire treatments (independent variables) and response (dependent) variables, I

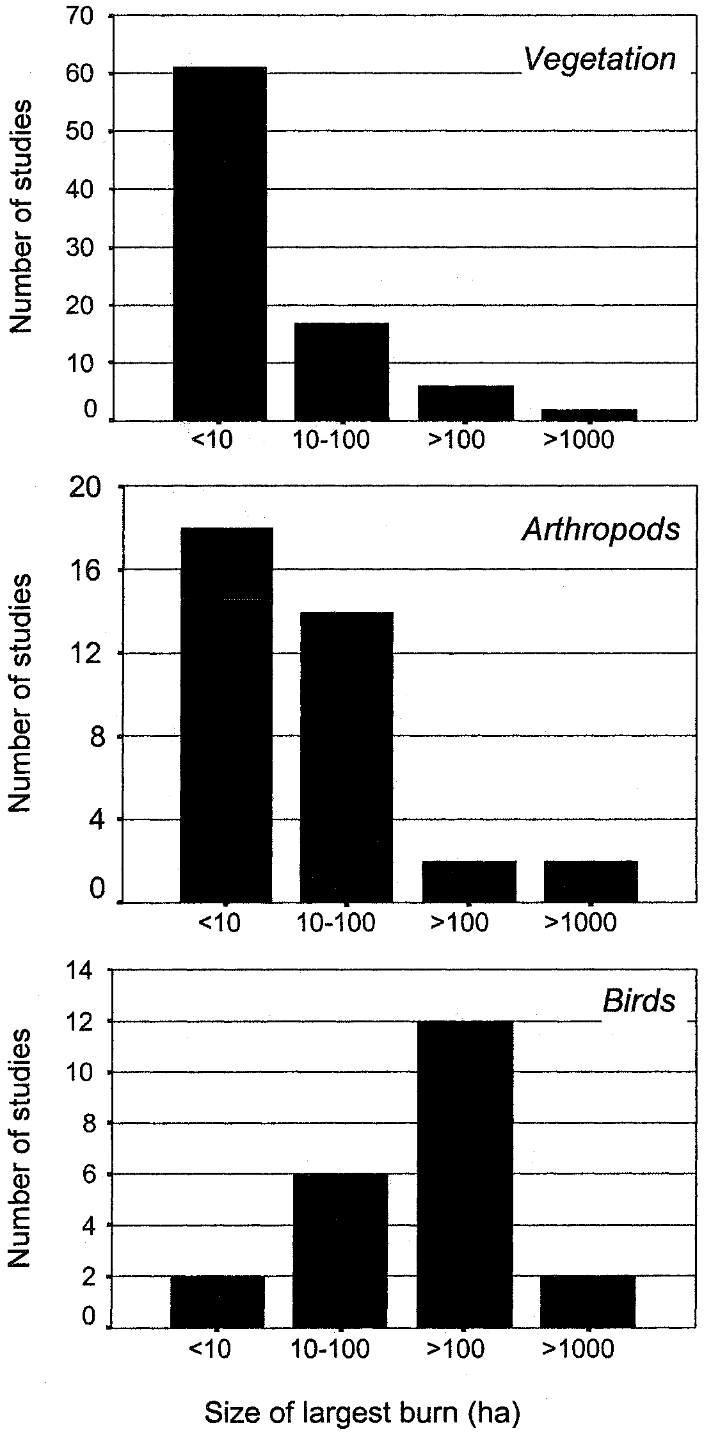

Figure 1.08. Distribution of studies that examine effects of prescribed burning on vegetation, arthropods, and birds by size of largest burn treatment. Studies describing effects on plants tended to capitalize on relatively small fires (<10 ha), whereas those describing bird responses tended to incorporate at least one relatively large (100-1000 ha) fire. Arthropod research was typically conducted in conjunction with burns smaller than 100 ha.

was able to discern focal areas of independently conducted research within each of these domains (Tables 1.01, 1.02). Of 25 studies of herbaceous response to burning in tallgrass prairie and included in this review, eight were the sole sources of information regarding the effects of a particular fire treatment on a given vital attribute (Table 1.01; i.e., the effect of summer burning on herbaceous production: Ewing and Engle 1988). Of 10 studies reporting vegetation responses to prescribed fires in southwestern ponderosa pine forest, half provided information not contained in any other study (Table 1.02). Of these 10 and five studies that lacked counterparts, 62 and 40%, respectively, were unreplicated case studies (Tables 1.01, 1.02). Only a couple of topics appear to have received relatively great attention even with my coarse-scale categorization (lumping all herbaceous vegetation together) — both from tallgrass prairie. The effects of spring burning on some metric of herbaceous production and species richness or diversity were reported in eight and five papers, respectively (Table 1.01). About half of these were case studies, and only one included well-described fire treatments (Table 1.01). This cursory evaluation suggests that, to date, fire-effects research has been extremely diffuse and few relationships have received enough attention to merit quantitative review. Moreover, lack of well-described fire treatments may unecessarily confound future attempts to summarize existing data, to replicate findings, and to make meaningful management recommendations.

Table 1.01. Studies that (1) were published from 1950-2002 and included in this review, and (2) described the effects of prescribed burning on herbaceous vegetation in tallgrass prairie.

	Response variable			
Independent variable	abundance/cover	growth/biomass	reproduction	diversity/richness
Spring burning	14^{2-3}, 20^{1}, 25^{1}	1^{4}, 5^{5}, 6^{1-2}, 7^{1}, $13^{?}$, 16^{1}, 19^{4}*, 25^{1}	1^{4}, 5^{5}, 6^{1-2}, $13^{?}$	6^{1-2}, 14^{2-3}, 16^{1}, 20^{1}, 25^{1}
Summer burning	17^{1}*	17^{1}*	17^{1}*	
Autumn burning	12^{1}*			12^{1}*
Winter burning	8^{1}	8^{1}	8^{1}	8^{1}
Interval between spring fires	3^{1}, 18^{3-4}	4^{1}, 18^{3-4}, 21^{1-2}	21^{1-2}	3^{1}, 18^{3-4}
Interval between summer fires				24^{3}
Date of spring fires			22^{2}	
Season of burning	9^{1} 15^{1}, $23^{?}$*	10^{1-2}, 11^{3}		9^{1}, 10^{1-2}, $23^{?}$*
Season and frequency of burning	15^{1}	2^{1}	2^{1}, 15^{1}	15^{1}

Notes: Studies: 1 = Kucera and Ehrenreich (1962), 2 = Hadley and Kiekhefer (1963), 3 = Kucera and Koelling (1964), 4 = Vogl (1965), 5 = Old (1969), 6 = Zedler and Loucks (1969), 7 = Peet et al. (1975), 8 = Anderson and Van Valkenberg (1977), 9 = Adams et al. (1982), 10 = Towne and Owensby (1984), 11 = James (1985), 12 = Schwegman and McClain (1985), 13 = Knapp and Hulbert (1986), 14 = Abrams and Hulbert (1987), 15 = Bacone and Post (1987), 16 = Blankenspoor (1987), 17 = Ewing and Engle (1988), 18 = Gibson (1988), 19 = Bidwell et al. (1990), 20 = Anderson and Schwegman (1991), 21 = Hartnett (1991), 22 = Benning and Bragg (1993), 23 = Howe (1995), 24 = Engle et al. (2000), 25 = Kost and De Steven (2000). Superscript is number of replicates per treatment in each study. Asterisk denotes that the fire treatment(s) were well described (see text).

Table 1.02. Studies that (1) were published from 1950-2002 and included in this review, and (2) described the effects of prescribed burning on vegetation in southwestern ponderosa pine forests.

	Response variable							
	Ponderosa pine				Herbaceous vegetation			
Independent variable	abundance/ cover	growth/ biomass	survival/ condition	reproduction	abundance/ cover	growth/ biomass	survival/ condition	reproduction
Autumn burning	2^{2}*, 8^{1}*	8^{1}*	2^{2}*, 8^{1}*	8^{1}*	7^{1}*, $9^{3\text{-}21}$*	3^{11}*, 5^{1}, $9^{3\text{-}21}$*	7^{1}*, $9^{3\text{-}21}$*	7^{1}*, 10^{1}*
Interval between autumn fires	—	—	$4^{3\text{-}18}$	—	—	—	—	—
Date of autumn fires	1^{2}*	—	1^{2}*	—	—	—	—	—
Season of burning	—	—	—	—	—	—	6^{6}	—

Notes: Studies: 1 = Gaines et al. (1958), 2 = Lindenmuth (1960), 3 = Harris and Covington (1983), 4 = Sackett (1984), 5 = Andiarese and Covington (1986), 6 = Harrington (1987), 7 = Vose and White (1987), 8 = Ffolliott and Guertin (1990), 9 = Vose and White (1991), 10 = White et al. (1991). Superscript is number of replicates per treatment in each study. Asterisk denotes that fire behavior and burning conditions were well described (see text).

DISCUSSION

Why plants?

Data describing the responses of plants and animals to prescribed burning have accumulated at an increasing rate over the past half century. Many of these data can be found in USDA Forest Service documents and refereed journals like *American Midland Naturalist*, and *Journal of Range Management*. The apparent emphasis on plants versus animals in this body of research (Figure 1.01) is likely due to the relative ease with which fire effects on sessile organisms may be observed and quantified (Sousa 1984), the practical importance of plant data to timber and livestock producers, the assumption that fire-caused changes in vegetation are, in large part, the basis for the responses of animal populations to burning. Consequently, fire management objectives are often expressed in terms of vegetative change (i.e., USDI 2001). However, this focus discounts the direct effects of fire on animal populations and the complexity of post-fire interactions among various plants and animals (Bailey and Whitham 2002). The direct effects of fire on populations of some animals, like arthropods, may be quite dramatic and entirely independent of fire effects on vegetation.

Is pseudoreplication a thing of the past?

Not surprisingly, case studies were pervasive in this body of literature, regardless of target taxon. The modal level of replication was one unit per treatment; the median was two (Figure 1.02). The proportion of unreplicated studies in the literature published since the mid-80s appears to have fallen steadily since the mid-1980s (Figure 1.03). It is probably not coincidence that the inflection point coincides well with the 1984 publication of Stuart Hurlbert's exposition about the common statistical pitfalls in the analysis of unreplicated experiments. Hurlbert (1984) effectively warned ecologists and editors of ecological journals of the limited inferences that can be drawn from case studies. According to Hargrove and Pickering (1992), Hurlbert's paper ". . . created a preoccupation with . . . classical experimentation in ecology." Yet, despite any newfound zeal to replicate treatments and continued prodding (most recently by Morrison and Morris 2000, van Mantgem et al. 2001) of those ostensibly content with "pseudoreplication" in the study of fire effects, nearly one in four studies published from 1998 to 2001 and included in this review were wholly unreplicated; nearly three-quarters averaged three or fewer replicates per treatment. The utility of unreplicated or poorly replicated studies as impact assessments, in hypothesis generation, or even in future meta-analyses depends upon the strength of assertions that significant differences of interest represent fire effects (Hurlbert 1983, Carpenter et al. 1989, Hargrove and Pickering 1992, Gurevitch and Hedges 1993).

How can we enhance the validity and scope of our inferences?

Although 40% of the studies that I reviewed relied upon relatively rigorous BACI designs to discern fire effects (Figure 1.04), the remainder (60%) could have increased their ability to discriminate background noise from the true effects of fires by collecting additional baseline or reference data. When treatments cannot be replicated, BA and BACI designs that include data collected for multiple years pre- and post-fire will allow the strongest objective causal inference (Likens 1985, James and McCulloch 1995, van Mantgem et al. 2001). When treatments are replicated, their locations are still seldom under control of the researcher, hence the lack of randomization in many CI and BACI studies. Close matching of control and treatment units at the outset of BACI studies can minimize group differences, serving essentially the same purpose as random assignment of treatments to experimental units (subjective randomization *sensu* Rubin 1974). *A-posteriori* matching in CI comparisons is likewise important, but such pairings necessarily rest upon untestable assumptions of pre-fire similarities.

In replicated studies, the application of findings to domains greater than those of the experiments is statistically valid only when study units have been randomly sampled from the population of interest (James and McCulloch 1995). Random sampling is distinct from randomization, although these principles are often conflated (e.g., van Mantgem et al. 2001). Fire ecologists may seldom, if ever, have the ability to randomly select experimental units from a target population. Instead, extrapolation of results to a given region of interest must be subjectively justified (Rubin 1974, USDI 1999), with the spatial or temporal scale of replication largely dictating the valid scope of inference (Andersen et al. 1998). Only a handful of the studies that I reviewed reported fire treatments that were replicated at a regional scale (> 10 km apart) despite the desire of researchers to apply findings to larger areas. I could deem only four of 229 studies exemplary with regard to their experimental rigor (Barker and Williamson 1988, Brose and McCormick 1992, Busse et al. 2000, and Artman et al. 2001). Notably, the study areas of Brose and McCormick (1992), Busse et al. (2000) Artman et al. (2001) effectively extended across more than 60 km of their regions of interest, which were sugar maple-dominated hardwood forest (sugarbushes) of Pennsylvania, ponderosa pine forest of central Oregon, and mixed-oak forest of southern Ohio, respectively.

Other promising directions

Regionally-coordinated experiments

Although it is clearly possible to conduct experimentally rigorous research in conjunction with prescribed fires at a regional scale, few ecologists may have the means or opportunity to do so independently. Well-replicated research at the "scale of management" will usually require the coordinated efforts of a number of scientists as well as "dedicated sites with sustained funding" (Carpenter et al. 1995). The "Birds and Burns Network" is a newly established multi-million dollar cooperative effort among several university and agency scientists to evaluate the short-term effects of various fire treatments on breeding birds within ponderosa pine forests throughout the Intermountain West (Saab et al. 2002, V. Saab *pers. comm.*). With study areas in eight western states, this project exemplifies the tremendous spatial coverage attainable through coordinated research (Saab et al. 2002). The "Birds and Burns Network" is sure to provide valuable fire effects information when it comes to full fruition over the next few years. Opportunities for similar projects at a range of spatial scales surely exist within other fire-prone habitats and should be seized upon promptly.

Metareplication

Despite the value of cooperative experiments, less attentively coordinated research has and always will play a crucial role in the quest for patterns and explanations of fire effects and in the evolution of state and federal fire management policies. For example, it was the collective research linking the persistence of longleaf pine (Chapman 1926, 1932; Heyward 1939), ponderosa pine (Weaver 1943), and Northern Bobwhite

(Stoddard 1931, 1935, 1936) to periodic burning that demonstrated that some of the nation's most valued resources actually benefited from, and possibly depended on, regular disturbance from fire. These data were instrumental in garnering institutional acceptance of the use of fire to manage natural resources in the face of a burgeoning national movement to exclude all fire from public lands (Kilgore 1976, Carle 2002). The accelerated growth of fire use programs that descended from this early research has fostered an increasing need for precise information describing how the fires we have chosen to set in the name of resource conservation and fire protection have shaped and will continue to affect biotic communities and their constituents. Although no single study may ever satisfy much of this need, data gathered in different studies of similar phenomena can be compiled and synthesized much in the same way that data from large-scale experiments can be digested to provide a general overview of certain relationships between fire and the biota at multiple spatial scales (Johnson 2002).

The potential for meaningful review of data from wholly independent sources depends on the often serendipitous accumulation of information from repeated study of a given relationship. Because meta-analyses of data from haphazardly replicated studies of prescribed fires must contend with sampling error inflated by disparities in research objectives and experimental design (Gurevitch and Hedges 1993, Whelan 1995), the existence of only a handful studies of a particular topic of interest will generally preclude meaningful quantitative review. The search for generality through evaluation of findings from a number of independent studies of fire effects should be most fruitful when plants are the focus, as there have simply been more studies to date of the effects of prescribed burning on flora than fauna in any vegetation type within the conterminous U. S. (Figure

1.01). Growing efforts to mitigate or reverse the effects of 20th century fire exclusion in fire-prone habitats historically dominated by longleaf pine, tallgrass prairie, and ponderosa pine have afforded many opportunities for research, which, in turn, has yielded a great deal of fire effects information from these areas (Hulbert 1973; Noss 1989; Brockaway and Lewis 1997; Busse et al. 2000; USDI 1999, 2002; Figures 1.05, 1.06). Yet, even in the veritable hotbeds of fire-effects research (i.e, tallgrass prairie, southwestern ponderosa pine), the existing information may be too limited and too diffuse (i.e., few studies include the same dependent and independent variables) with treatments too poorly replicated and described to discern signal from noise via quantitative review (Tables 1.01, 1.02).

Filling in the gaps

There are a great many more “cold spots”, or gaps, in research coverage within key short-return ecosystems of the conterminous U. S. than there are hotbeds of information (Figures 1.05, 1.06). This discrepancy is most strikingly evident in the western states, where published studies of animal responses to prescribed burning are few (Figure 1.06). Although fire-caused changes in vegetation are at the root of most wildlife responses to burning,we seldom have sufficient knowledge of wildlife-habitat relationships (i.e., vegetation attributes associated with fitness indices) and species interactions (i.e., how changes in plant quality/quantity effect changes in arthropod populations, which, in turn, affect vital rates of populations of insectivorous birds) to reliably translate fire-caused vegetative change into wildlife population responses (Johnson and Temple 1986, O’Neil and Carey 1986). At present, studies of plant responses to may provide only a weak basis for understanding and predicting the effects of fire on wildlife populations. As McMahon and deCalesta politely chided in their 1990 review, "In the future, for managers to make more definitive statements about the implications of prescribed fire on wildlife, . . . it would help if wildlife responses were monitored directly." Moreover, data describing fire's effects on plants and one or more types of animals that are collected simultaneously (i.e., Forde et al. 1984, Boyd and Bidwell 2001) may illuminate relationships between first- and higher-order effects of fire and other fascinating, fire-induced ecological cascades (Whelan 1995, Reed 1997).

Identifying mechanisms

Regardless of focal environments and organisms, the objectives and reporting of fire-effects research could be modified in ways that would expedite the generation of information necessary to direct the use of fire as an effective resource conservation tool. The objective of fire-effects studies has commonly been to describe how burning in a particular way in a given vegetation type acutely affects the abundance of target organisms (Figure 1.07). However, the abilities of populations to persist in the face of repeated fires (or lack thereof) are best gauged through studies of disturbance effects on demographic rates (Pendergrass et al. 1999, Sallabanks et al. 2000). Future research should have a heightened focus on fire-induced changes in vital rates of populations and the mechanisms underlying observed patterns. Because mechanisms often operate at smaller scales than those at which effected patterns are observed (Levin 1992), well-designed studies within a relatively small portion of a region of interest could explain fire effects that are documented within the larger domain (Vose and White 1991, Whelan

1995, Marzluff et al. 2000, Sallabanks et al. 2000; i.e., productivity changes because fire affects availability of some key resource). Such data could be used to make testable predictions of population responses to alternative treatments (i.e., if fire reduces availability of resource "X," possibly to some threshold level, productivity will fall such that $\lambda < 1$). Short-term, small-scale fire experiments to elucidate mechanisms are practical for graduate students and scientists for whom the costs of large-scale pattern generation may be prohibitive. On the other hand, identification of latent responses to or chronic effects of a particular treatment may take decades, as will experimental comparisons of alternative regimes (Whelan 1995; i.e., fires of high versus low frequencies). Studies that continue long enough to document effects beyond the first year post-fire and the cumulative effects of repeated burning (i.e., Waldrop and Thomas 1991) are essential.

A final word on treatment descriptions

Regardless of research focus and study duration, clear descriptions of the fire behavior and burning conditions responsible for observed responses are required not only to permit meaningful categorization of fire treatments but also to effectively direct future management and research (Figure 1.09). A fire simply characterized as "clean and hot" (Anderson and Van Valkenburg 1977) or a "cool spring burn" cannot be objectively replicated for either study or management purposes (Johnson and Miyanishi 1995). Convergence in descriptions of fire treatments according to fire behavior and burning conditions should facilitate the syntheses and communication of findings from the collective study of prescribed fires.

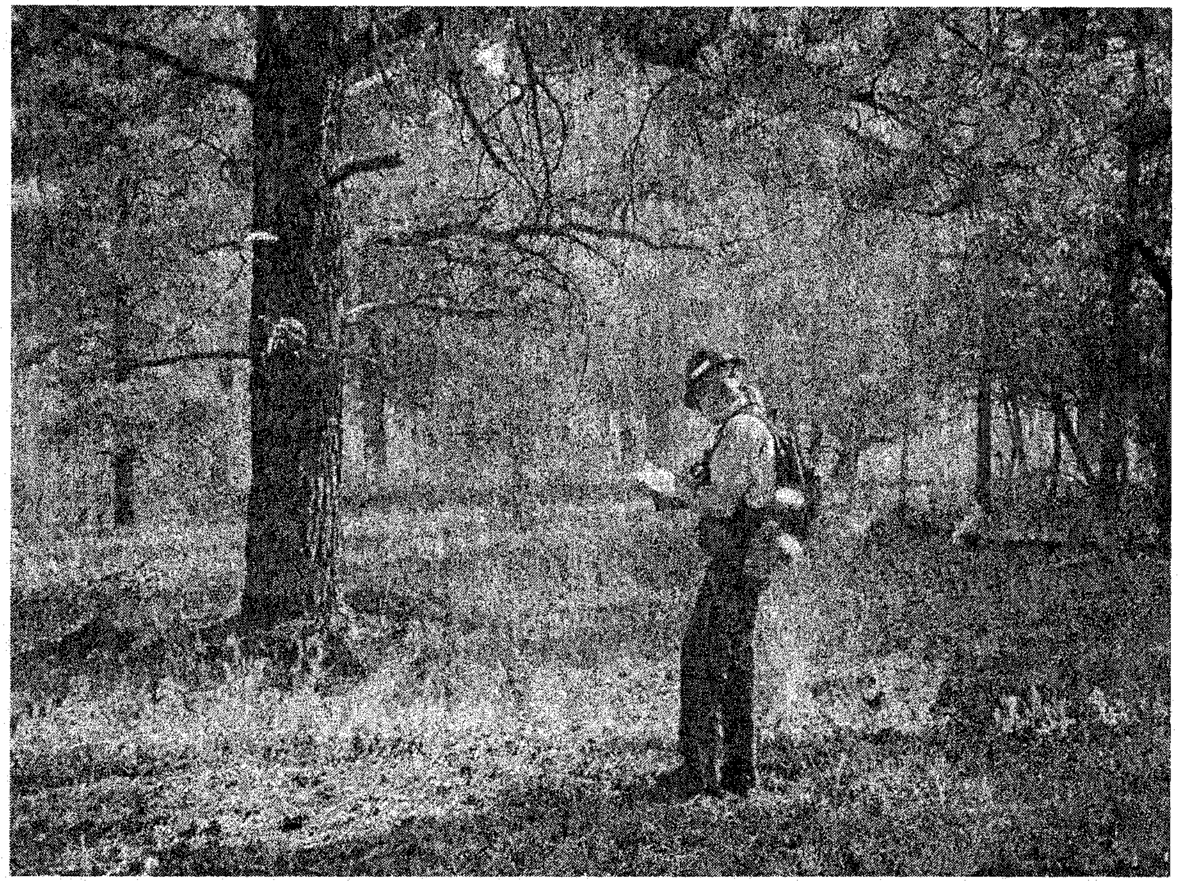

Figure 1.09. National Park Service employee documents fire behavior and burning conditions during a prescribed fire in Walnut Canyon National Monument. Such information is necessary to categorize fire treatments for meaningful synthesis of data from different studies and to allow replication of fire treatments by managers and other researchers (photo courtesy of Kathy Schon).

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—CHAPTER 2—

RESPONSES OF ARTHROPODS TO PRESCRIBED AUTUMN FIRES IN SOUTHWESTERN PONDEROSA PINE FORESTS: A QUASI-EXPERIMENTAL, FUNCTIONAL APPROACH

INTRODUCTION

The response of any given plant or animal population to burning depends not only on the type of fire, the vital attributes of the species in question (*sensu* Noble and Slatyer 1980), and the post-fire weather, but also on any fire-caused changes in the activity or density of biota — from microbes to vertebrates — with which the target individuals reliably interact (reviewed in Whelan 1995). Indeed, the literature is replete with reports of fire-caused changes in the nature or intensity of biotic interactions effecting outcomes of burning on study organisms that could not be predicted from fire behavior, vital attributes, and post-fire weather alone (e.g., Lawrence 1966, Gillon 1972, Bendell 1974, Whelan and Main 1979, Oswald and Covington 1984, Collins 1987, Brewer and Platt 1994, Hanley and Lamont 2001, Bailey and Whitham 2002). Fire-caused changes in the activity or density of arthropod folivores, wood-feeders, or seed predators, can, for example, enhance first-order plant mortality (Ryan and Amman 1996, Santoro et al. 2001), or check the stimulatory effects of burning on plant productivity (Reid 1999, Bailey and Whitham 2002), or both, while effecting marked attractions or aversions of insectivorous birds and mammals to the recently burned habitat (Gillon 1972).

To date, however, plants have been the sole focus of an inordinate amount of fire-effects research (Chapter 1). Even in some of the most heavily fire-managed environments, there have been astonishingly few studies of fire effects on any of the myriad other biota, including the range of arthropods, that occur in these habitats and are likely to interact with the vegetation, or any taxon, of interest. In this paper, I provide the first estimates of the short-term responses of a wide range of arthropods to one of the most commonly applied fire treatments in forests of the American West. I describe short-term changes in trap rates of insects, arachnids, and myriapods attributable to autumn (dormant-season) fires in southwestern ponderosa pine forests.

Although many of the first-order effects of these low-severity fires on forest vegetation may pale in comparison to those effected by stand-replacing wildfires, the influences of these treatments on the forest floor and understory, which may house 90% of forest arthropods for at least part of their life cycle (Klein 1988), are likely to be marked enough to affect the activity or density of these animals both directly, via lethal injury, and indirectly, by changing environmental conditions and resource availability. Such responses should be manifest in one of the first few growing seasons post-fire (Panzer 2001), if not longer. Here, I characterize these effects functionally, by grouping arthropods according to their general ecological roles within the forest community, and quasi-experimentally, by capitalizing on three nominally similar prescribed fires set within widely separated stands of comparable forest. Although these approaches promise to yield data with compelling implications for post-fire ecosystem dynamics and general relevance to the management of southwestern ponderosa pine forests, truly general patterns effected by prescribed fires will be most effectively gleaned through the synthesis of data from a number of independently replicated studies of this type (Chapter 1). To direct future research and facilitate future syntheses, I include detailed descriptions of the fire treatments and their effects on forest vegetation.

STUDY AREA AND METHODS

Study area

I considered all forest within Arizona or New Mexico classified as Rocky Mountain (Petran) and Madrean Montane Conifer Forests by Pase and Brown (1994) with overstories dominated by ponderosa pine as my target study area. I selected study sites within this area that had prescribed fires slated for Autumn 1998-2000 but were otherwise undisturbed by recent logging or grazing and were to remain unlogged and ungrazed during the study period. Three study sites in Arizona met these criteria, all within national parks (NP) and monuments (NM) (Figure 2.01).

I established the Grand Canyon NP (GRCA) site on the north rim of the canyon at 2200-2500 m atop Walhalla Plateau. The soil within this site was derived primarily from Kaibab Limestone (Opperman and Kerr 1999, *unpubl. rep.*). Cattle, horses, and sheep grazed the plateau from the mid to late 1800s until 1938, when the park boundary fence was constructed (Hughes 1991). The Walnut Canyon NM (WACA) site was situated on the south rim of the canyon at about 2010-2080 m on soil derived largely from Kaibab Limestone (Davis 1987). Cattle and sheep were grazed on WACA's south rim from the late 1800s to 1979, when the boundary fence was erected (Davis 1987). The Saguaro NP (SAGU) site was located within the park's Rincon Mountain District, just east of Tucson. This site included forest atop Mica Mountain at 2260-2560 m on soil derived from a mixture of Pinal Schist, Continental Granodiorite, and Wrong Mountain Quartz Monzonite (Bowers and McLaughlin 1991). Cattle and sheep lightly grazed the mountain from the late 1800s until 1958 (Turner 1992).

Ponderosa pine was the dominant overstory tree species within all sites, although

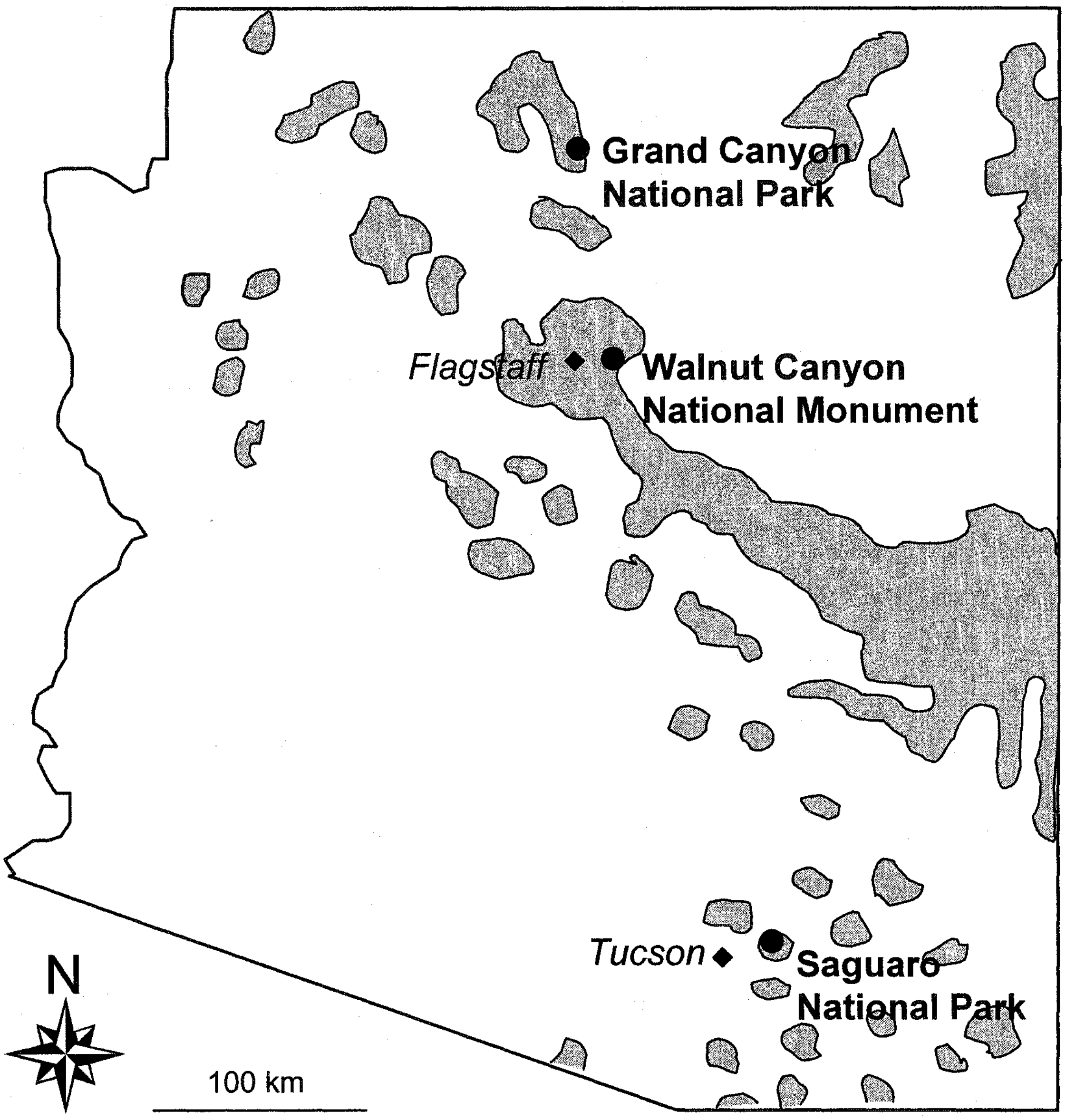


Figure 2.01. Arizona, showing general distribution of ponderosa pine (in gray, after Little 1971) and locations of study sites (black circles) with nearby cities.

overall species composition varied (Table 2.01, Figure 2.02). All sites had experienced decades of fire exclusion. For example, the last extensive wildfire in ponderosa pine forest at SAGU occurred in 1954 (K. Schon, *pers. comm.*). Further descriptions of the topography, vegetation, soils, and fire and weather patterns of Southwestern ponderosa pine forests can be found in Wagle (1981), Pase and Brown (1994), and Swetnam and Baisan (1996). Additional details specific to the GRCA, WACA, and SAGU sites are provided, respectively, by White and Vankat (1992) and Wolf and Mast (1998); Joyce (1974) and Davis (1987); Marshall (1956), Baisan and Swetnam (1990), and Bowers and McLaughlin (1994).

Experimental design and sampling protocol

I capitalized on the fires slated to burn within my study area and used a quasi-experimental approach (*sensu* Manly 1992) to isolate their effects on forest vegetation and arthropod groups. I chose 40-ha forest plots as my experimental units because I intended to conduct nest searches for a related study of breeding birds (see Chapter 3), and 35- to 50-ha plots are often necessary to find sufficient numbers of nests to estimate productivity of forest birds (Ralph et al. 1993; Martin et al. 1996, *unpubl. ms.*). I positioned a treatment unit within the perimeter of each planned burn and located a matched control nearby (Figures 2.03-2.06). Within each unit, I installed a 100-m by 100-m sampling grid, starting from a randomly selected location within 100 m of the primary access road or trail. I sampled forest vegetation and collected arthropods along each grid during the year before and during the first two years after the fall burns. At the SAGU site, I sampled vegetation during the third year post-fire as well (Figure 2.07).

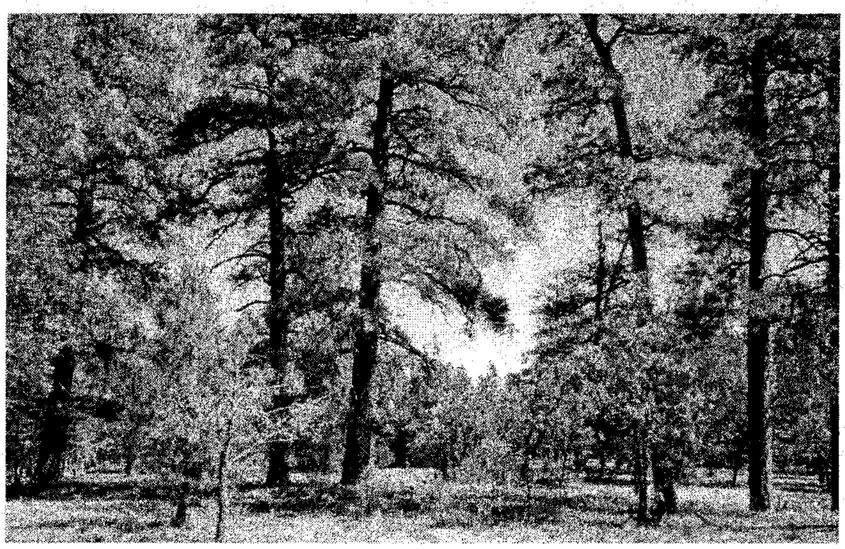
Table 2.01. General plant composition of the three study areas. Overstory and midstory tree species are listed in descending order of relative abundance. Tree species capable of vegetative reproduction (sprouting) are denoted by "(s)".

Site	Overstory trees[a]	Midstory trees	Understory woody spp.	Herbaceous spp.
GRCA	*Pinus ponderosa* var. *scopulorum* *Abies concolor* *Pseudotsuga menziesii* *Populus tremuloides* (s)	*Robinia neomexicana* (s) *Quercus gambelii* (s)	*Amelanchier utahensis* *Arctostaphylos patula* *Berberis repens* *Ceanothus fendleri* *Rosa fendleri*	*Achillia lanulosa* *Bouteloua gracilis* *Carex* spp. *Fragaria ovalis* *Lotus utahensis* *Lupinus* spp. *Poa fendleriana* *Sytanion hystrix* *Viguiera multiflora*
WACA	*P. ponderosa* var. *scopulorum* *P. menziesii*	*Q. gambelii* (s) *Juniperus osteosperma* *J. monosperma* *J. scopulorum* *J. deppeana* (s) *Pinus edulis*	*A. utahensis* *C. fendleri* *Cowania mexicana* *Purshia* spp. *Rhus trilobata* *Tetradymia canescens*	*A. lanulosa* *B. gracilis* *Elymus* spp. *Festuca arizonica* *Koeleria cristata* *Muhlenbergia montana* *P. fendleriana*
SAGU	*P. ponderosa* var. *arizonica* *Pinus strobiformis* *P. ponderosa* var. *scopulorum*	*Q. hypoleucoides* (s) *Q. rugosa* (s) *Q. arizonica* (s) *J. deppeana* (s) *Q. gambelii* (s) *Pinus cembroides* *R. neomexicana* (s)	*Arctostaphylos pungens* *Berberis repens* *C. fendleri* *Holodiscus dumosa* *Prunus serotina* *Symphoricarpos oreophilus*	*Blepharoneuron tricholepsis* *E. arizonicus* *Dugaldia hoopesii* *K. cristata* *M. virescens* *Pteridium aquilinum* *Stipa pringlei*

[a] Classification into strata is based upon average height attained by species in Southwestern ponderosa pine forests.

Grand Canyon
National Park

Walnut Canyon
National Monument



Saguaro
National Park

Figure 2.02. Photos of ponderosa pine forest typical of the three study areas.

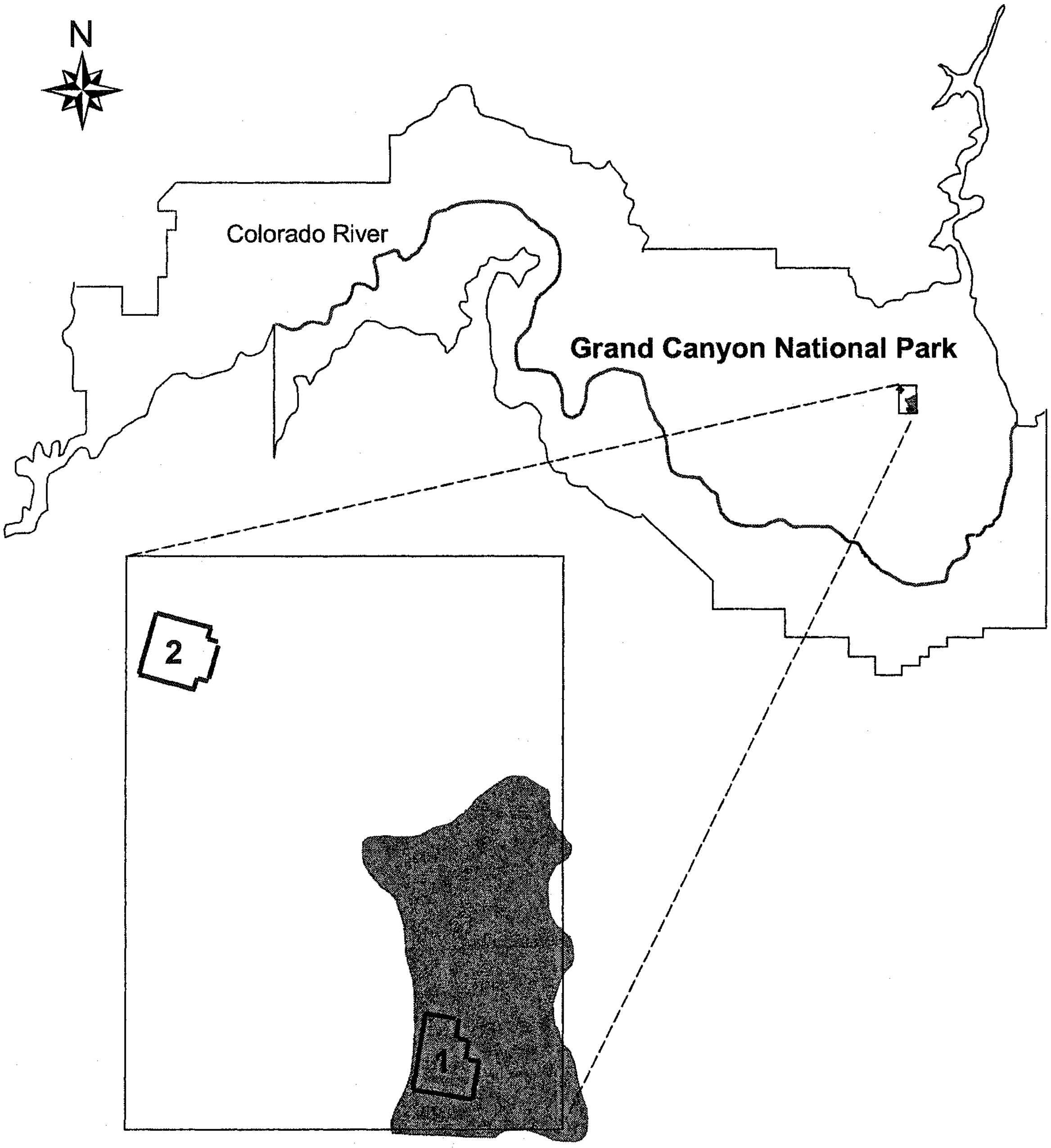


Figure 2.03. Locations of two, 40-ha sampling units within Grand Canyon National Park. Unit 1 (~12415600E, 4005275N) was burned in November 1999 as part of the 742-ha Atoko subunit of the Walhalla Burn (red hatching). Unit 2 (~12412900E, 4008384N) is the matched control for Unit 1. See Figure 2.04 for detail map.

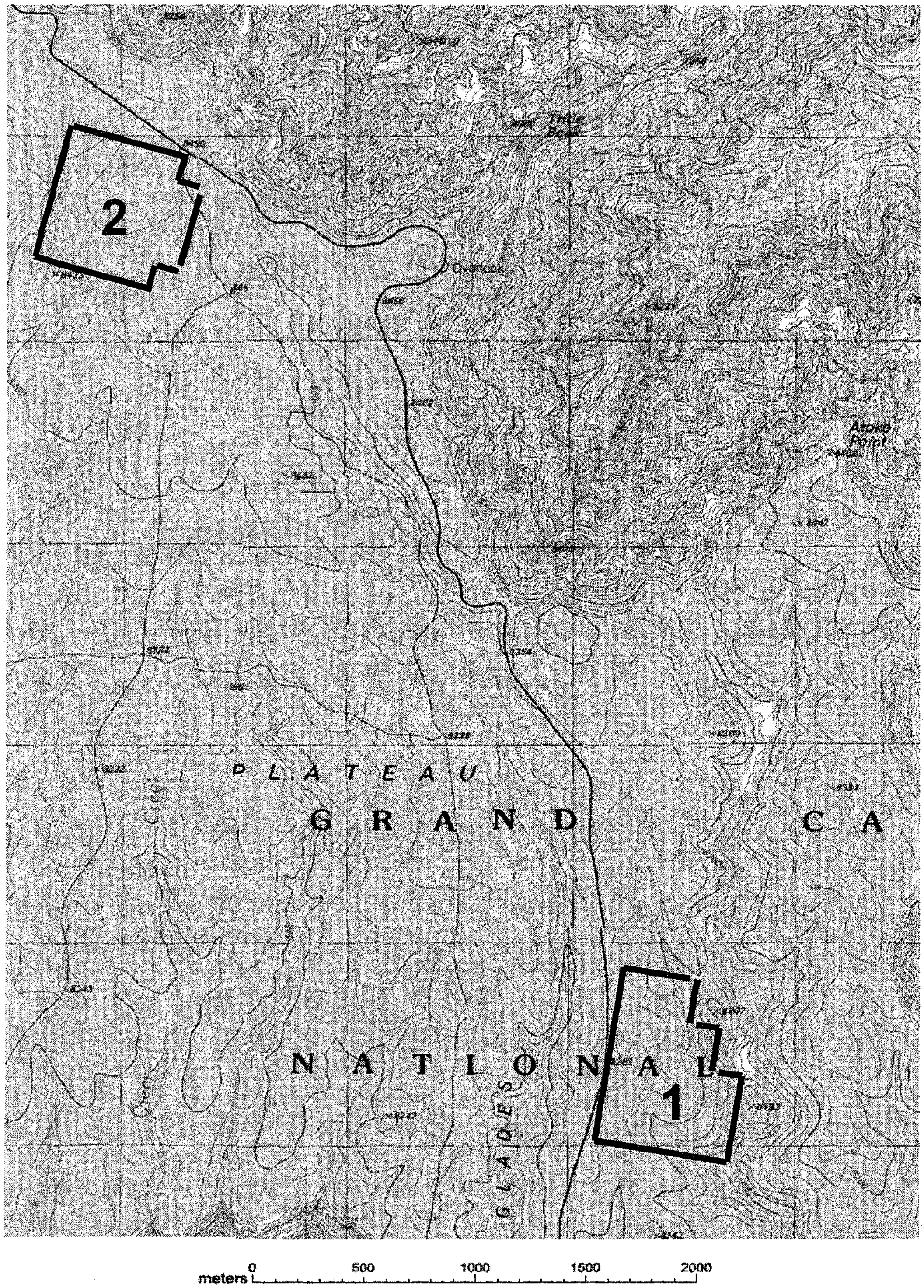


Figure 2.04. Detail of Figure 2.03 from USGS topographic map of Walhalla Plateau Quadrangle.

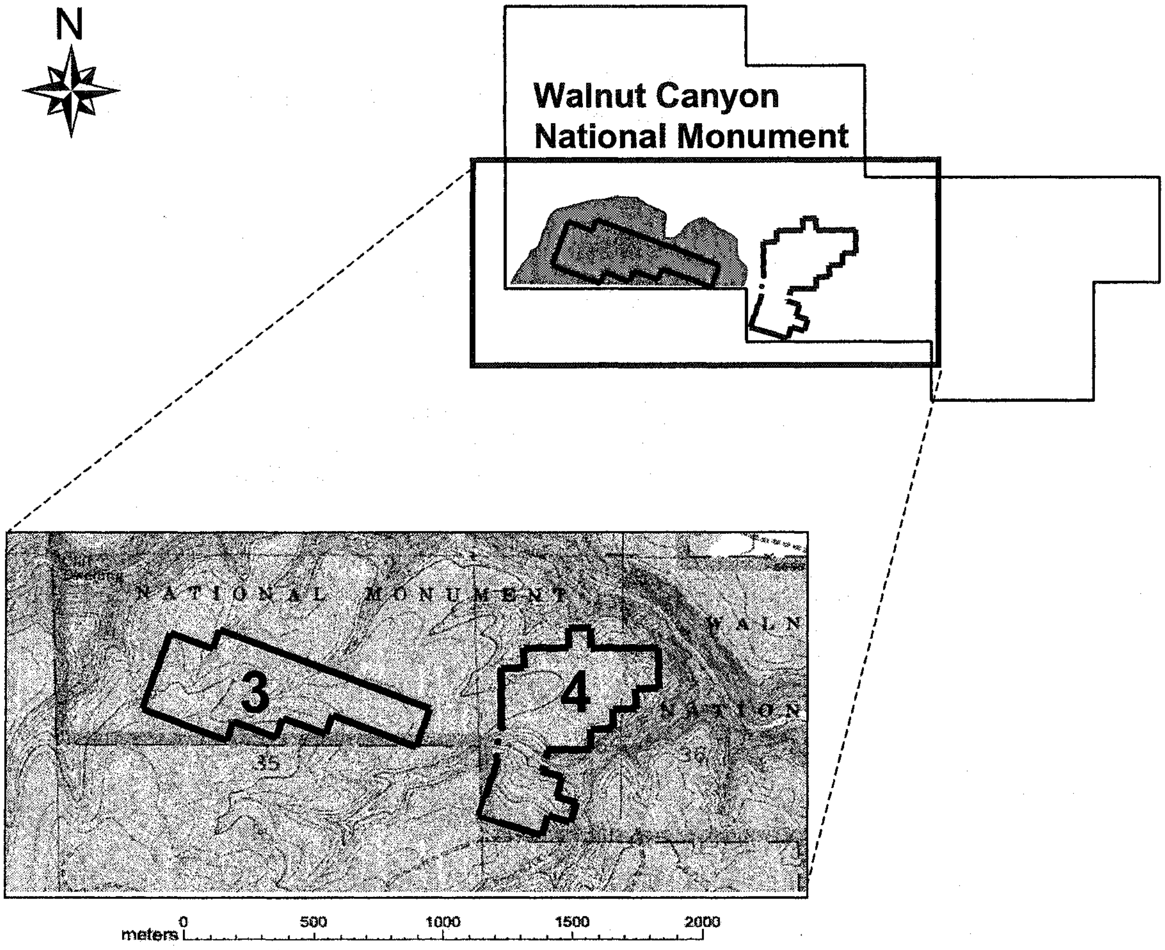


Figure 2.05. Locations of two, 40-ha sampling units within Walnut Canyon National Monument. Unit 3 (~12453200E, 3891050N) was burned in October 1999 as part of the 64-ha Pictograph Burn (red hatching). Unit 4 (~12454250E, 3890770N) is the matched control for unit 3. Detail is from USGS topographic map of Walnut Canyon Quadrangle.

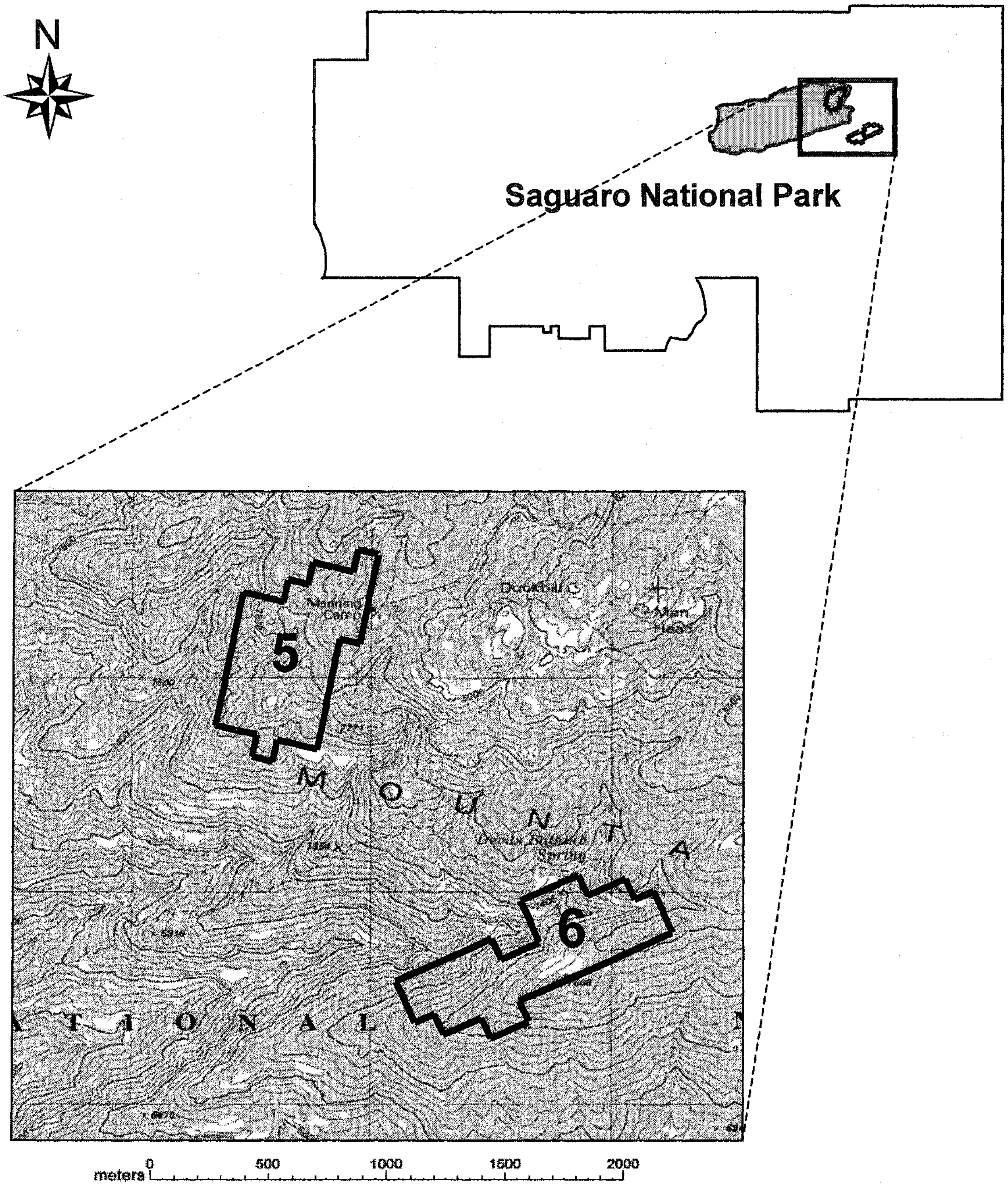


Figure 2.06. Locations of two, 40-ha sampling units within Saguaro National Park, Rincon Mountain Unit. Unit 5 (~12541625E, 3564200N) was burned in October 1998 as part of the 800-ha Chimenea Burn (red hatching). Unit 6 (~12542825E, 3562380N) is the matched control for Unit 5. Detail is from USGS topographic map of Mica Mountain Quadrangle.

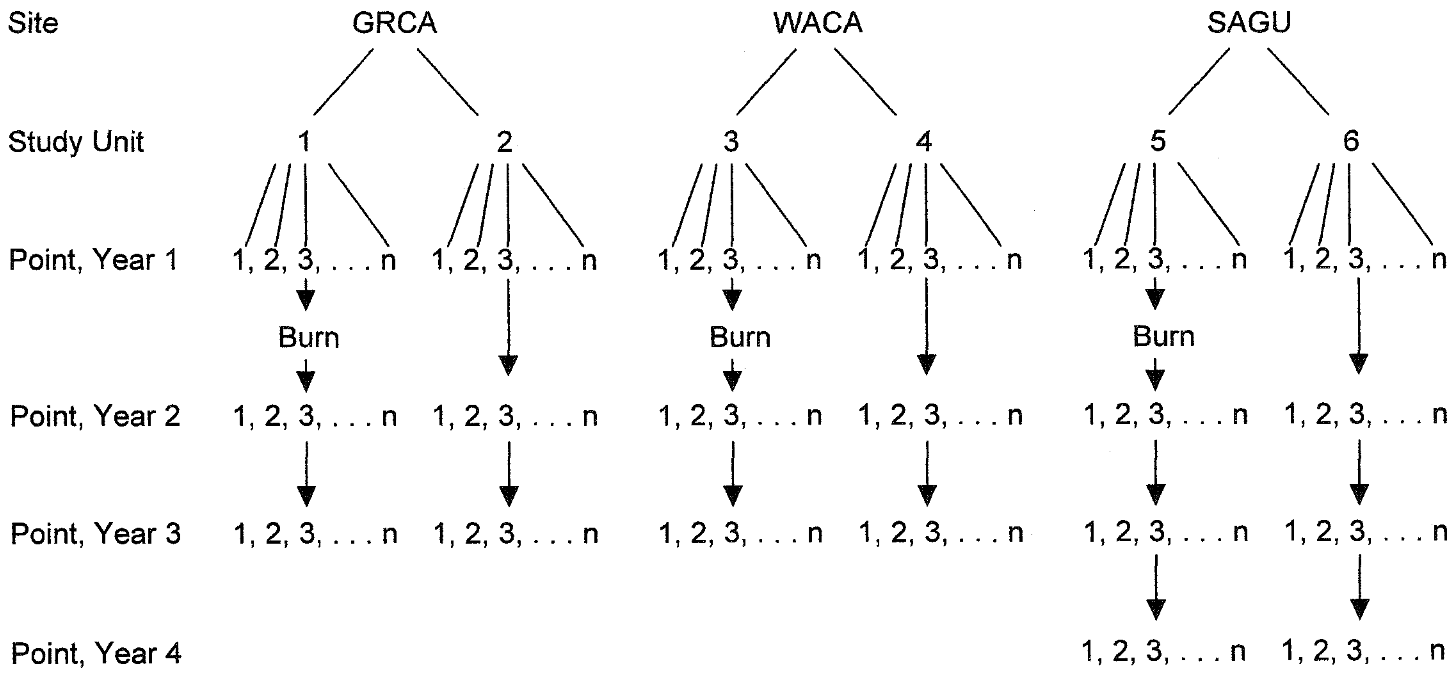


Figure 2.07. General experimental design of the study. I used site as a blocking factor and included two matched, 40-ha plots within each site. Each plot received one level of treatment: burn or no burn. Repeated measures were taken on each plot (during the summer before burning and then on approximately the same dates for 2-3 years following the fires).

Vegetation

Within each unit, I selected ~24 points at which to sample vegetation by choosing one gridpoint at random and then alternating across the grid (Figure 2.08). With the vegetation sampling, I sought to define the fire treatments in terms of habitat changes potentially important to forest arthropods and, for a related study, birds (see Chapter 3) while also conveying meaningful information to researchers and managers interested in replicating these treatments. To this end, I generally followed the Breeding Biology Research and Monitoring Database (BBIRD) sampling protocol (Martin et al. 1996, *unpubl. ms.*).

At each point, I laid two measuring tapes crosswise to delineate nested subplots of 5 and 11 m radii (Figure 2.08). In the larger subplot, I recorded:

1) *Burn severity.* Based on ocular estimates of average conditions, I rated burn severity of litter/duff, vegetation ≤3 m, and vegetation >3 m using standard National Park Service (NPS) burn severity codes (USDI 2001, Table 2.02).
2) *Number of trees >3 m tall by species, size class, and condition.* I measured the diameter of trees at breast height (dbh), except for basally sprouting species (see Table 2.01), which I measured at root crown (drc), and classed trees as <8.0, 8.0-22.9, 23.0-37.9, or >38.0 cm in size. For basally sprouting species, I recorded the condition of each individual based on proportion of main stems >3 cm drc supporting any green foliage. Sprouters in the smallest diameter class generally had only a single main stem, and I classed them simply as live or dead based on the presence or absence of any green foliage. I noted ponderosa pines as having either 0-15% or 15-100% green needles to discriminate standing-dead trees (snags) from live trees,

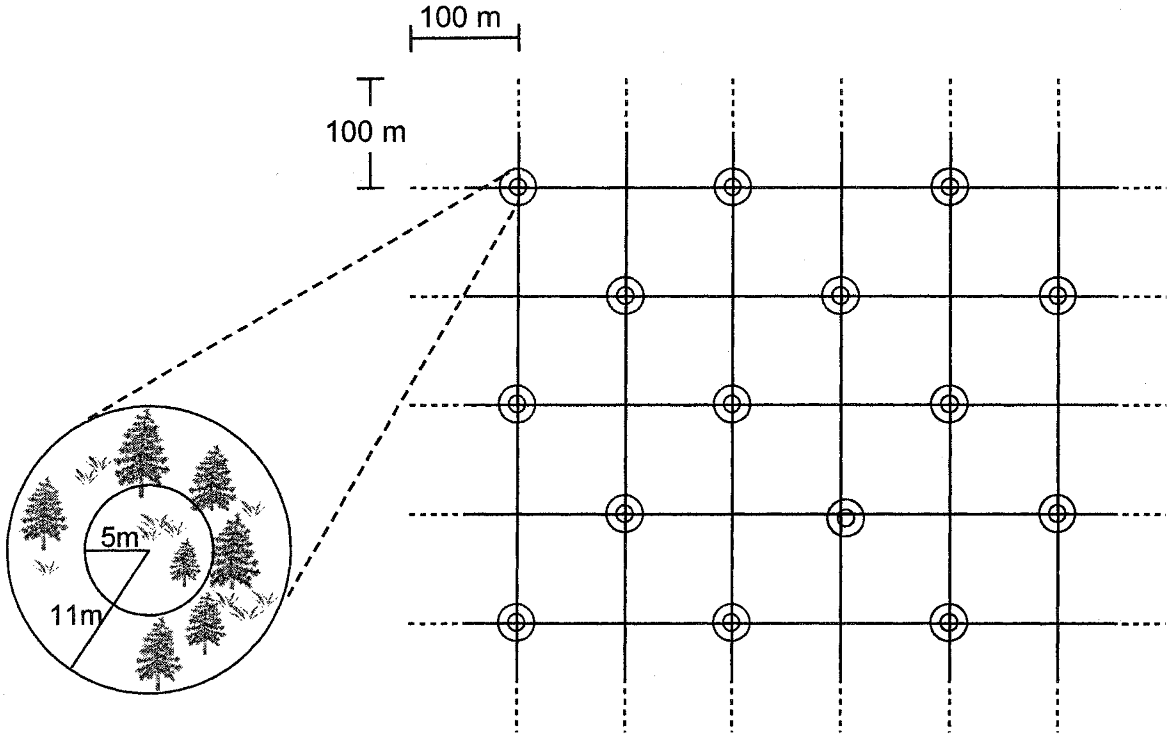


Figure 2.08. Schematic of vegetation sampling protocol. Within each experimental unit, I sampled vegetation in nested, 5- and 11-m radius subplots centered on 23-24 grid intersections.

Table 2.02. Fire-severity coding matrix used to characterize the fires in this study. Adapted from USDI (2001).

	Fire Severity Rating and Description					
Substrate	0 - Not Applicable	1- Heavily Burned	2 - Moderately Burned	3 - Lightly Burned	4 - Scorched	5 - Unburned
Litter/duff	Inorganic	Litter and duff consumed, leaving fine white ash; mineral soil visibly altered, often reddish	Litter mostly to entirely consumed, leaving coarse, light-colored ash; duff deeply burned; wood/leaf structures charred but recognizable	Litter charred to partially consumed, upper duff layer burned; wood/leaf structures charred but recognizable	Litter partially blackened; duff nearly unchanged; wood/leaf structures unchanged	Not burned
Vegetation $\leq$3m and >3m	None present	All plant parts consumed, leaving some or no major stems/trunks	Foliage, twigs and small stems consumed	Foliage and smaller twigs partially to completely consumed	Foliage scorched and attached to supporting twigs	Not burned

respectively (Lynch 1959, Harrington 1993).

3) *Percent cover from scorched and green vegetation by height class and form.* I estimated percent cover from woody plants in each of three height classes: > 3 m, 1-3 m, <1 m; and from herbaceous plants <1 m tall. I calculated percent cover as the proportion of the 45 meter-marks along the tapes with the target vegetation directly overhead. I used a moosehorn densiometer to determine presence of cover from woody vegetation >3 m and 1-3 m tall. I noted presence of woody and herbaceous cover >1 m tall simply by looking down while standing over each meter mark. Cover at each meter was recorded as either fully green or scorched somewhere within the given stratum.

I used the 5-m-radius subplot to further describe the understory, noting:

1) *Number of woody stems by tree species, height class, and condition.* I counted only basal (main) stems of overstory and midstory tree species (Table 2.01) – not subsequent branches. For example, I counted basal resprouts of *Quercus* species, but not individual branches of a given *Quercus* sprout. I classed stems as <1m or 1-3 m tall and as live or dead based on presence or absence of green foliage.
2) *Percent ground cover by form.* I made ocular estimates of percent cover from charred and unburned coarse woody debris (logs and branches ≥8 cm diameter, or 1000-hour fuels *sensu* Sackett and Haase 1998), other debris, litter, and organic matter in various stages of decomposition (≤ 100-hour fuels plus the L, F, and H layers of the forest floor *sensu* Sackett and Haase 1998), and bare ground (rock and mineral soil).

Arthropods

I expected the effects of these fires to be concentrated in low forest strata and focused my arthropod sampling efforts at the forest floor. Within each unit, I randomly selected 20 of the 23-24 vegetation sampling points at which to collect arthropods in pitfall traps, excluding any points that fell on rock outcrops, where it was impossible to bury the traps, or within 50 m of a road or trail, where the traps could be seen or disturbed by park visitors. Offset 0.5 m from the center of each of the 20 chosen vegetation sampling points, I installed a crosswise array of nine traps at 1 m intervals. Each trap consisted of a 10-oz, white, plastic cup buried in the soil so that the 8-cm opening was level with the litter surface. I filled each trap halfway with a killing solution of unscented castile soap and water (Figure 2.09). I ran the traps during two sampling periods of four days each on the same Julian dates during the late spring and summer of the year before and during each of the first two years after the fires. At the end of each sampling period, the contents of all nine traps at each point were pooled, fine-sieved, and transferred to Whirl-Pak™ bags containing 95% ethanol. I always collected from matched control and treatment plots on the same or consecutive days. Arthropods >3 mm in length were sorted, identified to family or thereabout (following Borror et al. 1992), and counted in the laboratory. I categorized taxa as decomposers, fungivores, sap and wood feeders, herbivores, predators, parasites, and parasitoids, or "other" (i.e., omnivores) depending on the typical habits of species therein (following Borror et al. 1992).

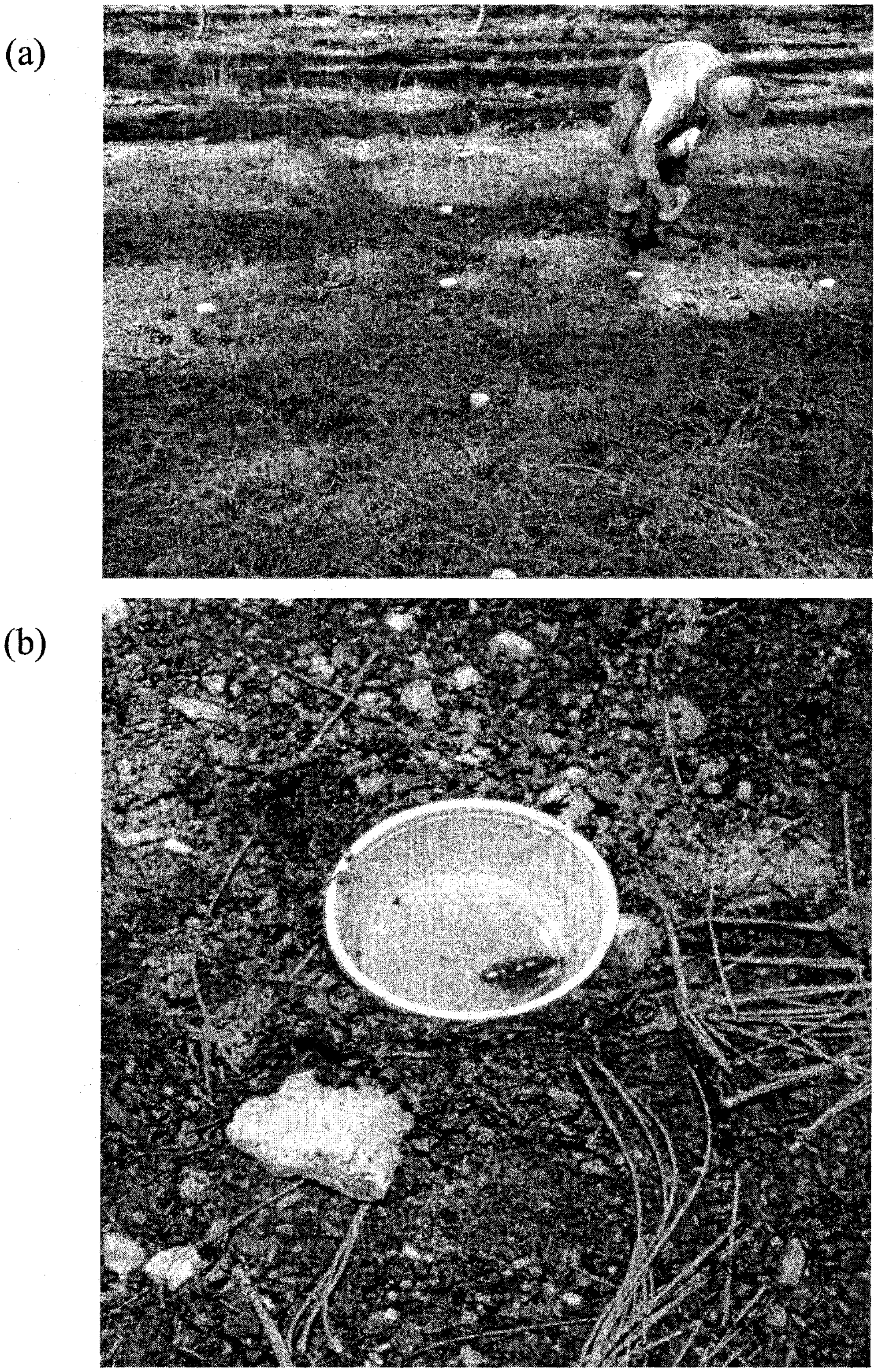


Figure 2.09. I used pitfall traps to assess the effects of the fire treatments on arthropods. (a) At each sampling point, I installed a crosswise array of nine traps at 1-m intervals. (b) Each pitfall trap consisted of a 10-oz, white, plastic cup buried in the soil so that the 8-cm opening was level with the litter surface. I filled each trap halfway with a killing solution of unscented castile soap and water.

Statistical analyses

From my repeated subplot measures, I calculated the average values of response variables within treatment versus control units for each year of study. For the arthropod data, I first averaged values from the two sampling periods per year, such that, ideally, each year of study yielded trap rate per unit effort (36 trap-days) from the same 20 sampling points within each of the six experimental units. However, a number of pitfall "failures" occurred when traps were unearthed by wildlife or filled with debris. I excluded data from point-visits with any of these failures (and therefore missing data) before calculating descriptive statistics.

I considered changes in mean values of response variables on the control plots to approximate the changes in means that would have occurred on the treatment plots in the absence of burning. For each variate, y_{ij}, and each interval, (1, 1 + n), I compared changes in paired treatment and control means to estimate a relative change function, r_n, or a difference score, d_n, as my fire effect estimate, where i = 0 (control) or 1 (treatment), j = 1 (pre-fire) or 1 + n (post-fire), n = number of years post-fire,

$$r_n = (\overline{y}_{1,1+n} / \overline{y}_{1,1}) / (\overline{y}_{0,1+n} / \overline{y}_{0,1}) \text{, and}$$
$$d_n = (\overline{y}_{1,1+n} - \overline{y}_{1,1}) - (\overline{y}_{0,1+n} - \overline{y}_{0,1})$$

I used these formulae to estimate fire effects both when data from sites were pooled (i.e., a single control or treatment mean was estimated from a given year's data pooled across sites) and when sites were considered singly, in which case I could assess the consistency of treatment effects across sites.

If pre-fire means are roughly equivalent, as in my estimates of forest floor attributes (see *Results*), either model provides a valid estimate of change due to fire. However, my three pairs of treatment and control plots were not perfectly matched on most variables of interest, and I generally accounted for baseline noncomparability among treatment groups by using the relative change in control means within a given interval as a proxy for the expected average change in the absence of fire on the treatment plots (r_n). I considered d_n to be an appropriate estimator of fire effects only for the proportion of dead or lethally injured trees of the total standing in each size class, as there is no reason to expect baseline changes in average condition of trees to be a multiplicative function of pretreatment values.

Because difference scores and relative change functions are both prone to highly skewed or asymmetric distributions (Bonate 2000), I used a bootstrap procedure (10000 iterations, S-PLUS 6.0) to generate sampling distributions and bias-corrected 95% confidence intervals (CI) for all r_n or d_n from the observed data. All data were resampled within units such that the number of observations per unit remained constant and the same subplots (sampling points within units) were represented in the repeated measures through all iterations. To ensure that the arthropod estimates were based on equal sampling effort over time within units, I included data from subplots with pitfall failures only when same number of traps failed across the years of interest.

I transformed relative change scores to percent changes, $(r_n - 1)*100\%$, so that, for all estimates, a value of zero would indicate no effect of burning. Here, I report findings as statistically significant at the unadjusted critical level of $P \leq 0.05$, that is, when the 95% CI do not include zero. Based on the sheer number of estimates that I was able to make, the true mean effect may lie outside the reported interval for a handful of variables. Nonetheless, as reported, my estimates should provide a valid indication of the relative magnitude and direction of most of the effects of the fires in this study.

RESULTS

The fire treatments and their effects on forest vegetation

The fires in my study were ignited in October or November of their respective years and burned from 64 to 800 ha under a range of weather conditions (Table 2.03). All were low-severity (Table 2.04), autumn burns. Because their effects were concentrated in low forest strata, all three would be similarly classified as surface or understory fires *(sensu* Agee 1993, Brown 2000). Despite their nominal similarities, the treatments differed in many of their effects on vegetation. In general, the GRCA fire was most severe at the forest floor and least severe in all foliage categories; the WACA fire was most severe in low foliage (≤3 m), with intermediate effects in upper foliage and at the forest floor; and the SAGU fire was most severe in upper foliage (>3 m) and least severe at the forest floor (Table 2.04). In the following sections I detail changes in vegetation – from the overstory to the forest floor – attributable to the three fire treatments, highlighting any marked disparities.

First-year changes

By the first summer post-fire, the treatments (pooled or otherwise) effected no significant change in total cover from trees >3 m tall (Table 2.05). All fires did, however, generate sufficient heat to kill foliage in all strata (Table 2.06) and to injure or kill significant numbers of ponderosa pines of all sizes except for those in the largest

Table 2.03. Characteristics of fire treatments applied to three, 40-ha experimental (study) units.

						Burning Conditions		Fire Behavior		
Site	Burn Unit	Burn Size (ha)	Study Unit[a]	Date and Time of Ignition	Ignition Method	Relative Humidity (%)	Dry Bulb (°C)	Midflame Windspeed (km/h)	Flame Length (m)	Rate of Spread (m/min)
GRCA	Walhalla (Atoko subunit)	297	1	17 November 1999, 1020 – 1330h; 20 November 1999, 1000 –1130h	Aerial	23-61	7-12	1.9-7.5	0.2-0.9	0.3-6.8
WACA	Pictograph	64	3	13-14 October 1999, 1000 – 1500h	Strip firing	20-33	20-24	0.6-3.1	0.1-0.9, up to 10	0.2-3.0
SAGU	Chimenea	800	5	11 October 1998, 1345 – 2030h	Strip firing, aerial	~19	~18	0-0.6	0.1-0.5, up to 15	~0.3

[a] See Figures 2.-3-2.06.

Table 2.04. Severity ratings (X ± 1SD) of the three fire treatments, as recorded during the first summer post-fire. Scores ranged from 1 (heavily burned) to 5 (unburned) (Table 2.02). Therefore, lower ratings indicate higher fire severities.

		Substrate		
Site	n	Forest Floor	Vegetation ≤3m	Vegetation >3m
GRCA	24	2.65 ± .81	3.96 ± .44	4.52 ± .43
WACA	23	2.96 ± .82	3.43 ± .73	3.85 ± .51
SAGU	24	3.21 ± .51	3.62 ± .58	3.75 ± .68

Table 2.05. Total cover and counts of standing vegetation and debris by forest stratum per 0.038 ha (0.008 ha, if denoted by an asterisk) as estimated during the summer before and the first summer after fire. Only trees common to all sites are included. Data are means ± 1SD for the three experimental units within each treatment-time combination. Estimates of fire-caused changes are based on data pooled across the three sites.

	Treatment		Control		% change due to fire: bootstrapped mean (95% CI)
Variable	Pre-fire	Post-fire Year 1	Prefire	Post-fire Year 1	
Vegetation > 3m					
percent cover	44.5 ± 10.9	42.1 ± 9.3	44.1 ± 7.6	42.6 ±7.4	-2 (-9, 4)
no. ponderosa pines					
> 38 cm dbh	3.2 ± 1.2	3.1 ± 1.3	2.5 ± 0.6	2.5 ± 0.6	-3 (-7, 0)
23 -37.9 cm dbh	3.1 ± 1.0	3.0 ± 0.8	2.5 ± 1.1	2.5 ± 1.1	-3 (-8, 0)
8 –22.9 cm dbh	8.3 ± 2.1	8.5 ± 2.4	6.5 ± 1.9	5.4 ± 3.1	2 (-1, 13)
<8 cm dbh*	0.7 ± 0.1	0.7 ± 0.2	0.9 ± 0.5	1.0 ± 0.5	9 (-4, 36)
Vegetation 1-3 m					
percent cover	5.3 ± 5.0	5.4 ± 2.4	8.5 ± 3.5	8.6 ± 1.8	1 (-24, 27)
no. ponderosa pines*	1.0 ± 0.2	0.9 ± 0.2	0.9 ± 0.5	1.2 ± 0.4	-10 (-26, 4)
no. midstory sprouters*	3.3 ± 2.8	2.4 ± 1.9	3.7 ± 3.7	3.4 ± 4.4	-33 (-47, -18)
Vegetation <1m					
percent woody cover	4.3 ± 1.2	3.4 ± 1.0	8.7 ± 2.9	8.0 ± 3.6	-14 (-31, 14)
no. ponderosa pines*	7.7 ± 5.9	168.4 ± 291.0	12.3 ± 18.4	2.5 ± 2.0	9128 (3650, 21699)
no. midstory sprouters*	35.4 ± 27.2	42.9 ± 26.4	38.2 ± 29.6	25.9 ± 39.3	15 (-4, 40)
percent herbaceous cover	13.1 ± 4.9	5.5 ± 3.7	16.3 ± 7.3	11.2 ± 7.8	-40 (-51, -27)
Forest floor					
percent cover of logs >8 cm in diameter*	4.0 ± 2.3	2.0 ± 1.0	4.4 ± 3.1	4.7 ± 3.3	-54 (-66, -39)
percent litter cover *	85.6 ± 5.5	81.0 ± 5.5	85.2 ± 2.1	85.2 ± 2.6	-5 (-10, -3)
percent bare ground *	7.9 ± 4.4	17.0 ± 5.6	8.1 ± 3.4	8.8 ± 4.0	99 (53, 173)

Table 2.06. Proportion of scorched or standing dead vegetation and charred woody debris by forest stratum per 0.038 ha (0.008 ha, if denoted by an asterisk) as estimated during the summer before and the first summer after fire. Only trees common to all sites are included. Data are means ± 1SD for the three experimental units within each treatment-time combination. Estimates of fire-caused changes (differences in percentage points) are based on data pooled across the three sites.

	Treatment		Control		Difference due to fire:
Variable	Pre-fire	Post-fire Year 1	Pre-fire	Post-fire Year 1	bootstrapped mean (95% CI)
Vegetation > 3m					
scorched cover	—	40.5 ± 31.9	—	8.3 ± 14.4	37 (30, 43)
ponderosa pines with <15% green foliage					
> 38 cm dbh	8.9 ± 2.4	13.9 ± 7.8	7.0 ± 2.2	7.1 ± 2.1	4 (0, 12)
23 -37.9 cm dbh	6.5 ± 2.0	17.4 ± 6.1	2.6 ± 2.8	2.6 ± 2.8	11 (5, 20)
8 –22.9 cm dbh	3.2 ± 3.6	33.7 ± 20.9	6.4 ± 8.8	8.5 ± 8.6	26 (17, 37)
<8 cm dbh*	3.9 ± 6.8	47.9 ± 25.5	8.1 ± 10.5	8.1 ± 10.6	39 (17, 59)
Vegetation 1-3 m					
scorched cover	—	67.1 ± 36.8	—	1.9 ± 3.3	76 (66, 84)
ponderosa pines with <15% green foliage*	6.8 ± 3.5	67.5 ± 19.4	9.0 ± 9.4	10.0 ± 7.4	63 (48, 77)
midstory sprouters with no green foliage*	20.4 ± 19.9	86.3 ± 13.8	13.5 ± 10.5	6.4 ± 5.9	76 (62, 86)
Vegetation <1m					
scorched woody cover	—	56.4 ± 26.4	—	1.1 ± 1.6	54 (39, 70)
midstory sprouters with no green foliage*	7.1 ± 8.9	15.4 ± 7.8	2.0 ± 2.1	2.4 ± 3.4	11 (6, 17)
Forest floor					
percent cover of logs >8 cm in diameter*	—	87.8 ± 11.1	—	6.4 ± 1.6	86 (76, 93)

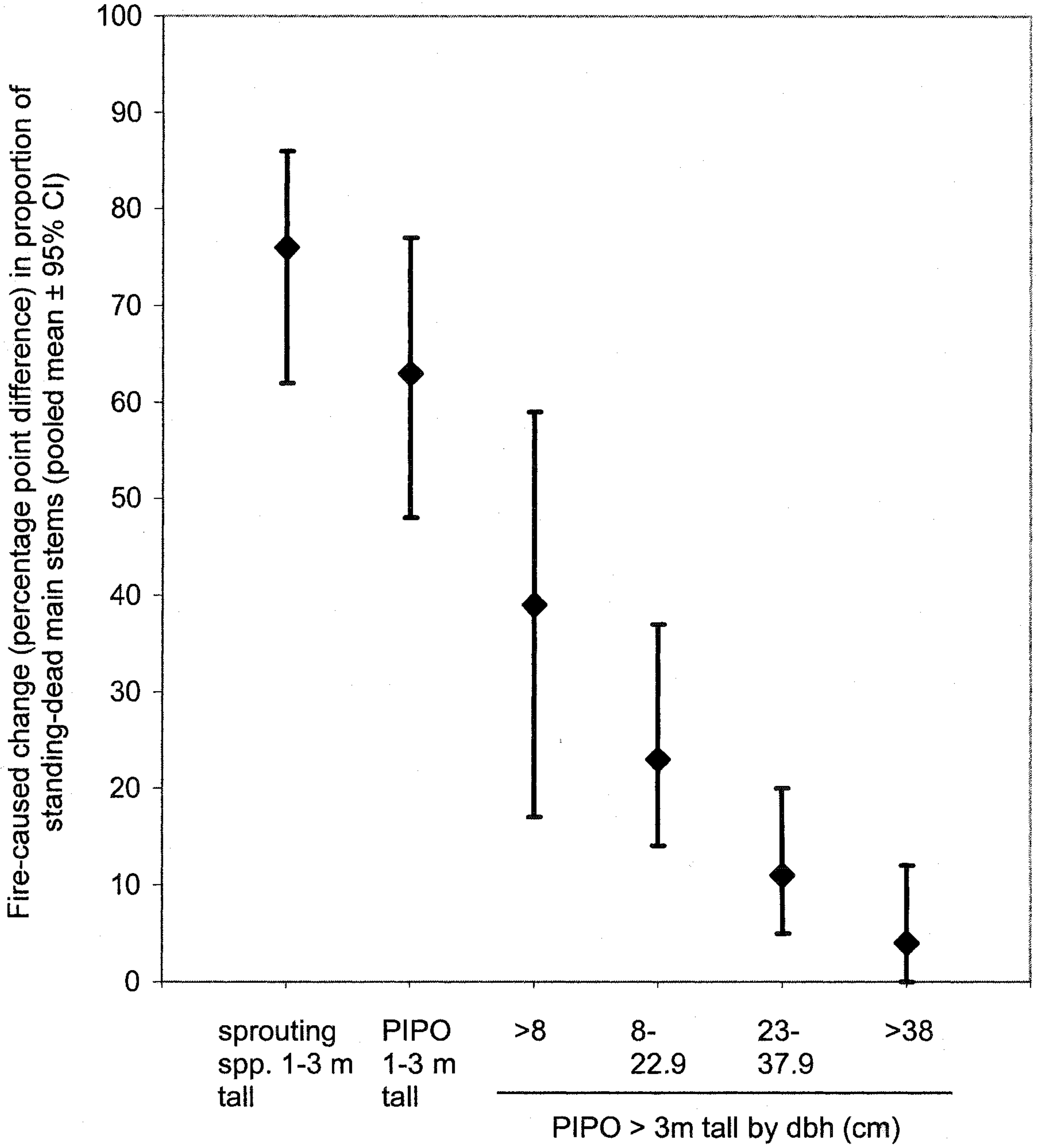


Figure 2.10. Smaller trees sustained greater fire-caused injuries, and main stems of sprouting species (i.e, oaks, Table 2.01) were more likely to be killed by the fires than the pines.

diameter class (Table 2.06, Figure 2.10). At WACA, 66% (51%, 79%) of the area covered by foliage in this stratum after fire had been scorched somewhere above 3 m, indicating that, on average, lethal heat was generated upwards of 3m over two-thirds of the area supporting midstory or overstory vegetation on the study plot. This figure for the SAGU and GRCA fires was 46% (34%, 59%) and 6% (3%, 9%) respectively. In general, smaller trees sustained greater fire-caused injuries, and main stems of sprouting species (i.e, oaks, Table 2.01) were more likely to be felled or killed by the fires than the pines (Table 2.06; Figure 2.10). The SAGU fire tended to cause the greatest increase in the proportion of dead trees per size and height class, with the WACA fire effecting fewer changes, and the GRCA fire effecting still fewer.

At both SAGU and WACA, most of the woody vegetation 1-3 m tall showed signs of lethal injury or topkill. However, there were only trivial changes in total cover from foliage in this stratum during the first year after the fires at SAGU and GRCA. In contrast, there was a significant first-year *increase* of 72% (19%, 177%) in cover within this stratum due to the WACA fire (Figure 2.11). This change was likely due to scattered treefall and the tendency for small-diameter stems to bend downward when fire-damaged. Losses of woody vegetation < 1 m tall due to burning were offset to a large degree at all sites by the vegetative regrowth of topkilled sprouters (Table 2.05, Figure 2.). However, there was still a 44% net loss (-64%, -19%) of shrub cover due to the fire at SAGU.

There was a tremendous flush in production of ponderosa pine seedlings after the SAGU fire, but not in response to the other two treatments. In fact, while the SAGU fire caused a 180-fold increase in the mean number of live ponderosa pine seedlings, the WACA fire caused no significant change, and the GRCA burn effected a 93% decrease (-

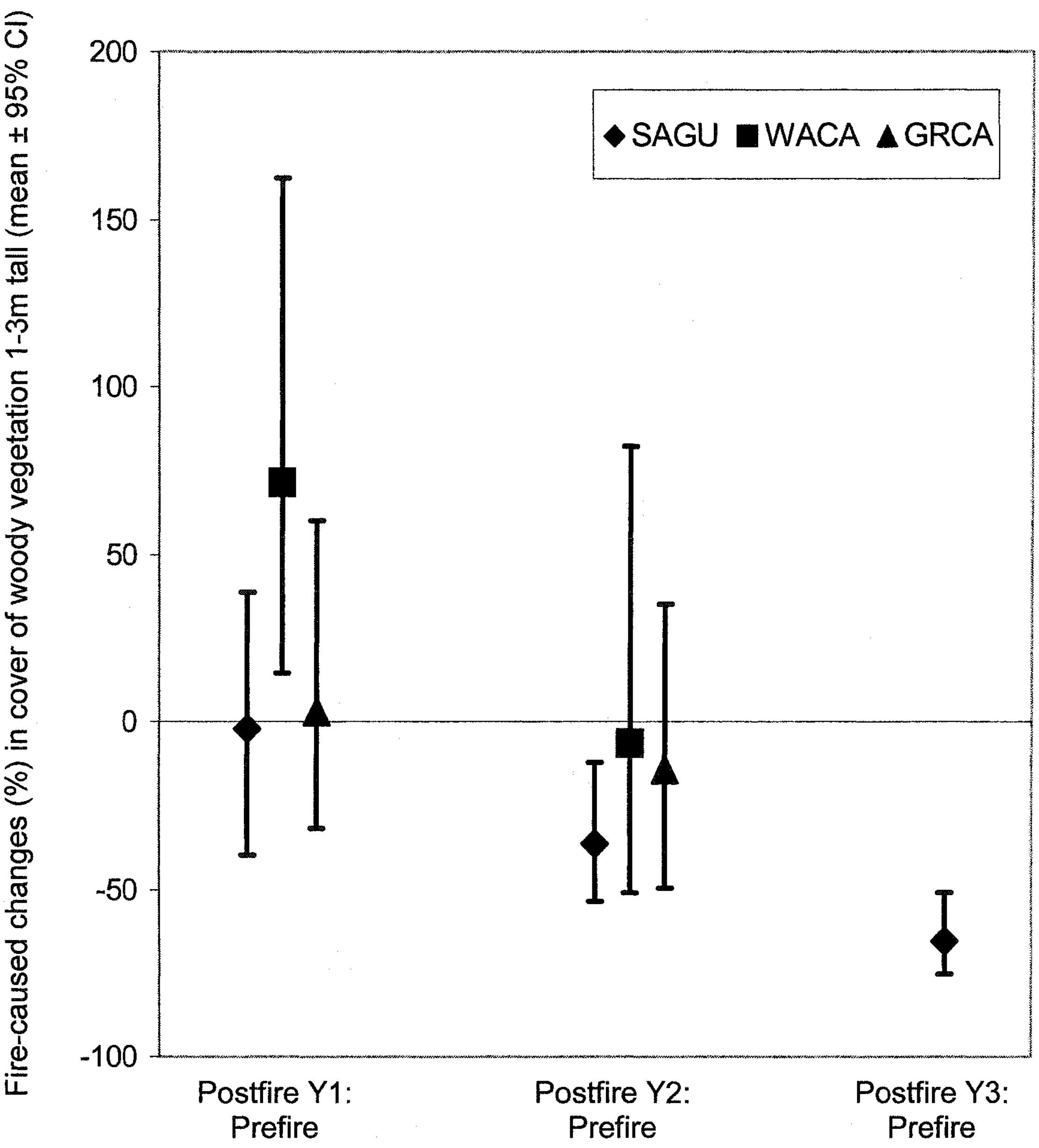


Figure 2.11. Fire-caused changes (%) in cover of woody vegetation 1-3m tall (mean ± 95% CI) from the summer before to the first, second, and third summers after fall burning. Note the significant first-year increase in cover within this stratum attributable to the WACA fire. This change was likely due to scattered treefall and the tendency for small-diameter stems to bend downward when fire-damaged.

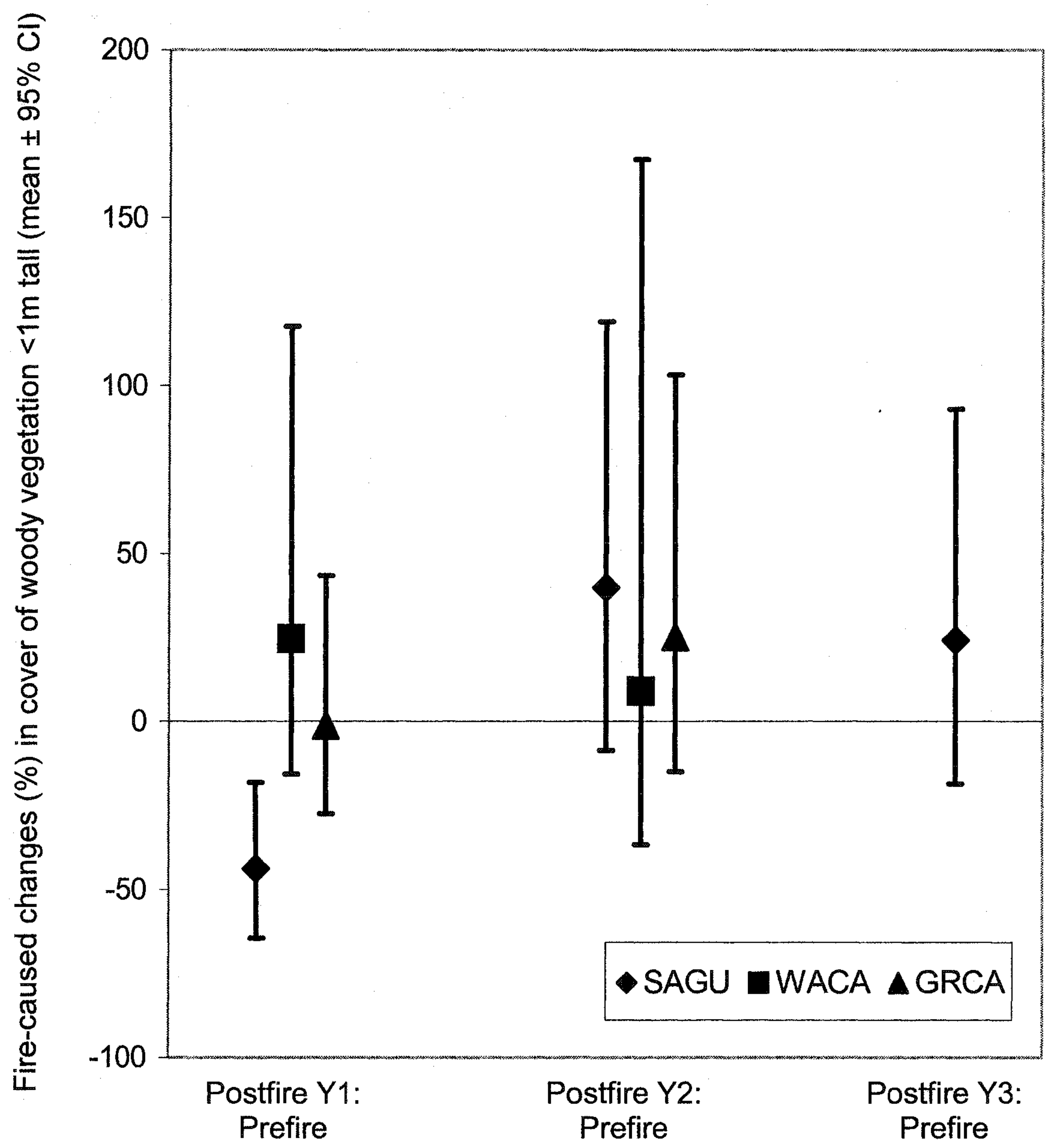


Figure 2.12. Fire-caused changes (%) in cover of woody vegetation <1m tall (mean ± 95% CI) from the summer before to the first, second, and third summers after fall burning. Only the SAGU fire had a significant influence on this forest attribute (first-year decrease).

98%, -81%) in numbers of these plants during year 1. None of these changes appeared to have any influence on the total cover of low woody vegetation after burning. Whereas average cover of low woody vegetation on treatment plots was not significantly affected in the short-term by the autumn burns, mean herbaceous cover fell at both SAGU and WACA (Figure 2.13), such that the overall effect was significant (Table 2.05).

In addition, the fires reduced the average cover of logs >8 cm in diameter by 54%, presumably via direct consumption of these fuels (Table 2.05, Figure 2.14). Of the residual coarse woody debris, 86% had been charred to some degree by the fires (Table 2.06). Cover of smaller-diameter woody debris and other fine organic material at the forest floor was 5% lower than expected on the treatment units in the first summer after burning (Table 2.05). These first-year changes at the forest floor, which were most marked at GRCA, translated into a short-term doubling of the average area of exposed mineral soil across the burned plots (Table 2.05, Figure 2.15).

Second-year changes

Most of the lethal injuries to forest plants were evident by the first summer following the fall burns. By the second summer post-fire, additional mortality was manifest only in the smallest class of ponderosa pines > 3 m tall (Tables 2.07, 2.08). Other second-year changes attributable to burning were generally functions of leaf-shed and enhanced growth of understory vegetation. Within the 1-3 m stratum, cover on the treated plots averaged 30% lower than expected in the absence of burning, largely due to the shedding of fire-killed foliage (Table 2.07). In the lowest stratum, the mean number of main sprouter stems was 80% greater than expected, and the new growth apparently

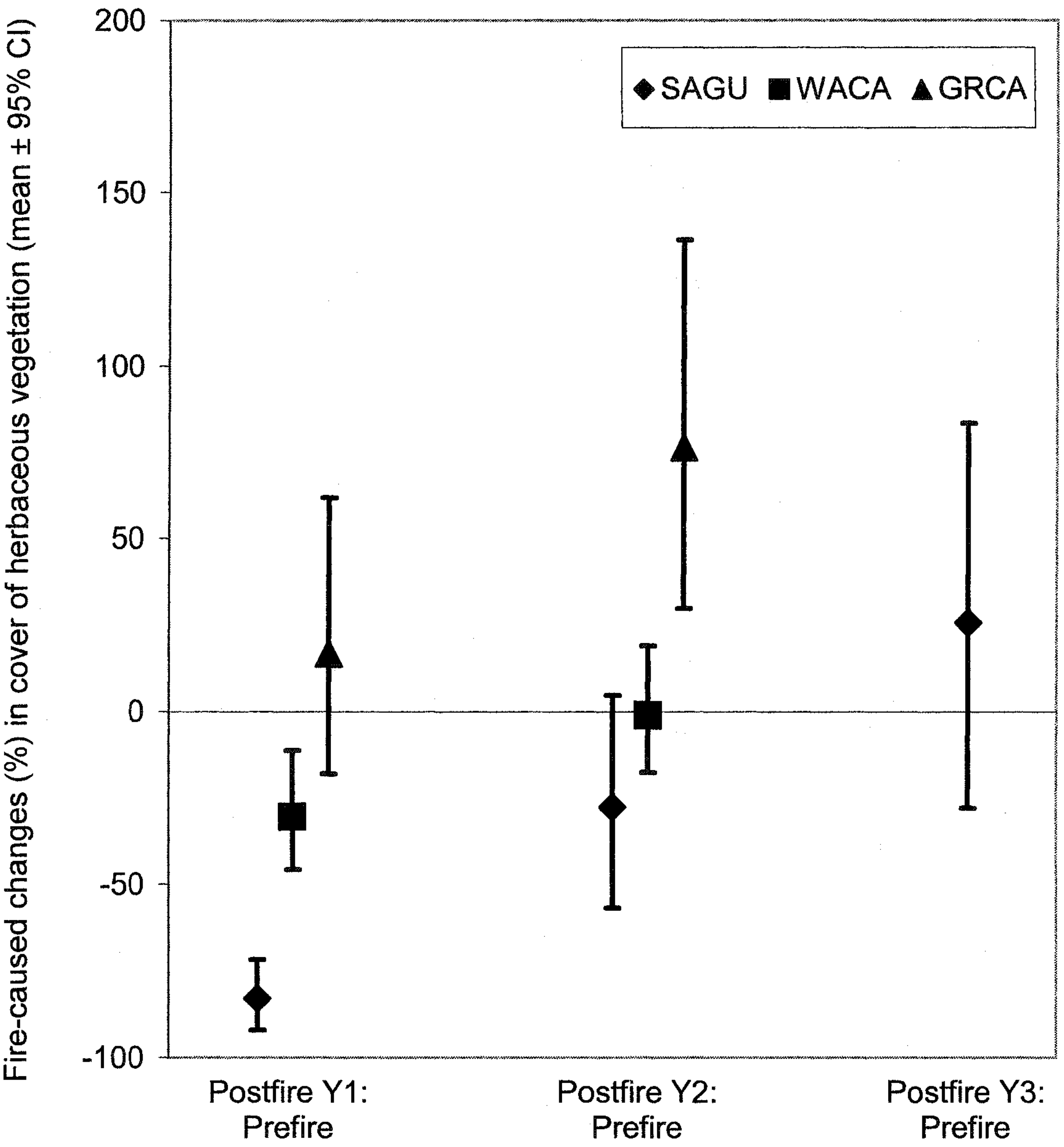


Figure 2.13. Fire-caused changes (%) in cover of herbaceous vegetation (mean ± 95% CI) from the summer before to the first, second, and third summers after fall burning. Additions to the understory appear to offset or exceed losses within the first two years postfire, with the precise timing differing among stands.

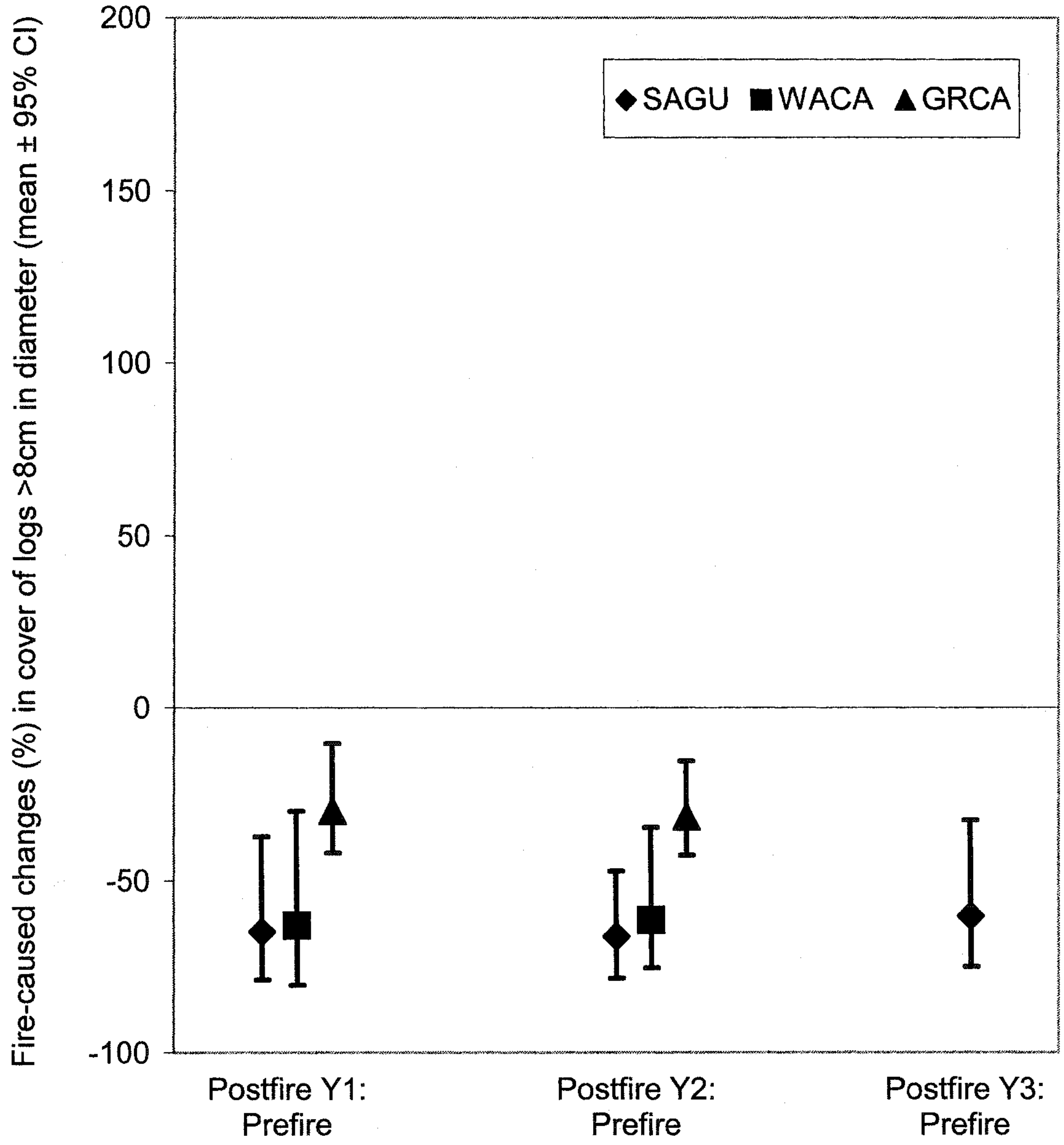


Figure 2.14. Fire-caused changes (%) in cover of logs >8cm in diameter (mean ± 95% CI) from the summer before to the first, second, and third summers after fall burning. This effect was relatively consistent both within and among the three fires.

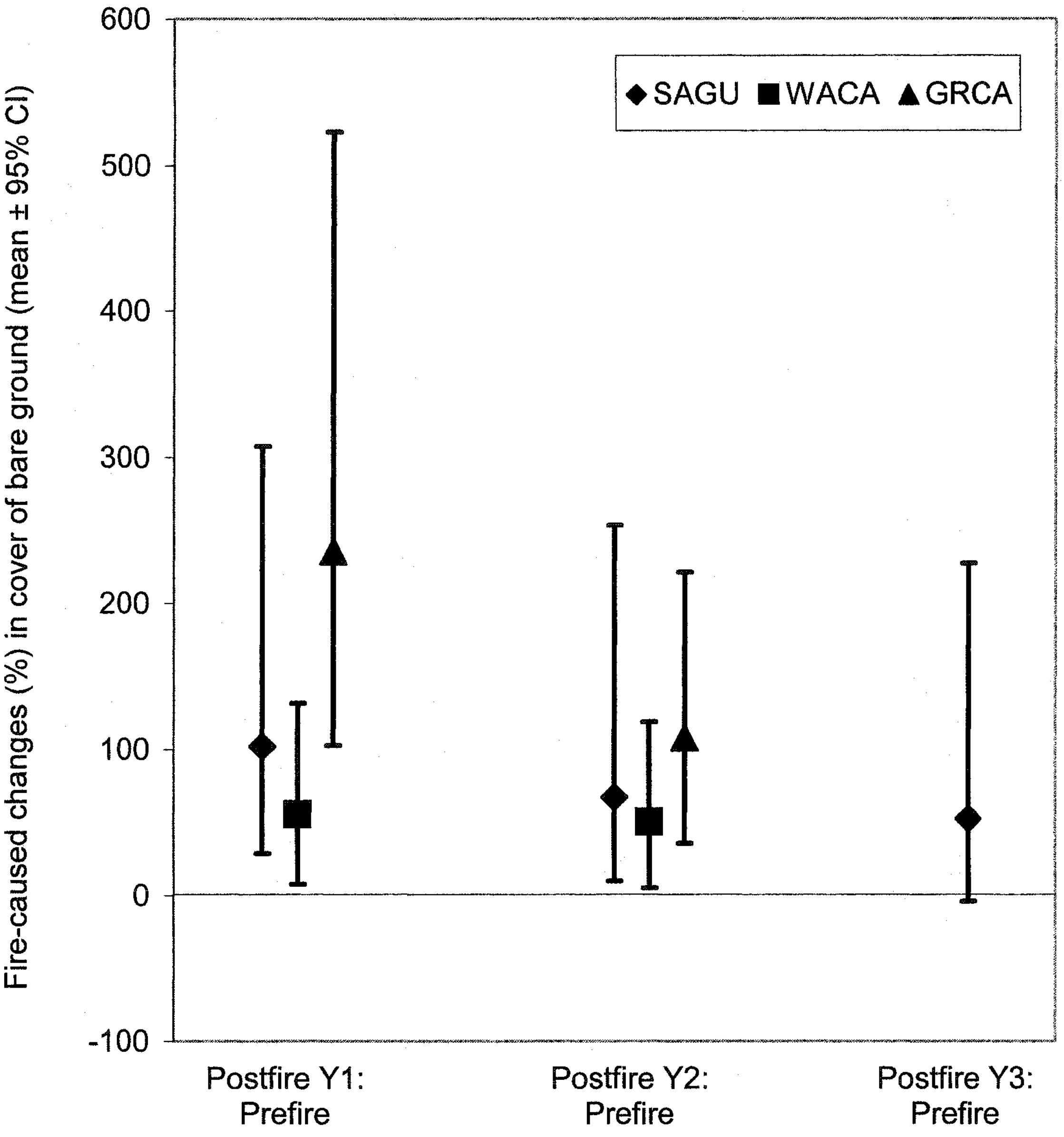


Figure 2.15. Fire-caused changes (%) in cover of bare ground (mean ± 95% CI) from the summer before to the first, second, and third summers after fall burning. The GRCA fire, which was most severe at the forest floor, effected the greatest first-year change in this attribute.

Table 2.07. Total cover and counts of standing vegetation and debris by forest stratum per 0.038 ha (0.008 ha, if denoted by an asterisk) as estimated during the summer before and the second summer after fire. Only trees common to all sites are included. Data are means ± 1SD for the three experimental units within each treatment-time combination. Estimates of fire-caused changes are based on data pooled across the three sites.

	Treatment		Control		% change due to fire:
Variable	Pre-fire	Post-fire Year 2	Prefire	Post-fire Year 2	bootstrapped mean (95% CI)
Vegetation > 3m					
percent cover	44.5 ± 10.9	38.5 ± 11.5	44.1 ± 7.6	40.6 ± 7.6	-6 (-13, 1)
no. ponderosa pines					
> 38 cm dbh	3.2 ± 1.2	3.1 ± 1.3	2.5 ± 0.6	2.5 ± 0.6	-4 (-9, -1)
23 -37.9 cm dbh	3.1 ± 1.0	2.9 ± 0.8	2.5 ± 1.1	2.5 ± 1.2	2 (-2, 14)
8 –22.9 cm dbh	8.3 ± 2.1	8.4 ± 2.3	6.5 ± 1.9	6.5 ± 1.9	2 (-1, 13)
<8 cm dbh*	0.7 ± 0.1	0.7 ± 0.1	0.9 ± 0.5	0.9 ± 0.5	2 (-16, 30)
Vegetation 1-3 m					
percent cover	5.3 ± 5.0	3.7 ± 2.3	8.5 ± 3.5	8.6 ± 2.5	-30 (-46, -10)
no. ponderosa pines*	1.0 ± 0.2	0.9 ± 0.1	0.9 ± 0.5	0.9 ± 0.4	-11 (-27, 8)
no. midstory sprouters*	3.3 ± 2.8	2.4 ± 1.8	3.7 ± 3.7	4.3 ± 4.0	-38 (-52, -23)
Vegetation <1m					
percent woody cover	4.3 ± 1.2	4.1 ± 1.8	8.7 ± 2.9	6.6 ± 2.8	25 (-2, 70)
no. ponderosa pines*	7.7 ± 5.9	20.0 ± 30.9	12.3 ± 18.4	1.5 ± 0.8	439 (117, 1190)
no. midstory sprouters*	35.4 ± 27.2	67.9 ± 59.0	38.2 ± 29.6	40.7 ± 34.0	80 (51, 136)
percent herbaceous cover	13.1 ± 4.9	9.4 ± 4.6	16.3 ± 7.3	10.7 ± 6.2	10 (-7, 31)
Forest floor					
percent cover of logs >8 cm in diameter*	4.0 ± 2.3	1.9 ± 1.0	4.4 ± 3.1	4.7 ± 3.2	-55 (-65, -43)
percent litter cover *	85.6 ± 5.5	83.0 ± 6.4	85.2 ± 2.1	85.7 ± 1.9	-4 (-8, -1)
percent bare ground *	7.9 ± 4.4	14.6 ± 6.8	8.1 ± 3.4	9.0 ± 3.9	67 (32, 132)

Table 2.08. Proportion of scorched or standing dead vegetation and charred woody debris by forest stratum per 0.038 ha (0.008 ha, if denoted by an asterisk) as estimated during the summer before and the second summer after fire. Only trees common to all sites are included. Data are means ± 1SD for the three experimental units within each treatment-time combination. Estimates of fire-caused changes (differences in percentage points) are based on data pooled across the three sites.

	Treatment		Control		Difference due to fire:
Variable	Pre-fire	Post-fire Year 2	Pre-fire	Post-fire Year 2	bootstrapped mean (95% CI)
Vegetation > 3m					
ponderosa pines with <15% green foliage					
> 38 cm dbh	8.9 ± 2.4	13.6 ± 7.3	7.0 ± 2.2	8.2 ± 2.8	3 (-2, 11)
23 -37.9 cm dbh	6.5 ± 2.0	18.6 ± 7.0	2.6 ± 2.8	3.6 ± 1.7	11 (5, 20)
8 –22.9 cm dbh	3.2 ± 3.6	36.7 ± 22.0	6.4 ± 8.8	9.1 ± 8.7	29 (19, 41)
<8 cm dbh*	3.9 ± 6.8	65.2 ± 30.7	8.1 ± 10.5	11.3 ± 8.0	65 (45, 79)
Vegetation 1-3 m					
ponderosa pines with <15% green foliage*	6.8 ± 3.5	75.3 ± 20.1	9.0 ± 9.4	9.8 ± 9.0	52 (31, 71)
midstory sprouters with no green foliage*	20.4 ± 19.9	83.8 ± 16.9	13.5 ± 10.5	13.3 ± 8.2	74 (59, 84)
Vegetation <1m					
midstory sprouters with no green foliage*	7.1 ± 8.9	9.7 ± 5.0	2.0 ± 2.1	6.0 ± 4.4	5 (1, 8)

compensated for any losses in total woody cover from leaf shed between the first and second summers after burning (Table 2.07). The number of new ponderosa pine seedlings fell dramatically from the first to second summer post-fire (Tables 2.05, 2.07); however, I still found, on average, five times as many on the treated plots in that second summer as one could have expected to find without burning (Table 2.07). In addition, herbaceous cover had rebounded to the unburned expectation by this time, and the cover of litter and bare ground approached pretreatment levels (Table 2.07).

Changes in arthropod trap rates due to burning

I collected and identified approximately 168,500 arthropods, representing at least 19 orders and more than 165 families of insects, arachnids, and myriapods, which I then categorized into functional groups (Table 2.09). Of all arthropods captured on both experimental and control plots before burning, approximately 1% were classified as sap and wood feeders, 2% as fungivores, 12% as decomposers, 13% as herbivores (or nectarivores), 32% as predators and the like, and 41% as "other" (i.e., omnivores). Over 75% of all captures from each of the latter three groups represented taxa that were abundant enough to allow for individual analyses of their responses to the fires. Sweat bees (Hymenoptera: Halictidae), leafhoppers (Homoptera: Cicadellidae), spider wasps (Hymenoptera: Pompilidae), weevils (Coleoptera: Curculionidae), and micromoths (Lepidoptera: Microlepidoptera) made up approximately 50%, 17%, 5%, 2%, and 2% of the average pre-fire herbivore pitfall collection, respectively. Ground beetles (Coleoptera: Carabidae), wolf spiders (Araneae: Lycosidae), other (non-lycosid) spiders, and spider wasps, respectively, made up about 51%, 22%, 5%, and 2% of all predators,

Table 2.09. Functional grouping of arthropod taxa represented by specimens collected in this study.

Detritivores	Fungivores	Herbivores	Sap and Wood Feeders	Predators, Parasitoids, and Parasites	Other
Diplopoda	Diplopoda	Insecta	Insecta	Arachnida	Arachnida
Insecta	Insecta	Orthoptera	Coleoptera	Scorpiones	Opiliones
Collembola	Hemiptera	Acrididae	Lucanidae	Araneae	Acari
Microcoryphia	Aradidae	Tettigoniidae	Buprestidae	Pseudoscorpiones	Insecta
Thysanura	Coleoptera	Hemiptera	Lyctidae	Solifugae	Orthoptera
Orthoptera	Leiodidae	Tingidae	Nitidulidae	Chilopoda	Gryllidae
Raphidophorinae	Cryptophagidae	Miridae	Cerambycidae	Insecta	Stenopelmatinae
Isoptera	Erotylidae	Berytidae	Scolytidae	Mantodea	Hemiptera
Termitidae	Endomychidae	Largidae	Diptera	Hemiptera	Lygaeidae
Coleoptera	Diptera	Alydidae	Periscelididae	Nabidae	Coreidae
Silphidae	Mycetophilidae	Rhopalidae		Anthocoridae	Cydnidae
Hydrophilidae	Sciaridae	Thyreocoridae		Cimicidae	Coleoptera
Histeridae	Platypezidae	Scutelleridae		Reduviidae	Bruchidae
Lucanidae		Pentatomidae		Neuroptera	Diptera
Scarabaeidae†		Acanthosomatidae		Coleoptera	Muscoidea
Lycidae		Homoptera		Cincindelidae	Sarcophagidae
Dermestidae		Coleoptera		Carabidae	Hymenoptera
Tenebrionidae		Scarabaeidae‡		Staphylinidae	Formicidae
Alleculidae		Byrrhidae		Phengodidae	
Lagriidae		Artematopidae		Cantharidae	

Table 2.09. Cont.

Detritivores	Fungivores	Herbivores	Sap and Wood Feeders	Predators, Parasitoids, and Parasites	Other
Insecta (cont.)		Insecta (cont.)		Insecta (cont.)	
Coleoptera (cont.)		Coleoptera (cont.)		Coleoptera (cont.)	
Oedemeridae		Elateroidea		Cleridae	
Diptera		Melandryidae		Melyridae	
Tipulidae		Mordellidae		Cucujidae	
Bibionidae		Alleculidae		Coccinellidae	
Synneuridae		Lagriidae		Diptera	
Stratiomyidae		Oedemeridae		Simulidae	
Scenopinidae		Anthicidae		Ceratopogonidae	
Phoridae		Euglenidae		Rhagionidae	
Micropezidae		Cerambycidae		Scenopinidae	
Piophilidae		Chrysomelidae		Asilidae	
Clusiidae		Curculionidae		Acroceridae	
Sepsidae		Diptera		Empididae	
Lauxaniidae		Cecidomyiidae		Dolichopodidae	
Heleomyzidae		Therevidae		Pipunculidae	
Sphaeroceridae		Bombyliidae		Conopidae	
Drosophilidae		Empididae		Sciomyzidae	
Calliphoridae		Syrphidae		Chamaemyiidae	

Table 2.09. Cont.

Detritivores	Fungivores	Herbivores	Sap and Wood Feeders	Predators, Parasitoids, and Parasites	Other
		Insecta (cont.)		Insecta (cont.)	
		Diptera (cont.)		Diptera (cont.)	
		Conopidae		Tachinidae	
		Tephritidae		Hymenoptera	
		Chloropidae		Ceraphronoidea	
		Lepidoptera		Braconidae	
		Hymenoptera		Ichneumonidae	
		Symphyta larvae		Chalcidoidea	
		Braconidae		Diapriidae	
		Ichneumonidae		Chrysidoidea	
		Melittidae		Sphecidae	
		Colletidae		Tiphiidae	
		Halictidae		Sapygidae	
		Andrenidae		Mutilidae	
		Megachilidae		Pompilidae	
		Anthophoridae		Vespidae	

Table 2.09. Cont.

Detritivores	Fungivores	Herbivores	Sap and Wood Feeders	Predators, Parasitoids, and Parasites	Other
		Insecta (cont.)			
		Hymenoptera (cont.)			
		Apidae			
		Pompilidae			

Notes: Detritivores include arthropods that feed upon plant debris, animal corpses, and dung. I also included predators that specialize on decomposer arthropods in this category and some fungivores that feed on both the dettritus and the fungal hyphae that coat and bind detritus (i.e., collembolans). *Fungivores* include arthropods that feed on fungi nearly exclusively . *Herbivores* include arthropods that feed on nectar, pollen, leaves, twigs, buds, or other tissues or fluids of live plants. *Sap and Wood Feeders* are herbivore allies that specialize on the sap, bark, or wood of live, injured, or dead trees. *Predators, Parasitoids, and Parasites* include arthropods that are carnivorous for at least part of their lives. I assigned arthropod taxa to these functional groupings based on the habits of most members as described by Borror et al. (1992). The final category, *Other,* includes taxa whose members range widely in feeding habits and therefore defy simple categorization, along with omnivores, root-feeders, and seed predators.

† Dung-feeding scarabs

‡ Plant-feeding scarabs

parasites, and parasitoids. Ants (Hymenoptera: Formicidae) made up nearly 82% of the "other" arthropods and 34% of total captures. Because total captures of sap and wood feeders and fungivores were relatively low, and because I expected the responses of taxa within these groups and the decomposers to be relatively consistent (i.e., decomposers may respond directly to changes in detritus supply, whereas predators and parasitoids are at least two to three steps removed from changing detritus levels, Schoenly et al. 1991), I lumped all representatives of these groups for fire-effects analyses.

During the first summer post-fire, I captured fewer detritivores, fungivores, weevils (herbivores), spiders (predators), and ground beetles (predators) per unit effort on the treatment plots than I would have expected to catch in the absence of burning (Table 2.10). In contrast, the fires apparently effected a marked increase in the number of sap and wood feeders active near the forest floor in post-fire year 1 (Table 2.10). No other significant fire-caused changes were evident at that time (Table 2.10).

By the second summer post-fire, trap rates of detritivores, fungivores, sap and wood feeders, and non-lycosid ("other") spiders on the experimental plots had returned to levels expected in the absence of burning (Table 2.11). Trap rates of weevils, wolf spiders, and ground beetles were still significantly lower than expected (Table 2.11). In addition, I detected latent responses of sweat bees and ants, with capture rates of these insects rising and falling, respectively, in response to burning. In sum, the fires reduced total second-year arthropod captures by about one-third (95% confidence interval: -43%, -20%; Table 2.11).

Table 2.10. Trap rates of arthropods (per trapping bout per sampling point) as estimated during the summer before and the first summer after fire. Data are means ± 1SD for the three experimental units within each treatment-time combination. To ensure that the arthropod estimates were based on equal sampling effort over time within units, I included data from subplots with pitfall failures only when same number of traps failed across the years of interest. Estimates of fire-caused changes are based on these data, pooled across the three sites.

	Experimental		Control		% change due to fire:
Taxon/Group	Pre-fire	Post-fire Year 1	Pre-fire	Post-fire Year 1	bootstrapped mean (95% CI)
Detritivores	32.4 ± 27.3	9.9 ± 2.8	32.8 ± 13.4	30.6 ± 11.5	-67 (-81, -50)
Fungivores	5.2 ± 8.3	0.3 ± 0.2	3.8 ± 5.4	0.5 ± 0.3	-71 (-86, -27)
Herbivores					
Cicadellidae	7.5 ± 2.8	3.8 ± 1.4	3.8 ± 1.7	1.5 ± 0.3	26 (-14, 80)
Curculionidae	0.7 ± 0.8	0.3 ± 0.4	0.8 ± 0.4	1.0 ± 1.1	-70 (-86, -33)
Microlepidoptera	0.7 ± 0.3	0.6 ± 0.6	0.5 ± 0.4	0.5 ± 0.4	-12 (-53, 65)
Halictidae	17.1 ± 20.8	18.4 ± 20.4	18.3 ± 18.1	16.8 ±23.2	15 (-15, 56)
Sap and Wood Feeders	2.4 ± 2.6	1.4 ± 0.9	1.9 ±1.8	0.9 ± 0.7	272 (73, 938)
Predators, Parasitoids, and Parasites					
Lycosidae	20.6 ± 7.9	11.7 ± 10.0	15.0 ± 1.8	13.9 ± 4.8	-38 (-51, -24)
Other spiders	3.4 ± 0.3	1.7 ± 0.7	4.4 ± 1.3	4.3 ±2.1	-59 (-70, -44)
Carabidae	54.9 ± 64.1	9.8 ± 14.7	30.9 ± 31.2	23.6 ±32.2	-74 (-84, -58)
Pompilidae†	1.9 ± 1.3	2.3 ± 0.6	1.9 ± 1.5	2.6 ± 2.2	-7 (-38, 40)
Other					
Formicidae	72.6 ± 16.4	142.4 ± 80.3	91.8 ±24.6	92.0 ± 42.1	28 (-13, 88)
Total Arthropods	275.6 ± 108.7	242.8 ± 98.7	241.0 ± 62.4	225.8 ± 98.7	-14 (-30, 5)

Note: †Because adult pompilids feed on pollen and nectar, the family is also included in the herbivore category.

Table 2.11. Trap rates of arthropods (per trapping bout per sampling point) as estimated during the summer before and the second summer after fire. Data are means ± 1SD for the three experimental units within each treatment-time combination. To ensure that the arthropod estimates were based on equal sampling effort over time within units, I included data from subplots with pitfall failures only when same number of traps failed across the years of interest (hence the differences in pre-fire means presented here and in Table 2.10.) Estimates of fire-caused changes are based on these data, pooled across the three sites.

	Experimental		Control		% change due to fire: bootstrapped mean (95% CI)
Taxon/Group	Pre-fire	Post-fire Year 2	Pre-fire	Post-fire Year 2	
Detritivores	31.3	28.3	31.7	32.5	-13 (-38, 25)
	± 28.3	± 24.7	± 14.4	± 22.6	
Fungivores	5.3	0.4	3.9	0.6	-55 (-87, 53)
	± 8.3	± 0.4	± 5.5	± 1.0	
Herbivores					
Cicadellidae	7.3	6.5	4.1	4.6	-24 (-57, 26)
	± 3.5	± 6.7	± 2.2	± 4.5	
Curculionidae	0.6	0.8	0.7	4.1	-78 (-89, -52)
	± 0.8	± 0.7	± 0.4	± 5.8	
Microlepidoptera	0.7	0.5	0.4	0.3	16 (-43, 113)
	± 0.4	± 0.4	± 0.4	± 0.1	
Halictidae	16.6	22.5	18.2	17.3	45 (9, 91)
	± 20.2	± 17.2	± 18.1	±17.1	
Sap and Wood	2.3	2.1	2.2	1.7	24 (-23, 96)
Feeders	± 2.7	± 1.1	±2.1	± 1.4	
Predators, Parasitoids, and Parasites					
Lycosidae	21.1	11.3	15.5	14.0	-40 (-53, -24)
	± 8.9	± 6.5	± 2.1	± 4.7	
Other spiders	3.5	3.1	4.6	3.9	4 (-21, 41)
	± 0.5	± 1.9	± 1.0	±1.3	
Carabidae	57.9	13.5	30.2	15.7	-54 (-70, -30)
	± 68.5	± 11.1	± 29.9	±22.6	
Pompilidae	1.9	2.9	1.8	3.4	-19 (-47, 24)
	± 1.2	± 2.1	± 1.8	± 3.7	
Other					
Formicidae	88.2	81.8	64.1	91.7	-36 (-57, -8)
	± 30.1	± 14.8	±20.0	± 24.7	
Total Arthropods	296.0	218.5	208.0	228.4	-32 (-43, -20)
	± 124.3	± 49.0	± 63.5	± 64.3	

DISCUSSION

Pre-fire forests, fire treatments, and forest changes

The pre-fire characteristics of the vegetation fell well within the contemporary range of variation that has been reported for forest stands dominated by ponderosa pine in Arizona (e.g., Covington and Moore 1994, Rosenstock 1996, Moore et al. 1999, Fulé et al. 2002a, b; Table 2.12). Moreover, the fires in this study burned under typical conditions and with characteristic behavior of October or November prescribed fires in southwestern ponderosa pine forests and effected short-term changes in vegetation and debris levels similar to those noted by others who have described the effects of such treatments (e.g., Gaines et al. 1958; Lindenmuth 1960; Cooper 1961b; Davis et al. 1968; Biswell et a. 1973; Wagle and Eakle 1979; Sackett 1980, 1984; Harris and Covington 1983; Covington and Sackett 1984; Oswald and Covington 1984; Vose and White 1991; Covington and Sackett 1992; Harrington 1993; Gordon 1996; Sackett and Haase 1998; Fulé et al. 2002a). My findings and the work of these many others indicate that the most marked short-term changes in vegetation and debris caused by fall burning occur within low forest strata. Of these effects, changes in cover of plant litter and other organic debris, which are largely due to the direct consumption of these fuels by fire and enhancement of microbial activity in the post-fire environment (Sackett and Haase 1998), tend to be more reliable (i.e., similar in magnitude and direction among treatments) than changes in low vegetation (Figures 2.11-2.15).

Litter and debris are invariably reduced in cover and volume by autumn prescribed fires in southwestern ponderosa pine forests (Figure 2.12; Gaines et al. 1958; Davis et al. 1968; Wagle and Eakle 1979; Covington and Sackett 1984; Sackett and

Table 2.12. Summary statistics for forest attributes measured within 23, 40-ha forest plots that were randomly located in ponderosa pine-dominated stands across six forest management districts in northern Arizona (from Rosenstock 1996) and my three, 40-ha study plots, before burning.

Variable	random sample (n=23)	my treatment units, prefire (n=3)
live overstory trees ≥ 2.54 cm in diameter (no./ha)	~175 to 2396 (median ~500)	723 ± 325[§]
canopy cover (%)	20 to 64	44.5 ± 10.9
shrub cover (%)	0 to 13.8 (median 0)	4.3 ± 1.2
herbaceous cover (%)	10-71 (median ~38)	13.1 ± 4.9

[§] 560 ± 116, if ponderosa pine only

Haase 1998; Fulé et al. 2002a; K. Schon, *unpublished data*; see also Kopper et al. 2002). The fires in my study likewise effected reductions not only in the cover of litter and downed woody debris but also on the total volume of these substrates. Following the standard NPS fire-effects monitoring protocol, K. Schon (*unpublished data*) determined that, by the first summer post-fire, the SAGU and WACA treatments had reduced the volume (kg/m^2) of coarse woody debris (1000-hour fuels) by an average of 86% and 60%, respectively, and the volume of litter and duff by 25% and 24%, respectively. Although I lack the same estimates for the GRCA fire, Fulé et al. (2002a) reported similar reductions in the volume of 1000-hour fuels (-53%) and depth of litter and duff (-27%) caused by a prescribed fire set in comparable ponderosa pine forest just north of my GRCA study site in late October 1999.

Fire effects on the forest understory are more complicated and idiosyncratic than fire effects on litter and debris. Prescribed burning tends to reduce the cover and biomass of low vegetation, including small-diameter trees, directly (i.e., via tissue consumption, heat kill, or injury; Fulé et al. 2002a) while stimulating understory production indirectly (i.e., by increasing nutrient availability, Harris and Covington 1983, Sackett and Haase 1998). In general, additions to the understory offset or exceed losses within the first two years post-fire (Harris and Covington 1983, Andiarese and Covington 1986, Figure 2.13), with the precise timing dependent, in part, on plant species composition and post-fire weather conditions, which may differ considerably among stands or years (Harris and Covington 1983, Vose and White 1991, Fulé et al. 2002b).

Ponderosa pine seedling establishment is likewise favored, but not ensured, by prescribed burning. Establishment depends on the coincidence of a good seed crop, favorable moisture conditions, and suitable seedbeds (Weaver 1951, Cooper 1961a, Sackett 1984, Haase 1986, Savage et al. 1996, Bailey and Covington 2002). By exposing patches of mineral soil, all three fires created excellent seedbeds for ponderosa pine regeneration. Yet, the significant increase in mean seedling abundance that I detected was an artifact of a tremendous flush in production that occurred only after the SAGU fire. The inconsistency among sites is not surprising, however, because ponderosa pine seeds are only episodically abundant and precipitation adequate to stimulate germination and growth of seedlings falls only periodically (i.e., every 3-4 years) in Southwestern ponderosa pine forests (Linhart 1988). Although I have no record of cone production during my study, the fire at SAGU must have occurred prior to, or coincided with, heavy seedfall in autumn 1998. The GRCA fire stimulated modest conifer seedling production during the second summer post-fire, suggesting that there was at least light seed shed in autumn 2000.

Changes in arthropod trap rates

Fire can affect the densities, activity patterns, and capture probabilities of forest arthropods, and changes in pitfall trap rates must be interpreted carefully in this light. While numbers and activity levels may rise or fall in response to burning, capture probabilities should increase, at least temporarily, as the removal of ground cover and low vegetation lessens the "environmental resistance" to movement of arthropods within the vicinity of the traps (Greenslade 1964a, Bess et al. 2002). Any reduction in trap rates attributable to fire treatments occurs despite this influence and can therefore be assumed to reflect a true decrease in the number of target arthropods active at or near the forest floor. Increased captures, on the other hand, could reflect increased abundance, activity, freedom of movement, or some combination of these effects. The lack of any significant change in trap rate for a particular group could indeed reflect no net effect of burning or, for example, a fire-caused reduction in density concurrent with an increase in activity (i.e., foraging effort) or capture probability of the remaining target individuals. In the following sections, I will discuss the observed fire-caused changes in trap rates of each arthropod group in light of such possibilities. Then, I will discuss some of the possible implications of the suite of observed effects in terms of the flow of nutrients and cycling of energy in the fire-prone ponderosa pine forests of the American Southwest and offer direction for future research along these lines.

Detritivores

Burning effected a temporary reduction in either the density of detritivores, their activity levels within the vicinity of the traps, or both numbers and behavior. Some of these animals were probably killed directly as fire burned through forest debris, litter, and duff (e.g., Wikars and Schimmel 2001; reviewed in Warren et al. 1987, McCullough et al. 1998). Then, at least during the first year post-fire, survivors seeking to reoccupy surface layers of the forest floor must have encountered diminished detrital resources and exceptionally warm and dry conditions due, in large part, to the increased absorption of light energy by charred organic residues (Ahlgren and Ahlgren 1960, Majer 1984, Raison et al. 1986). Litter removal and changes in microclimate presumably translated into reduced food availability or microhabitat suitability for the heat-sensitive and dessication-prone decomposers (Lussenhop 1976, Neumann and Tolhurst 1991, Collett 1998) thereby eliciting a numeric response that would compound any direct losses.

The high probability of a fire-caused reduction in the number of surface-dwelling (epigeic) detritivores is evinced by a wealth of data from other systems. Others have commonly reported: (1) positive correlations of actual detritivore numbers with percent cover, depth, or volume of litter and duff (Greenslade and Majer 1993; Chen and Wise 1997, 1999), (2) short-term reductions in the actual densities (as estimated from litter or soil samples) of these animals in upper litter or soil layers caused by the removal of litter and duff with and without burning (e.g., Rice 1932; Pearse 1943; Gill 1969; Buffington 1967; Springett 1976, 1979; Lussenhop 1976; Seastedt 1984a; Abbot 1984; Majer 1984; York 1999), and (3) ready movement of decomposer arthropods away from inhospitable (i.e., arid) microenvironments (horizontal movement: e.g., Levings and Windsor 1984; Klein 1989; vertical movement: e.g., Usher 1970; Springett 1971; Price 1973, 1975; van Amburg et al. 1981; Whitford et al. 1981). In contrast, no data suggest that epigeic decomposers become more sedentary in response to burning. Rather, the loss of detritus and higher temperatures at the forest floor should stimulate the activity of epigeic decomposers in burned forest, while the abundance of detrital resources should diminish "their need to move" in unburned forest (Hanula and Wade 2003). It is therefore likely that the transient change in capture rate caused by the fires in this study reflects, at least in large part, a true reduction in the abundance of detritivores at the soil surface. This effect is probably short-lived (i.e., 10 months: Neumann and Tolhurst 1991), as the microclimate of the forest floor should become increasingly favorable for decomposer organisms as understory cover re-develops and litter re-accumulates after burning (Raison et al. 1986).

Fungivores

The fires may have affected fungivore numbers both directly and indirectly by consuming fungal resources atop or within the forest floor. In addition to consuming a considerable portion of the fungi-laden woody debris, fires set in autumn in southwestern ponderosa pine forests apparently kill most of the fungi present within the L and upper F layers of the forest floor (Sackett and Haase 1998). Because populations of forest-floor fungivores appear to be food-limited (Chen and Wise 1997), losses of fungal resources should compound any lethal effects of burning.

Transient fire-caused reductions in fungivore densities have been documented in a variety of habitats (e.g., Springett 1976). Fungus gnats (Diptera: Sciaridae), which accounted for approximately 85% of total fungivore captures per unit effort from my study plots before burning, appear particularly sensitive to burning (Hanula and Wade 2003) and to experimental manipulation of fungal resources in forest litter (Chen and Wise 1997, Wise and Chen 1999). Although some fungi may be stimulated by fire-caused changes in soil and wood chemistry and microclimate at the forest floor (Ahlgren 1974, Pugh and Boddy 1988, Wicklow 1988, Olsson 2002, Wikars 2002), I detected no increase in observable fungal resources (i.e., mycelia) in lower forest strata of burned plots during either post-fire sampling period. If, as Sackett and Haase (1998) contend, fungi normally associated with unburned ponderosa pine litter and killed by burning are slow to recolonize post-fire litterfall, there was probably a first-year reduction in total food available in lower forest strata for polyphagous fungivores like the sciarids, and the first-year drop in pitfall captures can be reasonably attributed to a fire-caused reduction in fungivore density about the forest floor.

The abundance of any fire-stimulated fungi and associated arthropods should peak within the first two years after burning (Muona and Rutanen 1994, Wikars 2002). By the second summer post-fire, numeric responses of insects like flat bugs (Hemiptera: Aradidae), which feed on the fluids of fungi supported by dead and decaying trees (Borror et al. 1992), may have offset any losses of fungivores associated with forest litter. Indeed, I collected a trivial number of aradids from control plots over all years and from treatment plots before burning (>2% of fungivore captures per unit effort). However, flat bugs accounted for nearly 20% and 50% of all fungivore captures from burned forest during the first and second summers post-fire, respectively. These data indicate that while total fungivore captures may have recovered to unburned levels by the second summer post-fire, fire-caused changes in the relative abundance of fungivore taxa active in low forest strata persisted at least that long.

Herbivores

For each of the target herbivore taxa, I detected either no effect of burning or a fire-caused reduction in captures during the first summer post-fire. These first-year effects persisted at least nominally into the second summer post-fire for all but one taxon, the Halictidae. Because the influence of fire on pitfall captures differed among the target taxa, I will interpret my findings for each group separately. But first, I will review some likely influences of burning relevant to all assessments. Because responses of the nectivorous spider wasps (Hymenoptera: Pompilidae) must be considered also in light of fire effects on their spider prey, I defer my discussion of pompilid responses to a later section on predators and parasitoids.

Many forest herbivores are dormant in October and November (Mattson 1980), and therefore, the direct effects of burning in these months should depend, in large part, on the locations of overwintering sites. For example, eggs attached to grasses and larvae that overwinter in the uppermost layers of the forest floor should be more vulnerable to the direct effects of burning those insulated from lethal temperatures within the deeper recesses of the soil and vegetation (Simmons et al. 1977, Warren et al. 1987, Brose and McCormick 1992, Fay and Samenus 1993, Friend and Williams 1996). Survivors of fire events and immigrants to recently burned forest will generally encounter a resource base, predator assemblage, and environmental conditions (i.e., temperature, humidity) unlike those of unburned forest. Differences in these attributes are sure to translate into differences in vital rates or activity levels among herbivore populations occupying burned versus unburned areas (reviewed in Warren et al. 1987, McCullough et al. 1998). Of particular importance for herbivores should be the immediate reduction of plant biomass and the transient increase in soil nutrient availability caused by typical surface fires, as the latter can lead to enhanced productivity and nutritional and defensive potential of understory vegetation during at least the first growing season post-fire (Wan et al. 2001, Rieske 2002).

In the only published report of the effect of fall burning on nutrient concentration in plants of southwestern ponderosa pine forest, Harris and Covington (1983) indeed found nutrient concentrations (% ovendry weight of aboveground biomass) in understory vegetation to be significantly higher on burned (n = 11) than unburned (n = 7) plots during the first summer following replicated autumn fires. Nitrogen showed the greatest magnitude of increase: its concentration in *Festuca arizonica* and a pooled group of “miscellaneous grasses” apparently doubled due to fire in a number of subsamples (Harris and Covington 1983). In general, herbivore performance (i.e., larval survival, growth rate of the immature stage, adult body size, fecundity) is enhanced on young, vigorously growing, nutrient-rich plant tissues (e.g., Myers and Post 1981, Price 1991; reviewed in Slansky and Rodriguez 1987), and herbivore abundance is positively correlated with the biomass of high-quality plants (Ritchie 2000, Haddad et al. 2001). However, differences in rates of direct mortality or the abilities of survivors or immigrants to cope with or exploit any fire-caused changes in abiotic conditions or the quantity or quality of food resources can lead to differences in numeric or behavioral responses to burning among taxa.

Cicadellidae

The fire treatments had either no overall effect on the activity and abundance of leafhoppers in the lower forest strata or significant effects on some combination of abundance, behavior, and capture probability such that there was no net change in trap rate. The fires probably killed some of these insects directly. Eggs attached to grasses and larvae dormant in the upper layers of the forest floor were especially vulnerable to heat kill (Warren et al. 1987, Panzer and Schwartz 2000). Then, during the first summer post-fire, populations within the treatment units were probably stimulated by changes in plant quality. Individuals were probably attracted to the regrowth, and cicadellid survival may have increased with fire-caused increases in plant N content (Mattson 1980; e.g., Cancelado and Yonke 1970, Nagel 1973, Hansen 1986, Dunwiddie 1991). The probability of capturing these animals should have risen as well, due to lower environmental resistance to movement through the lower strata of recently burned forest. However, the lack of any strong signal in trap rates suggests that any local population additions (or increased capture probabilities) during the first year post-fire must have roughly offset direct losses. Alternatively, leafhoppers may have concentrated their activities within discrete pockets of tender new growth in recently burned forest (i.e., oak resprouts) and become relatively sedentary in these resource-rich patches (Whelan 1995), making it impossible to discern the true numeric response from pitfall captures (Gardner and Usher 1989, Koricheva et al. 2000, Andersen and Muller 2000). If this is true, I would expect the probability of detecting a positive influence of fire on leafhopper numbers to have been higher on the GRCA treatment plot, which supported few oaks or other basally resprouting woody plants, than on either of the other two treatment plots, which contained many such sprouters. Indeed, the first-year changes in mean trap rate (and 95% CI) attributable to the fires at GRCA, WACA, and SAGU were +47% (-9%, +151%), +8% (-52%, +103), and + 6% (-53%, +96%), respectively (Figure 2.16).

Curculionidae

The fires reduced the number of weevils active within the vicinity of the pitfall traps during the first year post-fire, with little change thereafter. This overall effect is largely attributable to the influence of the fire at WACA, as I rarely trapped these insects at SAGU and GRCA. The first-year decline in the abundance of weevils active within burned forest at WACA is likely an artifact of the direct influences of burning, fire-caused changes in food availability (Muona and Rutanen 1994, Orgeas and Andersen 2001), or both. Hiers et al. (2000) recently provided indirect evidence of a fire-caused

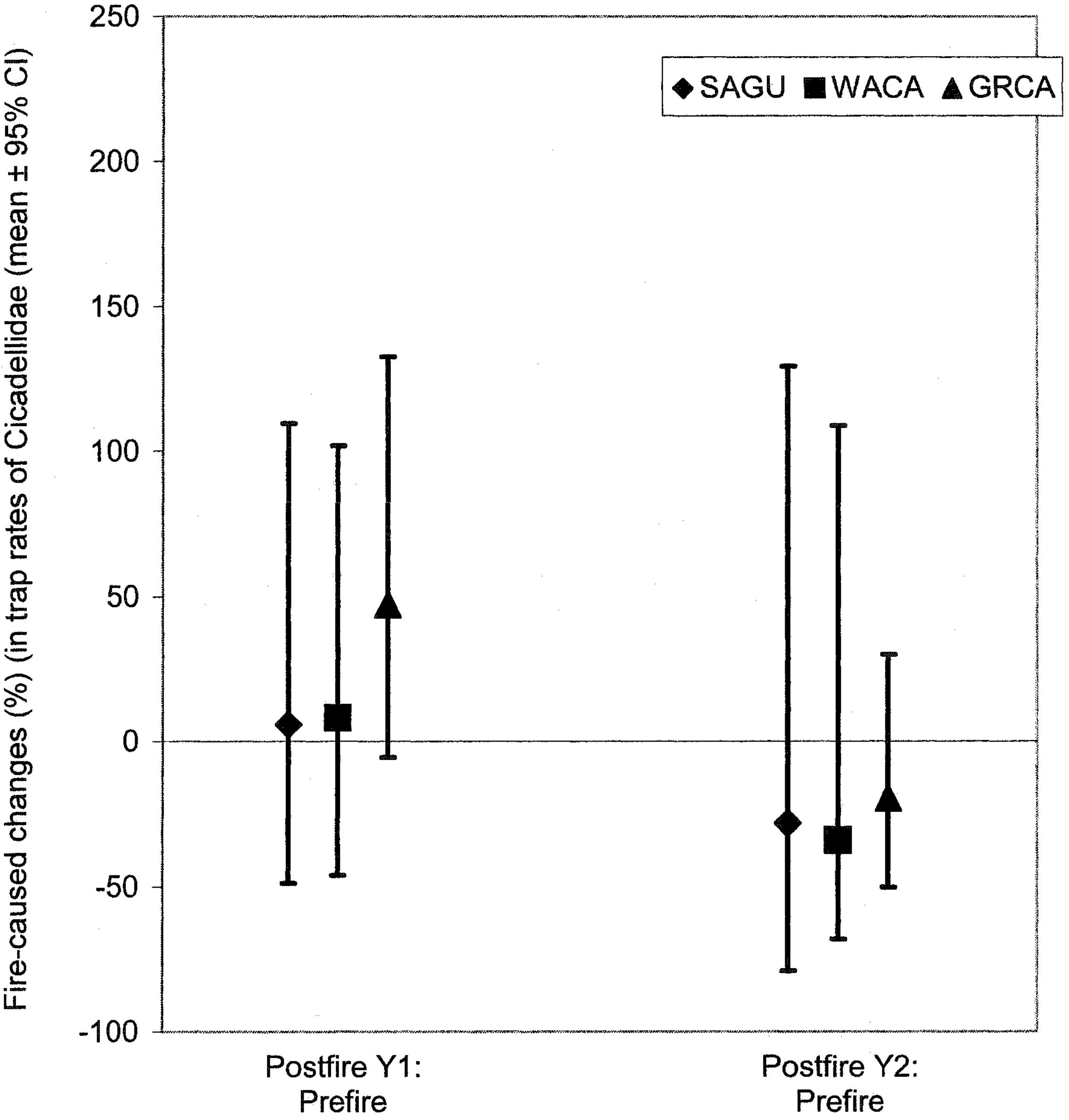


Figure 2.16. Fire-caused changes (%) in trap rates of leafhoppers (Homoptera: Cicadellidae) (mean ± 95% CI) from the summer before to the first and second summers after fall burning.

reduction in abundance of the sand weevil, *A. segnipes*, a seed predator of the legume, *T. virginiana,* in longleaf pine savanna. They noted that, regardless of burn season, the percentage of seed pods with predators was significantly lower (23.2% vs. 63.8%) in burned versus unburned savanna.

Microlepidoptera

The fires either had no overall effect on the density of active microlepidoptera in the lower forest strata or fire effects on density, activity, and capture probability canceled each other out. Microlepidoptera overwintering in leaf litter, seeds, or the buds or shoots of low vegetation can be killed by dormant-season fire (e.g., Simmons et al. 1977, Marini-Filho 2000). Larvae and pupae overwintering just a few centimeters below the soil surface should survive a fall burn, although those overwintering in the uppermost soil may suffer increased mortality upon litter removal due to exposure to extreme winter temperature fluctuations in the post-fire environment (Warren et al. 1987, Marini-Filho 2000). However, these effects may have been patchy and largely swamped by subsequent changes in vital rates or behavior (i.e., due to fire-caused changed in food quality or quantity), or they may have been countered by increased capture probability. Data from other habitats suggest that numeric responses of micromoths to prescribed fall burns may differ based on diet: seed predators and budworms decrease in abundance during the first summer post-fire (McCullough and Kulman 1991, Vickery 2002), while leaf miners are largely unaffected (Kerstyn and Sitling 1999). If there were numeric or behavioral responses among the micromoths in my study areas, the effects were not strong and/or consistent enough to register as significant within any experimental plot.

Halictidae

The fires apparently caused a latent increase in the density of sweat bees active in forest understory. These insects were probably relatively well protected from the direct effects of fire as they overwintered in the forest soil (Yanega 1990, Potts and Willmer 1997, Soucy 2002). Halictids are generally philopatric (Yanega 1990, Potts and Willmer 1997), and individuals emerging from burned forest during the first spring post-fire likely encountered an altered microenvironment upon return to their natal territories. Yet, because females tend to excavate their nests in well-insolated areas of bare soil, their site fidelity was probably not diminished by litter removal. Moreover, young sweat bees are reared on a mixture of pollen and nectar from variety of forbs and shrubs (Waddington 1987), and fire may have actually enhanced reproductive success during at least the first breeding season post-fire by stimulating the production of flowers and enhancing the quantity or quality of pollen and nectar produced within the forest understory (e.g., Menges 1995). First-year effects of fire on vital rates (i.e., increased survival, lower emigration) could account, at least in part, for the increased captures within the burned forest during the second summer after treatment. Also, any increase in the proportion of nectar-rich blossoms should have stimulated flower-to-flower movement by foraging bees (Slansky and Rodriguez 1987), which, coupled the increased probability of capture effected by burning, may account for the nonsignificant increase in trap rate evident in the first summer post-fire and for part of the increase apparent in the following year.

Sap and wood feeders

Although the transient fire-caused increase in mean trap rate of sap- and wood-feeding arthropods reflect a change in their abundance, activity, capture probability, or some combination of these phenomena, similar responses in other forest systems have been invariably attributed to true influxes of these animals into recently burned areas (Hansen 1986, Ryan and Amman 1996, Santoro et al. 2001, Wikars 2002). Sap and wood feeders are generally attracted to dead, injured, or stressed trees and woody vegetation (Hansen 1986, Borrror et al. 1992, Ryan and Amman 1996), and some, including wood-boring beetles (Coleoptera: Buprestidae), which accounted for about 92% of all pre-fire captures, are known to use the smoke, heat, and volatiles emitted by burning vegetation to help locate heat-killed cambium in which to lay their eggs (Gardiner 1957, Chénier and Philogène 1989, Borror et al. 1992, Ryan and Amman 1996, Werner 1997). The density of sap and wood feeders active in recently burned forest tends to decrease, however, as individuals locate suitable host trees. Consequently, there is usually only a short-term increase of these animals after fire (Granholm 1982). Offspring of immigrants may not be apparent for 2-5 years and not all live to emerge from their hosts, as sap and wood feeders are preyed heavily upon by birds and other vertebrates.

Predators, parasitoids, and parasites

Trap rates of key generalist predators, including spiders and carabids, showed largely consistent and persistent declines in response to the fire treatments, while mean captures of spider wasps, which are nectivorous as adults but carnivorous as larvae (i.e., parasitoids), were unaffected by burning. I interpret these findings as follows:

Spiders and ground beetles

Spiders and ground beetles active on or seeking refuge within surface litter at the time of burning may have been killed by the fires (e.g., Winter 1984, Wikars and Schimmel 2001), while those in subsurface burrows, under rocks, or in clumps of dense vegetation probably escaped lethal temperatures (Komarek 1969, Riechert and Reeder 1972, Warren et al. 1987). Survivors then faced warmer and drier conditions and encountered less litter and debris cover and fewer arthropod detritivores and fungivores active within the upper layers of the forest floor than before burning. Carabids and spiders are notably sensitive to changes in microclimate (Thiele 1977, Carrington 2002) and will readily disperse from inhospitable (i.e., arid) microenvironments (Greenslade 1964b, Thiele 1977, Riechert and Bishop 1990), including those within recently burned areas (e.g., Riechert and Reeder 1972). Furthermore, both spider and carabid abundances or vital rates (i.e., survival, fecundity) are generally positive functions of litter and debris levels and tend to track concomitant or independently manipulated changes in the abundances of their detritivore and fungivore prey (e.g., spiders: Riechert and Reeder 1972; Seastedt 1984 a, b; Riechert and Bishop 1990; Spiller 1992; Haila et al. 1994; Polis et al. 1998; Chen and Wise 1999; Wise and Chen 1999; Wise et al. 1999; Heliola et al. 2001; Kreiter and Wise 2001; carabids: Edgar 1969; Thiele 1977; Seastedt 1984 a, b; Brust et al. 1985; Weseloh 1985; McCoy 1987; Bommarco 1988; Niemela et al. 1993; Manley 1996; Spence et al. 1996; Spieles and Horn 1998; Wise and Chen 1999; Carrington 2002). It is therefore likely that a fire-caused reduction in actual numbers is to some degree responsible for the drop in capture rates of these generalist predators.

While total numbers of spiders and carabids are likely to fall shortly after fire, activity levels (i.e., rates and changes in direction of travel) of remaining animals should increase in the upper layers of the forest floor due to the loss of litter (Greenslade 1964a, b) and low vegetation (Greenslade 1964a, b; Pajunen et al. 1995), increased temperature (Briggs 1961; Greenslade 1964a, b; Markl 1974; Evans 1983; Dennison and Hodkinson 1984; Niwa and Peck 2002), and reduced availability of detritivore and fungivore prey (Bommarco 1998). Therefore, the change in trap rates caused by burning probably underestimates the true reduction in total carabid and spider abundances (Greenslade 1964a, Spence and Niemela 1994). Many researchers, working in a variety of habitats, have documented short-term, fire-caused reductions in actual densities (as estimated from litter samples) of spiders (e.g., Rice 1932, Heyward and Tissot 1936, Buffington 1967, French and Keirle 1969, Reichert and Reeder 1972, Nagel 1973, Ahlgren 1974, Springett 1976, Winter 1984, Dunwiddie 1991, Friend 1996, York 1999) and carabids (e.g., French and Kierle 1969, Rickard 1970, Ahlgren 1974, Van Amburg et al. 1981, Holliday 1992).

Effects of prescribed burning on carabids and lycosids may persist for several years post-fire. My data suggest that numbers may remain depressed for at least two summers post-fire. Similar studies of low-severity fire treatments in pine forests likewise suggest a slow recovery by affected populations. For example, Hanula and Wade (2003) reported that trap rates of 61% of all spider genera fell in response to fall burning in longleaf pine. Of these, 65% showed no sign of recovery to unburned levels within four years of treatment. Within the Lycosidae alone, 83% of the genera were negatively affected by fall burning and none recovered to control levels within the first two years post-fire; 40% had not recovered within four years post-fire. Likewise, of the carabid genera apparently negatively affected by burning, 66% did not recover to control levels until three to four years post-fire (Hanula and Wade 2003).

Spider wasps

The lack of any significant effect of burning on pompilid captures indicated that the fire treatments either had no overall effect on the number of spider wasps active in the lower forest strata or caused significant changes in some combination of abundance, behavior, and capture probability such that there was no net change. Preliminary analyses indicated that mean pompilid captures during the first summer after the SAGU fire were 75% (95% CI: 6%, 209%) higher than expected from control values. Clearly the other fires did not effect similar first-year increases, and the disparate influences cancelled each other out in the pooled analysis. Indeed, the SAGU, WACA, and GRCA fires respectively effected an increase, decrease, and no significant change in spider wasp captures during the first summer post-fire (Figure 2.17). In each case, the effects persisted into year 2 (Figure 2.17).

Spider wasps overwinter in burrows within forest soil and should, therefore, be well-protected from the direct effects of fall burning. Moreover, given the persistence of the apparent fire effects over two growing seasons, I reject direct mortality as the primary source of any differences among sites and contend that the indirect effects of burning were largely responsible for the observed changes in each case. Adult spider wasps feed on pollen and nectar of understory plants, but provision their young with spiders (i.e., lycosids) collected from the forest floor (Alm and Kurczewski 1984, Deyrup et al. 1988, Field 1992, Koomen and Peeters 1992, Rayor 1995, Wagner and Wise 1996, Evans and

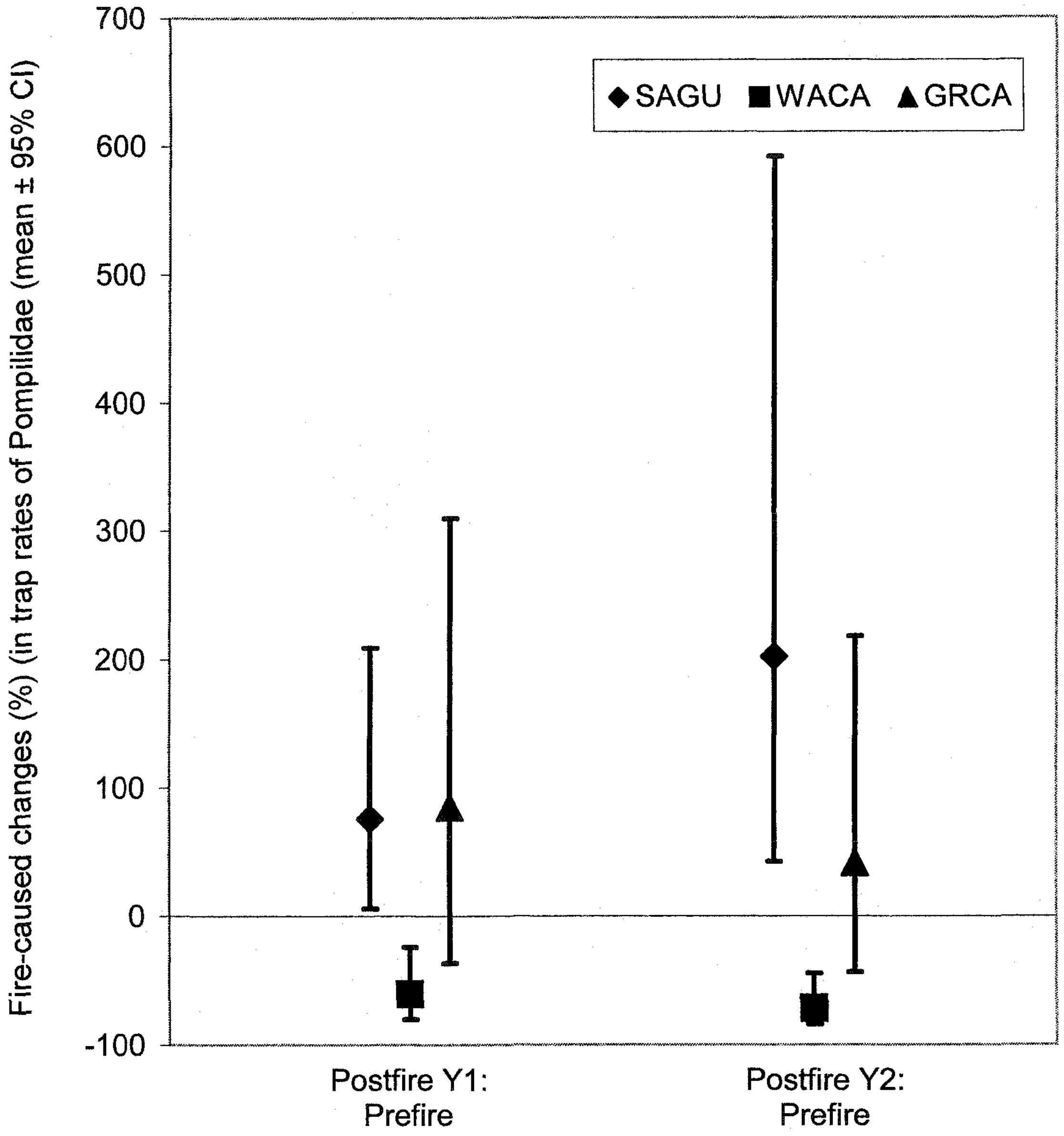


Figure 2.17. Fire-caused changes (%) in trap rates of spider wasps (Hymenoptera: Pompilidae) (mean ± 95% CI) from the summer before to the first and second summers after fall burning.

Shimizu 1996, Polis et al. 1998). Both nesting and foraging activities are often focused within patches of mineral soil, presumably because spider prey are more readily captured and nest burrows are more easily located or excavated in these bare areas (Alcock 1983, Alm and Kurczewski 1984, Jennings and Parker 1987, Kurczewski et al. 1988, Martins 1991). By exposing more mineral soil, prescribed burning should increase the availability of favorable foraging and nesting microhabitat for these insects. Given ample floral resources and spider prey, pompilid populations may flourish in the face of such changes.

However, spider abundances were largely diminished by the fires in this study, and the fire at WACA effected a far greater first-year reduction in the mean trap rate of lycosids, which are key spider wasp prey, than did the fires at SAGU and GRCA (Figure 2.18). Moreover, trap rates remained depressed into the second summer post-fire, except at SAGU, where average second-year captures of both lycosids and pompilids exceeded those expected based on control values (Figures 2.17, 2.18). These data suggest a conditional response to burning by spider wasps. That is, the total density of pompilids active near the forest floor may increase in response to fire-caused changes in microhabitat as long as prey abundance is not diminished below some critical level by the same treatment.

Ants

All else equal, the probability of capturing surface-active ants in pitfall traps increases with heightened freedom of movement during the first few growing seasons following fire (e.g., Whelan et al. 1980, Abbott 1984, Andersen and Yen 1985, York

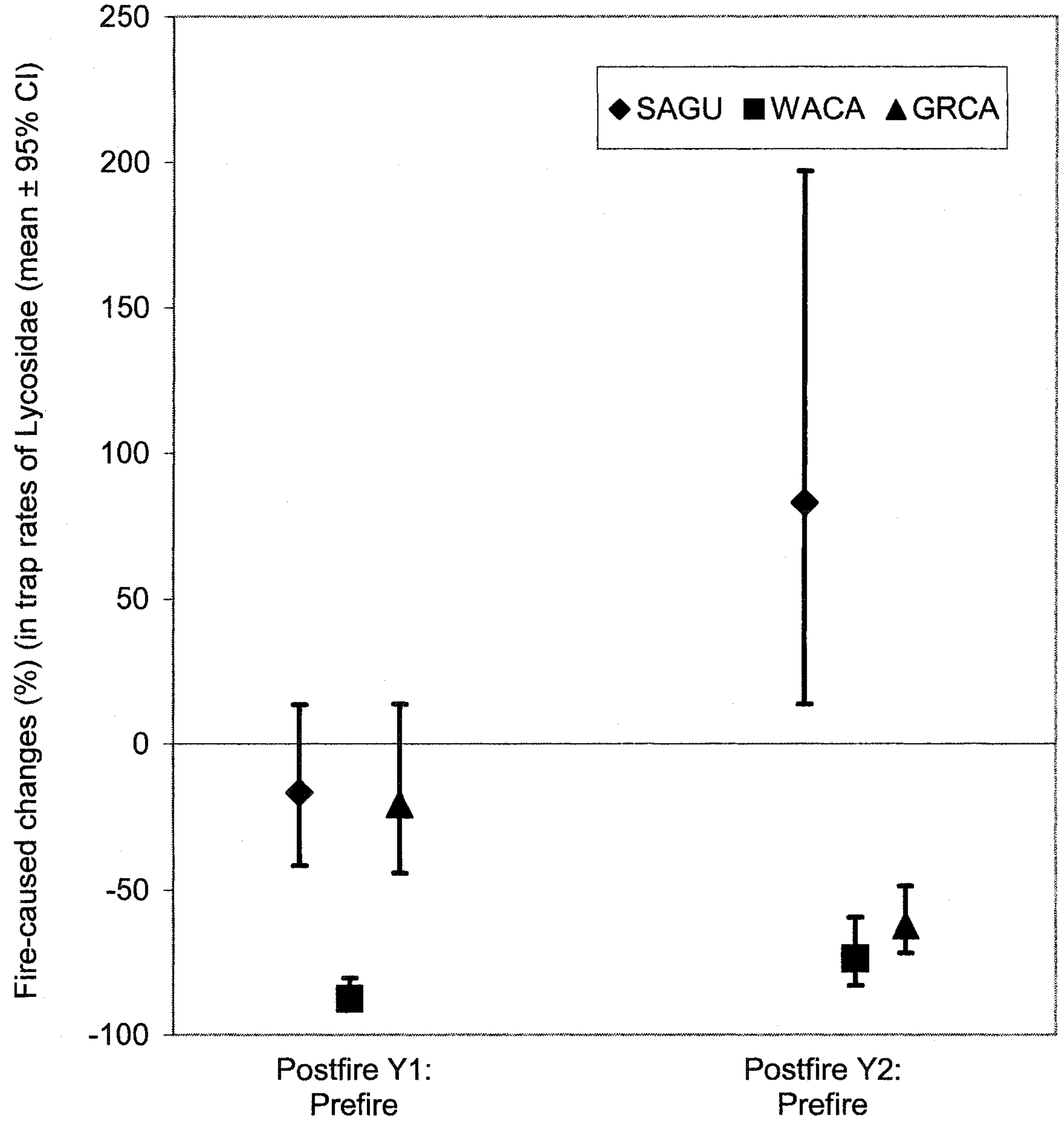


Figure 2.18. Fire-caused changes (%) in trap rates of wolf spiders (Araneae: Lycosidae) (mean ± 95% CI) from the summer before to the first and second summers after fall burning.

2000). Thus, the fire-caused reduction in trap rates from before burning to the second summer post-fire probably underestimates a true decrease in the number of ants active at or near the forest floor. Direct losses, which should have been evident during the first summer post-fire, probably contributed little, if any, to this effect. Most ants are protected in nests deep within the ground or inside the boles of trees during the passage of fire; only workers active at the soil surface would be vulnerable to the direct effects of burning (Andersen and Yen 1985, Warren et al. 1987, McCoy and Kaiser 1990, Andersen 1991, York 2000). Instead, the second-year reduction in trap rate probably reflects increased emigration from burned forest (Komarek 1969), diminished surface activity (Schowalter et al. 1981, McCoy and Kaiser 1990), or some combination of these factors.

Information gleaned from other habitats indicates that understory burning reduces populations of ants that forage and nest in soil and litter or are associated with vegetation and downed woody debris (e.g., *Camponotus*) while favoring seed harvesters and xeric specialists (e.g., *Lasius, Solenopsis, Pogonomyrmex, Pheidole* spp.) at least during the first year post-fire (Buffington 1967, Andersen 1991, Neumann 1991, Collett et al. 1993, York 2000, Farji-Brener et al. 2002, Hanula and Wade 2003). The heightened activity of both the emigrants and the ants favored by burning generally translates into first-year increases in total ant captures in pitfall traps (e.g., O'Dowd and Gill 1984, Andersen and Yen 1985, McCoy and Kaiser 1990, Neumann 1991, Collett et al. 19931 Collett 19981 Andersen and Muller 2000). I likewise captured more ants than expected during the first summer post-fire at both GRCA and WACA, but not at SAGU (Figure 2.19). The difference could be due to differences in food availability, ant communities, or fire severity.

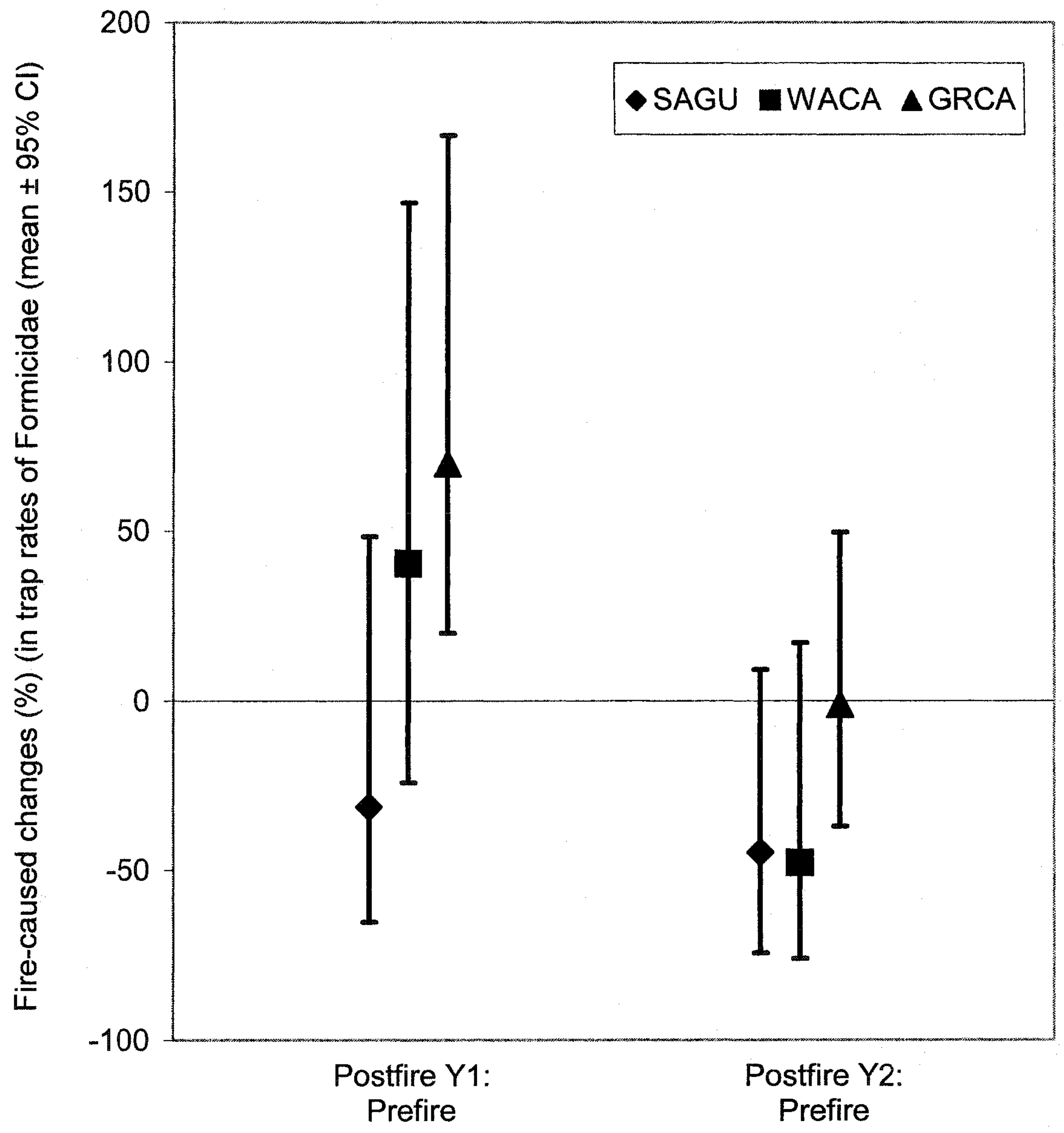


Figure 2.19. Fire-caused changes (%) in trap rates of ants (Hymenoptera: Formicidae) (mean ± 95% CI) from the summer before to the first and second summers after fall burning.

Functional significance

The arthropod responses that I detected are similar to those reported by other researchers who have conducted comparable investigations of the effects of dormant-season prescribed fires in U.S. pine forests. For example, Rambo (1999) compared pitfall captures from unburned ponderosa pine grasslands to those from stands burned at 1-, 4-, and 8-year intervals and noted that trap rates of epigeic detritivores, fungivores, and generalist predators (i.e., carabid beetles) were lowest in stands that had been burned one year prior, whereas trap rates of herbivores (i.e., orthopterans, mirids, aphids), sap and wood feeders (i.e., buprestids), spider wasps, and ants were highest in these same plots. More recently, Hanula and Wade (2003) compared pitfall captures from unburned longleaf pine (*Pinus palustris*) stands to those from forest plots burned at 1-, 2-, and 4-year intervals and reported that total predator abundance was diminished by burning regardless of burn frequency. Although total herbivore captures did not differ among treatments, Hanula and Wade (2003) trapped significantly more herbivore genera in annually burned than unburned stands. Assuming that these changes or differences in trap rates indeed signify consistent numeric or functional responses to the fire treatments, the patterns beg speculation on their implications for nutrient cycling and energy flow in recently burned forest.

Fire is a potent agent of decomposition, and as forest fuels burn, the textbook detrital pathway within the forest food web is circumvented, and a flush of nutrients is availed to the base of the grazing food chain. Consequently, for at least the first growing season post-fire, the contributions of surface-active decomposers and generalist predators to community assembly and ecosystem function are probably diminished, while those of arthropods associated with both live and dead plant materials are enhanced. In other habitats, fire-caused reductions of epigeic detritivores have been shown to retard the decay of newly cast leaf and needle litter for a number of years posttreatment (Springett 1976, Raison et al. 1986, Greenslade 1997). Similar processes likely contribute to the rapid post-fire accumulation of fine fuels in ponderosa pine forest (e.g., Monleon and Cromack 1996, Sackett and Haase 1998). Meanwhile, any fire-caused reduction in predation pressure should facilitate the exploitation of nutrient-rich post-fire plant production by herbivorous arthropods (reviewed in Halaj and Wise 2001).

Although I cannot argue that the fires in my study effected increased herbivore pressure during either of the first two growing seasons post-fire, burning has been repeatedly shown to stimulate insect herbivory in other fire-prone environments (e.g., Dolva and Scott 1982, Raw and Hay 1985, Prada et al. 1996, Viera et al. 1996, Steinbauer et al. 1998, Negron-Ortiz and Gorchov 2000, Radho-Toly et al. 2001). The potential for a similar influence of fire in ponderosa pine forest merits investigation, as the intensity of post-fire herbivory can affect the structure and composition of forest vegetation as well as the degree of nutrient uptake in new growth (e.g., Schowalter et al. 1981, Radho-Toly et al. 2001). The latter can be enhanced via compensatory growth or the induction of chemical defenses in response to tissue removal or damage by herbivores (Detling et al. 1980, Matson 1980, Huntly 1991, Mikola et al. 2001), particularly upon fertilization of otherwise nutrient-poor environments (Chapin 1980, McNaughton and Chapin 1985). Enhanced nutrient uptake by plants during the first few growing seasons after burning would translate into greater retention of mobile nutrients (i.e., nitrogen) within the affected ecosystem. Thus, by enhancing the nutrient sink in post-fire plant production, fire-stimulated herbivory should conserve nutrients that would otherwise be leached from recently burned forest (e.g., Schowalter et al. 1981).

As post-fire plant growth accumulates in the form of nutrient-rich detritus, and these inputs along with the shade from developing vegetation again moderate the microclimate of the forest floor, populations of epigeic decomposers, including fungi and associated fungivores, should flourish (Seastedt 1984a, Hendrix et al. 1986, Stinner and House 1990). Thereafter, the decay rate of surface litter and abundances of generalist predators should approach or exceed pre-fire levels, and the potential for top-down control of herbivore populations should rise accordingly. I reiterate that although understory production tends to increase in response to fall burning in southwestern ponderosa pine forest, this effect is reliably detected only after the second growing season post-fire (reviewed in Andiarese and Covington 1986). Andiarese and Covington (1986) attributed the variation in short-term, fire-caused changes in herbaceous production to intersite differences in plant species composition and fire severity. However, it is unclear why the influences of any such disparities would consistently wane after the second year post-fire. It is at least as likely that this pattern is an artifact of the time necessary to reestablish top-down control of herbivore populations after this influence is disrupted by burning (Schoener 1993).

Direction for future research

The data presented here indicate that arthropods of southwestern ponderosa pine forest are keenly sensitive to even the most outwardly benign fire treatments. Because these animals heavily influence so many key ecosystem processes, fire-caused changes in the arthropod community are surely responsible at some level for what we perceive as indirect effects of burning on other forest components, including plants and vertebrates. While it has long been recognized that the exploitation of fire-damaged trees by wood-feeding insects can account for much latent tree mortality attributable to burning and for much of the attraction of birds like woodpeckers to recently burned forest, the potential for the attractions and aversions of other types of arthropods to shape post-fire forests has been under-appreciated. Surely, if we understood the relationships between, for example, plants of the forest understory and their arthropod pollinators, herbivores, and their predators at least as well as we understand the influence of forest pests on timber production, we would look to fire's influence on a wide range of insects and spiders to explain or predict the response of understory vegetation to any type of burning in southwestern ponderosa pine forests. Indeed, research to detail the ecological roles of a wide range of arthropods seems prerequisite to the development of robust models of fire effects on any forest attributes of interest. More fundamentally, inventories and expositions on the natural histories of non-pest invertebrates of southwestern ponderosa pine forests are long overdue (Lightfoot 1996).

Here I report changes in trap rates that, with careful consideration of the biology of the target organisms and the inherent biases in the capture method, I have argued to reflect certain numeric or behavioral responses of arthropod groups to burning and have interpreted in terms of their potential functional significance. However, I do not intend such inferences to substitute for direct measurement of the numbers, rates, or processes of interest. Instead, I hope that my findings will stimulate rigorous investigations of the phenomena upon which I have speculated (*sensu* Didham et al. 1996). In particular, I hope that research to examine links between particular invertebrate taxa and aspects of ecosystem structure or function and to explore the numeric and behavioral responses of these animals to a range of fire management alternatives are soon to follow.

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—CHAPTER 3—

EFFECTS OF AUTUMN PRESCRIBED FIRES ON UNDERSTORY BIRDS (*JUNCO* SPECIES) IN SOUTHWESTERN PONDEROSA PINE FORESTS

INTRODUCTION

Wildlife populations change in the face of fire as a function of changing rates of survival, reproduction, or movement into or out of altered habitat (Sousa 1984, Whelan 1995). These demographic parameters are usually not directly affected by the disturbance *per se* but are instead affected indirectly by changes in the availability of food, feeding or breeding microhabitat, or numbers of predators, parasites, or competitors (Komarek 1969, Bendell 1974, Sousa 1984, Rotenberry et al. 1995, Whelan 1995, Lyon et al. 2000). A given type of habitat alteration may have predictable and consistent effects on wildlife populations only when it has predictable and consistent effects on resources or conditions that influence rates of survival, reproduction, and dispersal. However, subtle differences in pre-fire conditions, fire behavior, subsequent weather among treatments can lead to important differences in the effects of nominally similar fires on key habitat attributes for any given wildlife species (i.e., Kapler-Smith et al. 1993). If fire-caused changes in key resources differ considerably among replicated treatments, then our ability to predict consequences of prescribed burning for wildlife may rest squarely upon our understanding of the mechanisms that translate fire-caused changes in forest structure and condition into changes in the abundance, survival, productivity, and movement of animals (Marzluff et al. 2000).

Birds that depend heavily on the forest understory for food, cover, or both, are commonly assumed to be sensitive to prescribed burns in ponderosa pine forests, because the treatments are sure influence the availability of these key resources at multiple scales (Finch et al. 1997, Arno and Allison-Bunnell 2002). Specifically, Finch et al. (1997) predicted that "ground- and shrub-nesting [birds] may suffer reduced reproductive success and may decrease in abundance when the understory vegetation necessary for structural support, cover, and protection of the nest has been reduced or altered." Tiedemann et al. (2000) even warned that, in these forests "a spring burn can eliminate reproduction in ground-nesting birds." There are, however, only a handful of data describing numeric responses of understory birds to low-severity fires in Western conifer forests. Granholm (1982), Bock and Bock (1983), and Horton (1987) noted both short-term increases and decreases in abundance of ground-nesting birds in response to understory burning in these forests, suggesting that the effects of fire treatments on populations of these animals are conditional and variable. Yet there are no compelling explanations for any of the observed responses and there has been no study of the fires' effects on the reproductive success of these birds.

Here, I used Southwestern ponderosa pine forests as a model system in which to examine the effects of understory burning on the abundance and productivity of ground-nesting and ground-foraging birds. In this forest type, understory birds like the Yellow-eyed Junco (*Junco phaeonotus*; bird species nomenclature follows AOU 1998, 2000) and its ecological equivalent, the Dark-eyed Junco (*Junco hyemalis*) have presumably persisted for centuries or even millennia in the face of chronic perturbation via understory burning. Low-severity, understory fires burned frequently (i.e., every 2-12 years) through this habitat for centuries or even millennia, until they were excluded throughout the 20th century (Weaver 1951, Cooper 1960, Dieterich 1980, Covington and Moore 1994, Swetnam and Baisan 1996). Today, these low-severity fires persist in Southwestern ponderosa pine forests largely via prescribed burning. Although the historic fire season peaked in the late foresummer (Baisan and Swetnam 1990, Swetnam and Baisan 1996), prescribed fires are now commonly ignited in autumn, when risk of wildfire is low. I capitalized upon these planned, cool-season burns as the experimental treatments for my study (Whelan 1995) and used a Before-After-Control-Impact design (Stewart-Oaten et al. 1986) to isolate the influence of prescribed burning on the abundance and productivity of understory birds. Here I (1) report changes in abundance and nesting success of juncos attributable to the fires in my study and (2) develop a population growth model to examine the long-term consequences of any demographic influences. Identification of mechanisms behind the observed demographic effects should increase the likelihood of correctly predicting the outcomes of similar fire treatments (Marzluff et al. 2000). To enhance the utility of my findings in the management of Southwestern ponderosa pine forests, I link observed changes in abundance and nesting success of juncos to fire-caused changes in the availability of food and nesting microhabitat.

STUDY AREA AND METHODS

Study area

I considered all forest within Arizona or New Mexico classified as Rocky Mountain (Petran) and Madrean Montane Conifer Forests by Pase and Brown (1994) with overstories dominated by ponderosa pine as my target study area. I selected study sites within this area that had prescribed fires slated for Autumn 1998-2000 but were otherwise relatively undisturbed by logging or grazing and were to remain unlogged and ungrazed during the study period. Three study sites in Arizona met these criteria, all within national parks (NP) and monuments (NM) (Figure 2.01).

I established the Grand Canyon NP (GRCA) site on the north rim of the canyon at 2200-2500 m atop Walhalla Plateau. The soil within this site was derived primarily from Kaibab Limestone (Opperman and Kerr 1999, *unpubl. rep.*). Cattle, horses, and sheep grazed the plateau from the mid to late 1800s until 1938, when the park boundary fence was constructed (Hughes 1991). The Walnut Canyon NM (WACA) site was situated on the south rim of the canyon at about 2010-2080 m on soil derived largely from Kaibab Limestone (Davis 1987). Cattle and sheep were grazed on WACA's south rim from the late 1800s to 1979, when the boundary fence was erected (Davis 1987). The Saguaro NP (SAGU) site was located within the park's Rincon Mountain District, just east of Tucson. This site included forest atop Mica Mountain at 2260-2560 m on soil derived from a mixture of Pinal Schist, Continental Granodiorite, and Wrong Mountain Quartz Monzonite (Bowers and McLaughlin 1991). Cattle and sheep lightly grazed the mountain from the late 1800s until 1958 (Turner 1992).

Ponderosa pine was the dominant overstory tree species within all sites, although overall species composition varied (Table 2.01, Figure 2.02). All sites had experienced decades of fire exclusion. For example, the last extensive wildfire in ponderosa pine forest at SAGU occurred in 1954 (K. Schon, *pers. comm.*). Further descriptions of the topography, vegetation, soils, and fire and weather patterns of Southwestern ponderosa pine forests can be found in Wagle (1981), Pase and Brown (1994), and Swetnam and Baisan (1996). Additional details specific to the GRCA, WACA, and SAGU sites are provided, respectively, by White and Vankat (1992) and Wolf and Mast (1998); Joyce (1974) and Davis (1987); Marshall (1956), Baisan and Swetnam (1990), and Bowers and McLaughlin (1994).

Target species

Dark-eyed Juncos and Yellow-eyed Juncos are locally abundant, resident songbirds in Southwestern ponderosa pine forests. The species are ecological equivalents (Szaro and Balda 1979) with non-overlapping distributions during the breeding season in Arizona (Sullivan 1999). Yellow-eyed Juncos reach the northernmost extent of their range in southeastern Arizona, whereas Dark-eyed Juncos of the "Gray-headed" race (*J. h. dorsalis)* generally breed north of the Mogollon Rim in Arizona. Juncos are generally monogamous. They maintain all-purpose, <1 ha breeding territories, and have biparental care of the young (Sullivan 1999). In Arizona, juncos begin nesting in late April and continue until late August, successfully producing up to three broods each year (Sullivan 1999, Martin 2001). Average clutch size is 3-4 eggs (Sullivan 1999, Martin 1995, *pers. obs.*). Incubation begins with the penultimate egg and continues for 11-13 days (Sullivan 1989, Martin 1995, *pers. obs.*). Understory arthropods (primarily insects) make up more than 90% of the diet of adult juncos during the breeding season (Moore 1972, Ehrlich et al. 1988, Sullivan 1999). Young birds are reared entirely on arthropods (Hostetter 1961, Moore 1972, Sullivan 1999). Although juncos commonly forage on the ground in the shade of low vegetation, they may also glean prey from low branches of conifers (Moore 1972, Weathers and Sullivan 1989a,b). Juncos place their nests on the ground, often shaded by a tuft of grass, beneath a fallen log, or dried clumps of bracken fern (Sullivan 1989, Weathers and Sullivan 1989 a, b; *pers. obs.*). After fledging, young birds spend 22-28d with at least one parent in a family flock (Sullivan 1999). During this time, adults supplement foraging efforts of the juveniles. After young juncos are evicted from the family territory at the end of the fledgling period, they join juvenile flocks and remain in the area for the rest of the breeding season (Sullivan 1999). In late August, all juncos move to lower elevations to overwinter (Sullivan 1988, 1989). Juncos can breed during the first breeding season that follows hatching (Weathers and Sullivan 1989b). Sullivan (1989) estimated annual survival rates of adult and recently fledged Yellow-eyed Juncos as 59 and 16%, respectively. Similar figures have been noted by Wolf et al. (1988) and Martin (1995) for adult Dark-eyed Juncos.

Experimental design and sampling protocol

I capitalized on the fires slated to burn within my study area and used a quasi-experimental approach (*sensu* Manly 1992) to isolate their effects on forest vegetation and arthropod groups. Because 35-50 ha plots are generally necessary to find sufficient numbers of nests to estimate nest success for species of forest birds (Ralph et al. 1993; Martin et al. 1996, *unpubl. ms.*), I chose 40-ha study plots as my experimental units. I positioned experimental units within study sites based on locations of the planned burns – not at random. I positioned a treatment unit within the perimeter of each planned burn and located a matched control nearby (Figures 2.03-2.06). In 1999, I installed a second control unit within the SAGU study area (in anticipation of a planned burn that was later cancelled). Within each unit, I installed a 100-m by 100-m sampling grid, starting from a randomly selected location within 100 m of the primary access road or trail. I sampled forest vegetation and collected arthropods along each grid during the year before and during the first two years after the fall burns. At the SAGU site, I sampled vegetation during the third year postfire as well (Figure 2.07).

Encounter rates of adult juncos

I selected six interior gridpoints at which to record the number of individuals of each bird species seen or heard within a 50-m radius during a 10-minute count per Ralph et al. (1993). I chose sampling points in a stratified random fashion to ensure that point count stations were spaced at least 200 m apart (Ralph et al. 1993). I visited matched control and treatment sites on consecutive mornings and surveyed from 0600-0900. I repeated counts 3 times in each year. Within each unit, I conducted counts at the same set of points on approximately the same Julian dates each year.

For each plot in each year, I calculated the grand mean annual encounter rate of each bird species by first averaging the number of adults detected over the three visits and then over the six sampling points within each plot. Therefore the standard deviation associated with each plot mean is a measure of spatial variation in encounter rate. I excluded "flyovers" from analyses.

Assessment of fire effects via the point-count method assumes that "a constant fraction of individuals is counted between areas at the same time, between areas over time, or within an area over time" (Pendleton 1995). I assume that detection probability did not change on treatment plots due to understory burning. I believe that this is a valid assumption given that much of the vegetation affected by these fires was scorched rather than consumed, such that burning did not enhance visibility or the ability to hear sounds through the forest. I conducted all counts at GRCA and WACA and most at SAGU. Additional field observers were trained extensively before assisting with surveys and spent equal effort sampling on control and treatment plots (per Ralph et al. 1993). Therefore, any differences in counts within a plot over time should reflect changes in the abundances, and not the detectability, of birds.

Number of territorial males

Within each plot at SAGU, I spot-mapped locations of adult Yellow-eyed Juncos and their nests on daily visit maps (per Ralph et al. 1993, Hutto unpubl.). I searched control and treatment sites on consecutive days, focusing effort between 0600-1200. I recorded locations of singing and countersinging males, nonsinging individuals, junco pairs, aggressive interactions between juncos, birds carrying food or nesting material, nest sites, and recently fledged young. These data were transferred onto composite maps for each plot after each visit. On these composite maps, I roughly estimated territory boundaries by extending circles about 10 m beyond the outermost points at which birds associated with a given locale were observed. Although territory boundaries drawn in this way could not be used to accurately estimate territory size, I was able to approximate the number of territorial males in each plot (per Kendeigh 1944, Hall 1964, Williamson 1964). If ≥ half of a territory fell within the perimeter of the study area, I counted it as a 0.5 territory (per Hansen 1978).

Nesting success

Nest-searching was concentrated within territories of males known or suspected to be mated at SAGU only. Searches were conducted from approximately 25 May to 10 August, 1998-2000, with consecutive visits and equal effort on all study plots. Nest locations were generally revealed by conspicuous activities of adult birds (e.g., carrying nesting material, food, or fecal sacs to or from a nest). Once an active nest was located, it was visited every 2-3 days to determine its fate (per Martin and Guepel 1993). A nest was considered successful if it fledged at least one young. Daily nest survival rates were calculated using the Mayfield (1975) method as modified by Johnson (1979) and Hensler and Nichols (1981). Daily survival probabilities were calculated based on 12d incubation and 12d nestling periods (Sullivan 1999, *pers. obs.*).

Nesting microhabitat

Upon termination of each nest, I characterized the surrounding vegetation following the Breeding Biology Research and Monitoring Database (BBIRD) sampling protocol (Martin et al. 1996, *unpubl. ms.*). At each nest, I laid two measuring tapes crosswise with 11 meters extending in each cardinal direction and delineated nested 5- and 11-m-radius circles centered upon the nest. I noted the type of vegetation or substrate that primarily concealed the nest from above (i.e., grass/fern, low woody stems, rock, litter). In the 11-m-radius circle, I then recorded:

1) *Burn severity*. Fire severity is a qualitative measure of the consumption of plant biomass by fire (Brown and Smith 2000). Based on ocular characterization of average conditions, I rated burn severity of litter/duff, vegetation ≤3 m, and vegetation >3 m using standard National Park Service (NPS) burn severity codes (USDI 2001, Table 2.04).
2) *Number of trees >3m tall by species, size class, and condition*. I classed trees as <8.0, 8.0-22.9, 23.0-37.9, or >38.0 cm in diameter. I measured diameter of trees at breast height (dbh) except for basally sprouting species (see Table 2.01), which I measured at root crown. For these sprouting species, I recorded the condition of each

individual based on proportion of main stems >3 cm diameter at root crown (drc) supporting any green foliage, using three classes: 0, 1-50%, and >50%. However, because sprouters in the smallest diameter class generally had only a single main stem, I classed them simply as live or dead based on the presence or absence of any green foliage. For conifers, the percentage of crown foliage killed (scorched) by fire is a good indication of postfire survival probability (Lynch 1959, Harrington 1993). Lynch (1959) found that few ponderosa pines >10 cm dbh died after burning if they retained >15% green foliage. Likewise, Harrington (1993) reported that most ponderosa pines >18 cm in diameter survived autumn fire injury, even with >90% scorching. To classify all trees >3m tall into condition categories best corresponding to "standing dead" (or "snag") versus "live," I used the 15% scorch threshold and recorded ponderosa pines as having either 0-15% or 15-100% green needles. For all other conifers, which are less tolerant of crown scorch, I used two classes to assess condition: 0-20, >20% green. I treated aspen like "other" conifers, measuring the diameter of individual clones at breast height and recording snags in the 0-20% foliage category.

3) *Percent cover from scorched and green vegetation by height class and form.* I estimated percent cover from woody plants in each of three height classes: > 3 m, 1-3 m, <1m; and from herbaceous plants <1m tall. I calculated percent cover as the proportion of the 45 meter-marks along the tapes with the target vegetation directly overhead. I used a moosehorn densiometer to determine presence of cover from woody vegetation >3 m and 1-3 m tall. I noted presence of woody and herbaceous cover >1 m tall simply by looking down while standing over each meter mark. Cover

at each point was recorded as either fully green or scorched somewhere within the given stratum.

I used the 5-m-radius circle to further describe the understory, including:

1) *Number of woody stems by tree species, height class, and condition.* I counted only basal (main) stems of overstory and midstory tree species (Table 2.01) – not subsequent branches. For example, I counted basal resprouts of *Quercus* species, but not individual branches of a given *Quercus* sprout. I classed stems as <1m or 1-3 m tall and as live or dead based on presence or absence of green foliage.
2) *Percent ground cover by form.* I made ocular estimates of percent cover from charred and unburned coarse woody debris (logs and branches >8 cm diameter), litter (all other dead plant matter and duff), and bare ground (rock and mineral soil).

I also sampled vegetation in the same manner at 23-24 sampling points spaced 150-200 m along a 100 x 100 m sampling grid within each experimental unit (hereafter referred to as "systematic" sampling points). I used these data to discriminate vegetation characteristics that were "used" by nesting juncos from those generally "available" within a study plot. In this way I could identify key microhabitat attributes of junco nest sites. To accomplish this, I subjected a subset of 10 uncorrelated vegetation variables ($r < .40$; Table 3.01) to a stepwise discriminant function analysis (DFA) to develop a linear model that would distinguish used from available nesting microhabitat on Treatment (Unit 1 in Figure 2.02) and Control 1 (Unit 2 in Figure 2.02), separately, based on preburn (1998) vegetation characteristics. Prior to these analyses, count data were square root transformed, while data measured as percentages were arcsine and square root transformed (Sokal and Rohlf 1995). With each DFA, I calculated the posterior probability of membership of each "available" or "non-nest" sampling point in the "used" or "nest" group for Treatment and Control 1 (separately) over all years, which I considered an index of abundance of nesting microhabitat in subsequent fire-effects analyses.

Trap rates of arthropod prey

Because Yellow-eyed Juncos concentrate their foraging efforts in the understory, and because I expected the effects surface fire on vegetation to be concentrated in the forest understory, I targeted this stratum for arthropod sampling using pitfall traps (Bland and Jacques 1978, Cooper and Whitmore 1990). Arthropod capture rates in pitfall traps reflect both the abundance and activity of the animals, thereby providing an index of arthropod activity-density (Greenslade 1964). I assume that with enhanced activity or density of junco prey, food availability is increased for these birds. Therefore, activity-density of arthropod taxa known to be eaten by juncos, estimated from pitfall captures, is a viable index of prey availability.

Within each plot, I selected 20 points along the 100 x 100 m sampling grid at which to install traps by choosing one gridpoint at random and the rest in a checkerboard pattern radiating outward from it. Sampling points that fell on rock outcrops or within 50 m of a road or campground were relocated to a randomly selected, vacant gridpoint within 100 m. At each point, I installed a crosswise array of nine pitfall traps set at 1 m intervals. Each trap consisted of a 10-oz., white, plastic SOLO™ cup buried in the soil so that the 8-cm opening was level with the litter surface. I filled each trap halfway with a mixture of Dr. Bronner's™ unscented castile soap and water as a killing solution. Traps were run for 96-h intervals, twice during each summer – once in June and once in July. Within each unit, I ran traps on approximately the same Julian dates over all years. At the end of each interval, the contents of all nine traps at each point were pooled, fine-sieved, and transferred to Whirl-Pak™ bags containing 95% ethanol. I collected from matched control and treatment plots either on the same or consecutive days. Arthropods >3 mm in length were sorted, identified to family or thereabout (following Borror et al. 1992), and counted in the laboratory.

Only trap rates of arthropods likely taken as prey by juncos (based on Sullivan's [1998] stomach samples and my own observations) were assessed. These taxa were: Araneae, Isoptera (Termitidae), Hemiptera, Homoptera, Coleoptera (Carabidae, Staphylinidae, Scarabaeidae, Buprestidae, Elateridae, Cleridae, Melyridae, Nitidulidae, Coccinelidae, Endomychidae, Melandryidae, Chrysomelidae, Curculionidae, Scolytidae, and unidentified larvae), Diptera (Dolichopodidae, Muscoidea, Calliphoridae, Sarcophagidae, and unidentified larvae), Lepidoptera (adults and larvae), and Hymenoptera (Symphyta larvae, Braconidae, Ichneumonidae, and Formicidae).

Prey capture rates

According to Morrison (2001), "it is usually the rate at which an animal encounters resources, and not the density (or abundance) of the resource, that is important. . . as such we should not assume that density of a resource is an appropriate surrogate to the encounter rate of a resource." Therefore I also described fire's effects on food availability based upon estimates of prey capture rates of adult juncos, assuming that trap rates of arthropods and rates of prey encounters by foraging juncos would be positively correlated, but that the latter would provide a more direct and reliable index of prey availability for the birds (Davies and Huston 1981, Hutto 1990). Whenever a target species was observed foraging, I waited 15 seconds and then recorded number of prey captures until the bird flushed, moved out of view, or stopped foraging (per Holmes and Robinson 1988, Hutto 1990). Prey capture rate was calculated as the number of items taken/minute. In the case that an individual bird disappeared from view before one minute passed, if it reappeared and continued foraging within a 5-m radius of the point at which it disappeared, I continued recording captures until a cumulative minute passed and subsequently added together the sequences. Because prey capture rates of juvenile birds largely reflect age and experience instead of prey availability (Sullivan 1988, Weathers and Sullivan 1991b), I recorded capture rates of adult juncos only. In order to ensure independent observations, prey capture rate was only recorded once for a single individual within a given territory (Martin and Bateson 1986, Bell et al. 1990). Hence, sampling variation is based on differences among individuals rather than the variance in observations within individuals.

Because I collected arthropods by pitfall trapping, capture rate reflects not only abundance but also activity of the animals, which Greenslade (1964) termed "activity-density." I assume that both abundance and activity of insects and spiders are positively correlated with prey capture rates of forest insectivores, making activity-density a particularly good index of the availability of arthropod prey for the birds in my study.

Statistical analyses

I isolated the effect of the fire treatment(s) on 1) encounter rates of juncos, 2) number of junco territories, 3) junco nesting success, 4) abundance of vegetation attributes associated with junco nests, 5) probability of classification of "available" vegetation (systematic sampling points) as potential junco nesting microhabitat, 6) prey capture rates of juncos, and 7) pitfall trap rates of junco prey by comparing changes in my estimates of these variables on treatment plots relative to changes on matched control plots over each year of study.

From my repeated subplot measures, I calculated the average values of response variables within treatment versus control units for each year of study. For the arthropod data, I first averaged values from the two sampling periods per year, such that, ideally, each year of study yielded trap rate per unit effort (36 trap-days) from the same 20 sampling points within each of the six experimental units. However, a number of pitfall "failures" occurred when traps were unearthed by wildlife or filled with debris. I excluded data from point-visits with any of these failures (and therefore missing data) before calculating descriptive statistics.

I considered changes in mean values of response variables on the control plots to approximate the changes in means that would have occurred on the treatment plots in the absence of burning. For each variate, y_{ij}, and each interval, (1, 1 + n), I compared changes in paired treatment and control means to estimate a relative change function, r_n, or a difference score, d_n, as my fire effect estimate, where i = 0 (control) or 1 (treatment), j = 1 (prefire) or 1 + n (postfire), n = number of years postfire,

$$r_n = (\bar{y}_{1,1+n} / \bar{y}_{1,1}) / (\bar{y}_{0,1+n} / \bar{y}_{0,1})\text{ , and}$$

$$d_n = (\bar{y}_{1,1+n} - \bar{y}_{1,1}) - (\bar{y}_{0,1+n} - \bar{y}_{0,1})$$

If prefire means are roughly equivalent, as in my estimates of forest floor attributes (see *Results*), either model provides a valid estimate of change due to fire. However, my three pairs of treatment and control plots were not perfectly matched on most variables of interest, and I generally accounted for baseline noncomparability among treatment groups by using the relative change in control means within a given interval as a proxy for the expected average change in the absence of fire on the treatment plots (r_n). I considered d_n to be an appropriate estimator of fire effects only for the proportion of dead or lethally injured trees of the total standing in each size class, as there is no reason to expect baseline changes in average condition of trees to be a multiplicative function of pretreatment values.

Because difference scores and relative change functions are both prone to highly skewed or asymmetric distributions (Bonate 2000), I used a bootstrap procedure (10000 iterations, S-PLUS 6.0) to generate sampling distributions and bias-corrected 95% confidence intervals (CI) for all r_n or d_n from the observed data. All data were resampled within units such that the number of observations per unit remained constant and the same subplots (sampling points within units) were represented in the repeated measures through all iterations. To ensure that the arthropod estimates were based on equal sampling effort over time within units, I included data from subplots with pitfall failures only when same number of traps failed across the years of interest. I transformed relative change scores to percent changes, $(r_n - 1)100\%$, so that, for all estimates, a value of zero would indicate no effect of burning.

Because nest success rates were essentially equivalent on matched control and treatment plots prior to burning, I simply tested the null hypothesis that post-fire rates were equivalent to assess statistical significance of the first-year fire effect. There was little change in daily survival probability on either control plot from 1999 to 2000, so I was able to test for a significant second-year effect by comparing the treatment estimates from those years. I tested for these differences in daily survival probabilities via the program CONTRAST, which compares rate estimates with a Chi-square test (Sauer and Williams 1989). The statistical significance of fire's effect on prey capture rates was evident from visual inspection of a graph of means and confidence intervals for all plots and years.

Here, I report findings as statistically significant at the unadjusted critical level of $P \leq 0.05$, that is, when the 95% CI do not include zero. Based on the sheer number of estimates that I was able to make, the true mean effect may lie outside the reported interval for a handful of variables. Nonetheless, as reported, my estimates should provide a valid indication of the relative magnitude and direction of most of the effects of the fires in this study.

Hereafter, I refer to the interval from the summer before burning to the first summer post-fire as "year 1," to the interval from the first to second summers post-fire as "year 2," and to the interval from the second to third summers after burning as "year 3."

Population growth models

To assess the population-level implications of any effects of fire on productivity, I determined the daily survival probability and nest success rate necessary to maintain populations of juncos in the absence of immigration. Using Sullivan's (1988) estimate of adult junco mortality (41%), the population declines by 0.82 adults per pair per year. Thus, for the population to remain stable in the absence of immigration, pairs must produce enough young for 0.82 per pair to enter the breeding population the following spring. Since only 15.7% of juncos are estimated to survive from pre-flight fledging to the following spring (Sullivan 1988), pairs must fledge an average of 5.2 young per year for $\lambda = 1$, which, given that a pair of juncos can produce up to 12 fledglings per year, translates into a 43% success rate or an average daily survival probability of 0.966 for junco nests.

Based on my estimates of Yellow-eyed Junco demographic parameters in burned versus unburned ponderosa pine forest and data from Sullivan (1999) I modeled 100 years of change in junco populations (1) in the absence of fire, (2) subject to autumn fires with a mean return interval of ~ 6.1 years, and (3) subject to autumn fires with a mean return interval of 16.3 years. I modeled a 6.1-year return interval because it was the mean fire frequency for mixed conifer and open pine forest near and within my SAGU study site over the period 1657-1893 (Baisan and Swetnam 1990) and it is the target frequency for prescribed burning in ponderosa pine at this site (Schon 2000, *unpubl. rep.*). Complete fire exclusion and high-frequency fire are two extremes along a continuum of possible fire patterns over 100 years in this dry forest type. I modeled a 16.3-year return interval to assess the population response to fires of intermediate frequency as well.

The models were based on a 100-year sequence of productivity estimates for

Yellow-eyed Juncos, each modified to account for the effect of fire as estimated from my field data. Base productivity estimates came from my own data and those of Sullivan (1988), who recorded nesting success of a population of Yellow-eyed Juncos in a montane ponderosa pine forest in southeastern Arizona near my SAGU study site. I pooled six years of data from Sullivan (1988) with those from Treatment (preburn) and Control 1 (all three years) to describe Yellow-eyed Junco nest success (x ± 1SD) in unburned ponderosa pine forest in southeastern Arizona (0.457 ± 0.130; n = 10). I then generated 120 random values from a normal distribution defined by these statistics. These data served as a pool of annual nest success estimates from which to draw values to span the hypothetical 100 year period. Because, controlling for fire's influence, junco nesting success is thought to be lowest in years of severe drought (Sullivan 1999, *pers. obs.*), I used Palmer Drought Severity Index (PDSI) values (grouped into six categories from extremely drought to extremely wet) for all years during the period 1895-1995 (as summarized by Cook et al. [1999] for southeastern Arizona) as a template to generate a biologically tenable pattern of nest success over 100 years. I ordered the nest success estimates generated by randomization from smallest to largest and then grouped them into six sets of 20 values. I then generated a 100-year sequence of productivity estimates by randomly selecting one value from the set that corresponded to the PDSI category for each year. For example, for a year with a PDSI index in category 1, the highest drought rating, I randomly selected a nest success estimate from the set containing the 20 lowest values. For each year, I calculated $\lambda = b - d$, where b = the per capita rate of increase based on juvenile recruitment into the population from time t to $t + 1$ and d = the adult mortality rate. Based on a possible six fledglings produced per adult junco per year, 15.7% survival from fledging to recruitment, and a 41% adult mortality rate, $\lambda = 0.942$ (nest success) - 0.41. From these estimates I produced a growth function describing 100 years of change in a population of Yellow-eyed Juncos in the absence of fire when $N_0 = 100$ and $N_{t+1} = \lambda N_t$.

I generated a growth function for a population of Yellow-eyed Juncos subject to frequent fires with only minor amendments to the series of nest success estimates. Baisan and Swetnam (1990) found that from 1657-1893, fires within or near my SAGU study plots typically occurred in years of moderate PDSI, but followed two years unusually wet years (high PDSI). Therefore, instead of randomly "applying" fires in this model, I designated 15 "fire years" consistent with this historic pattern of fire occurrence. I adjusted nest success rates in the two years following each fire based upon my estimates of first- and second-year effects of the SAGU burn (see Results). Thus, I multiplied the first value by 0.23 (a 77% reduction) to approximate the first-year effect of burning and then multiplied the resulting value by 5.86 (a 486% increase) to obtain the adjusted value for year 2. In sum, I adjusted 30 values associated with the 15 fires. I estimated λ for each year and modeled a century of population change as described above. To assess the potential influence of decreased fire frequency on junco populations, I developed a model of population change for juncos subject to fires with a mean return interval of 16.3 years by removing the influence of nine of the fifteen fires from the productivity series.

RESULTS

Changes in junco encounter rates due to three fires

Mean encounter rates of juncos tended to fall or remain unchanged in response to each fire in year 1 (Table 3.01), however none of the apparent first-year declines was statistically significant. In year 2, the treatments at SAGU and WACA effected 283% and 515% increases in junco detections, respectively. There was little evidence for second-year change in junco numbers on the GRCA treatment plot relative to its matched control.

Changes in number of territorial male juncos due to the SAGU fire

The number of territorial males on study plots at SAGU hovered around 20 throughout the study. In 1998, I identified 21 territories on the treatment plot and 23 on the matched control. The treatment plot was burned in October 1998. In the following summer I estimated 20 and 24 territorial male juncos on Treatment and Control 1, respectively. In 2000, there were 20 on treatment and 23 on Control 1. On Control 2, territory number rose from 19 to 22 during the interval 1999-2000. These data indicate that there was no effect of the SAGU fire on the number of territorial male juncos.

Changes in nesting success due to the SAGU fire

Of 139 junco nests located at SAGU over the 3-yr study period, 125 were active long enough to allow estimation of success based on exposure-days. In 1998, the success rate for junco nests on both Treatment and Control 1 was 48% (Figure 3.01). In 1999, the first breeding season after fire, these values had fallen to 7% and 32% on Treatment and Control 1, respectively (Figure 3.01). Assuming that the 32% success rate on the control plot in 1999 is a good proxy for the expected rate on the treatment plot had it remained unburned, the fire treatment appears to have caused a 77% decrease in nest success in

Table 3.01. Encounter rate of adult juncos, percent cover of understory microhabitat attributes, and capture rate of arthropod prey on all six plots over all years of study. Values are means ± 1SD.

	Treatment				Control			
Variable	Prefire	Postfire Y1	Postfire Y2	Postfire Y3	Prefire	Postfire Y1	Postfire Y2	Postfire Y3
Saguaro National Park								
Junco encounter rate	0.50 ± 0.35	0.28 ± 0.33	1.28 ± 0.39	0.61 ± 0.57	0.89 ± 0.58	0.83 ± 0.55	1.00 ± 0.70	0.61 ± 0.65
Understory cover								
Woody <1 m	5.3 ± 5.5	2.7 ± 3.9	6.1 ± 5.0	4.7 ± 3.9	8.7 ± 7.5	7.7 ± 5.1	7.1 ± 3.1	6.2 ± 2.6
Herbaceous	8.3 ± 8.5	1.2 ± 2.2	4.3 ± 5.0	5.8 ± 6.9	24.7 ± 9.3	20.0 ± 11.6	17.8 ± 9.9	13.7 ± 8.5
CWD	6.6 ± 4.3	2.8 ± 3.7	2.7 ± 2.6	2.8 ± 2.3	3.5 ± 4.9	4.1 ± 5.3	4.2 ± 5.1	3.7 ± 4.2
Capture rate of arthropod prey	213.78 ± 244.77	107.22 ± 77.11	180.68 ± 158.68	—	208.21 ± 214.92	95.84 ± 55.33	122.24 ± 109.80	—
Walnut Canyon National Park								
Junco encounter rate	0.83 ± 0.18	0.72 ± 0.68	0.56 ± 0.27	—	0.50 ± 0.66	0.44 ± 0.46	0.06 ± 0.14	—
Understory cover								
Woody <1 m	4.4 ± 3.9	4.4 ± 4.8	3.1 ± 4.8	—	5.7 ± 5.3	4.6 ± 3.2	3.7 ± 3.7	—
Herbaceous	18.0 ± 7.7	8.0 ± 5.4	10.5 ± 4.4	—	13.4 ± 6.5	8.3 ± 4.9	8.0 ± 4.5	—
CWD	2.3 ± 3.7	0.8 ± 1.3	0.8 ± 1.4	—	1.8 ± 3.3	1.7 ± 3.1	1.7 ± 3.0	—
Capture rate of arthropod prey	136.72 ± 71.80	266.56 ± 96.14	119.47 ± 70.50	—	96.93 ± 51.63	180.53 ± 76.76	141.30 ± 79.75	—
Grand Canyon National Park								
Junco encounter rate	0.67 ± 0.63	0.67 ± 0.47	0.56 ± 0.62	—	0.78 ± 0.54	0.89 ± 0.50	0.89 ± 0.27	—
Understory cover								
Woody <1 m	3.0 ± 5.0	3.0 ± 3.4	3.0 ± 3.6	—	11.6 ± 8.8	11.7 ± 8.7	9.1 ± 7.3	—
Herbaceous	13.0 ± 8.4	7.4 ± 5.9	13.3 ± 10.7	—	11.0 ± 8.8	5.3 ± 4.2	6.3 ± 3.2	—
CWD	3.2 ± 5.3	2.3 ± 3.9	2.2 ± 3.7	—	7.8 ± 5.3	8.2 ± 5.6	8.1 ± 5.6	—
Capture rate of arthropod prey	283.24 ± 72.94	250.29 ± 94.85	202.21 ± 77.28	—	200.12 ± 90.37	215.20 ± 89.37	232.10 ± 94.84	—

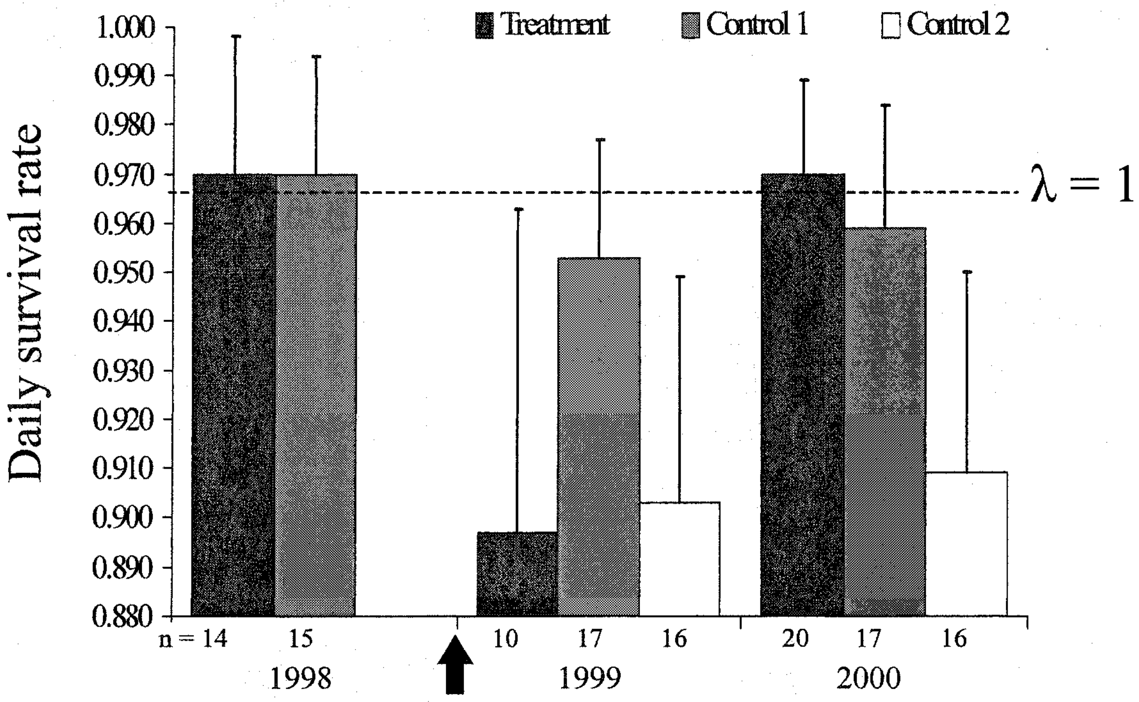


Figure 3.01. Daily survival rates (probability of survival per day + 95% CI) for Yellow-eyed Junco nests on control and treatment plots at SAGU before and after burning in the fall of 1998 (arrow). Sample size is listed below each bar. During the first breeding season postfire, productivity on the treatment plot fell below the level necessary to maintain junco numbers in the absence of immigration (~ 43% nest success for λ = 1, dashed line). By the second breeding season postfire, however, average nest success on the burned plot had risen from 7 to 49% - a nearly fivefold increase relative to corresponding changes on either control plot.

year 1 (Figure 3.02). Although the difference in nest success on the treatment versus Control 1 in 1999 was not statistically significant ($X^2 = 1.78$, 1 df, $P = 0.182$), the fire appears to have had a biologically meaningful effect on junco productivity in that first postfire breeding season. After burning, nest success fell below the estimated 43% necessary to maintain junco numbers in the absence of immigration (Figure 3.01). By the second breeding season postfire, this rate had rebounded to its prefire level (~48%). Nest success of juncos on Control 2 was significantly lower than the critical 43% in both 1999 and 2000. Change in nesting success during this period was comparable on both control plots.

Changes in availability of nesting microhabitat due to three fires

In 1998, percent cover from herbaceous vegetation within an 11-m radius best distinguished used from available nesting microhabitat on both Treatment (Wilk's $\Lambda = 0.783$, $X^2 = 8.68$, $P = 0.003$) and Control 1 (Wilk's $\Lambda = 0.865$, $X^2 = 5.31$, $P = 0.021$). Mean herbaceous cover (± 1SD) was significantly higher around nests than around systematic sampling points (Table 3.02, Figure 3.03). Moreover, on both plots, nests that fledged at least one junco ("successful" nests) were surrounded by more herbaceous cover than those that were abandoned or depredated ("failures") (Figure 3.04), although these differences were not statistically significant (Mann-Whitney *U* tests, $P > 0.23$).

In 1999 and 2000, juncos continued to place their nests in patches of forest with more herbaceous cover than the average "available" level on each study plot (Table 3.03, Figure 3.04). In 1999, these differences were significant on Control 1 ($U = 125$, 42 df, $P = 0.020$) and Control 2 ($U = 130$, 41 df, $P = 0.050$), but not on Treatment ($U = 92.5$, 35

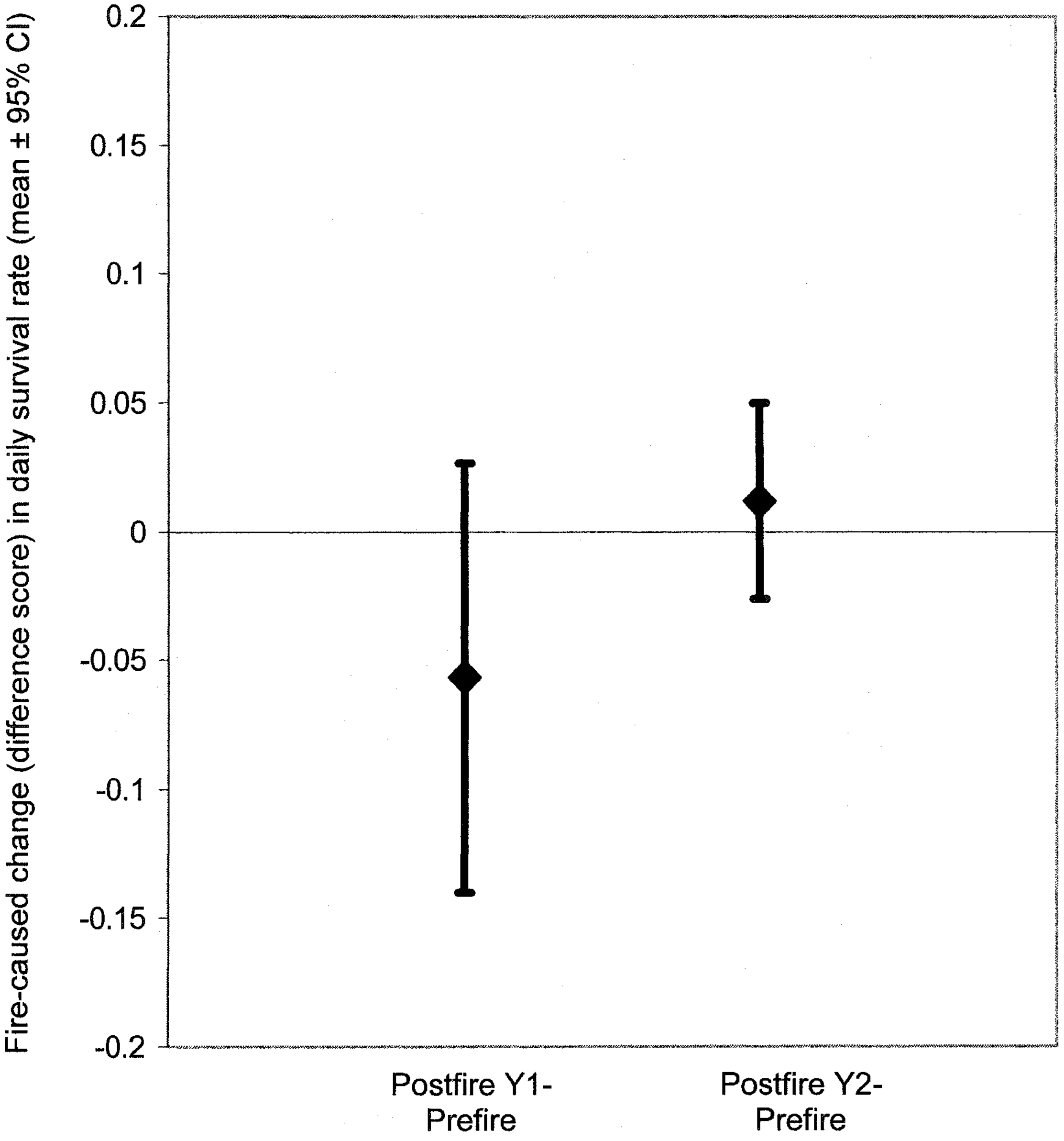


Figure 3.02. Fire-caused change (difference score) in daily survival rate of Yellow-eyed Junco nests from the summer before to the first and second summers after fall burning at SAGU.

Table 3.02. Vegetation (X ± 1SD) surrounding junco nests ("Used") and systematic sampling points ("Available") within SAGU study plots in 1998 ("Prefire"), 1999 ("Postfire Y1"), and 2000 ("Postfire Y2").

	Used			Available		
Variable	Prefire	Postfire Y1	Postfire Y2	Prefire	Postfire Y1	Postfire Y2
Treatment						
No. live trees within 11 m						
Conifers >38 cm dbh	0.6 ± 0.9	0.1 ± 0.3	0.2 ± 0.4	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3
Conifers 23-38 cm dbh	1.9 ± 1.6	0.5 ± 1.0	1.3 ± 1.4	1.3 ± 1.5	1.1 ± 1.5	1.0 ± 1.5
Ponderosa pines 8-23 cm dbh	7.6 ± 4.9	5.4 ± 4.0	8.9 ± 8.5	9.8 ± 9.4	6.5 ± 8.3	6.2 ± 7.6
Sprouters 8-23 cm drc	2.5 ± 2.8	1.3 ± 2.7	0.7 ± 1.0	1.9 ± 2.2	0.5 ± 0.9	0.7 ± 1.0
No. live stems within 5 m						
Ponderosa pines 1-3 m tall	1.8 ± 3.9	0.0 ± 0.0	0.7 ± 1.3	1.0 ± 1.6	0.2 ± 0.5	0.1 ± 1.3
Sprouts <1 m tall	50.3 ± 69.9	13.4 ± 39.8	84.7 ± 122.8	59.8 ± 78.2	50.8 ± 68.4	119.3 ± 140.6
Percent cover within 11 m						
Herbaceous	19.8 ± 12.3	5.0 ± 7.7	11.6 ± 15.5	8.3 ± 8.5	1.2 ± 2.2	4.3 ± 5.0
Percent cover within 5 m						
Coarse woody debris	5.1 ± 6.4	3.3 ± 3.1	3.4 ± 4.4	6.6 ± 4.3	2.8 ± 3.7	2.7 ± 2.6
Litter	86.6 ± 12.2	80.5 ± 15.4	78.9 ± 21.8	83.0 ± 11.2	77.0 ± 18.7	79.6 ± 19.8
Bare ground	7.8 ± 10.4	16.8 ± 16.0	12.4 ± 10.8	8.5 ± 11.9	20.5 ± 18.5	17.6 ± 19.4
Control 1						
No. live trees within 11 m						
Conifers >38 cm dbh	0.1 ± 0.3	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3
Conifers 23-38 cm dbh	0.4 ± 1.1	0.3 ± 0.6	0.2 ± 0.4	0.4 ± 0.9	0.5 ± 1.1	0.5 ± 1.1
Ponderosa pines 8-23 cm dbh	6.7 ± 7.3	9.7 ± 10.1	11.5 ± 13.8	8.5 ± 10.4	8.5 ± 10.4	8.4 ± 10.4
Sprouters 8-23 cm drc	2.5 ± 3.8	1.4 ± 1.3	0.7 ± 0.9	2.8 ± 3.5	2.7 ± 3.5	2.8 ± 3.6
No. live stems within 5 m						
Ponderosa pines 1-3 m tall	1.4 ± 1.9	1.4 ± 2.1	1.1 ± 1.2	1.4 ± 3.7	1.4 ± 3.7	1.2 ± 2.8
Sprouts <1 m tall	39.2 ± 62.3	77.3 ± 103.0	33.0 ± 34.7	65.4 ± 50.8	70.5 ± 52.3	73.4 ± 52.6
Percent cover within 11 m						
Herbaceous	34.3 ± 14.9	27.4 ± 12.0	20.7 ± 9.9	24.7 ± 9.3	20.0 ± 52.3	17.8 ± 9.9

Table 3.02. Cont.

	Used			Available		
Variable	Prefire	Postfire Y1	Postfire Y2	Prefire	Postfire Y1	Postfire Y2
Percent cover within 5 m						
Coarse woody debris	2.1 ± 3.4	3.7 ± 4.4	3.7 ± 3.2	3.5 ± 4.9	4.1 ± 5.3	4.2 ± 5.1
Litter	78.7 ± 13.8	76.6 ± 14.0	77.4 ± 23.6	84.1 ± 12.5	83.1 ± 12.3	84.5 ± 10.3
Bare ground	9.7 ± 11.8	11.4 ± 12.2	8.0 ± 10.0	7.3 ± 8.2	8.7 ± 8.8	9.0 ± 8.5
Control 2						
No. live trees within 11 m						
Conifers >38 cm dbh	—	0.0 ± 0.0	0.1 ± 0.4	—	0.2 ± 0.5	0.2 ± 0.5
Conifers 23-38 cm dbh	—	0.1 ± 0.2	0.7 ± 0.8	—	0.4 ± 0.9	0.4 ± 0.9
Ponderosa pines 8-23 cm dbh	—	4.7 ± 5.8	9.1 ± 8.2	—	4.7 ± 6.1	4.6 ± 6.2
Sprouters 8-23 cm drc	—	0.1 ± 0.2	0.1 ± 0.5	—	0.7 ± 1.6	0.6 ± 1.6
No. live stems within 5 m						
Ponderosa pines 1-3 m tall	—	0.7 ± 2.9	0.9 ± 2.5	—	0.5 ± 1.7	0.5 ± 1.7
Sprouts <1 m tall	—	9.9 ± 23.3	39.7 ± 50.7	—	21.0 ± 31.4	21.7 ± 32.7
Percent cover within 11 m						
Herbaceous	—	31.7 ± 15.6	22.6 ± 12.1	—	22.2 ± 18.4	17.8 ± 15.5
Percent cover within 5 m						
Coarse woody debris	—	4.2 ± 3.6	5.1 ± 4.3	—	4.1 ± 4.1	4.8 ± 4.8
Litter	—	83.2 ± 12.8	86.5 ± 12.7	—	81.0 ± 13.1	82.2 ± 11.3
Bare ground	—	7.2 ± 7.7	7.1 ± 9.7	—	13.1 ± 11.5	12.7 ± 10.9

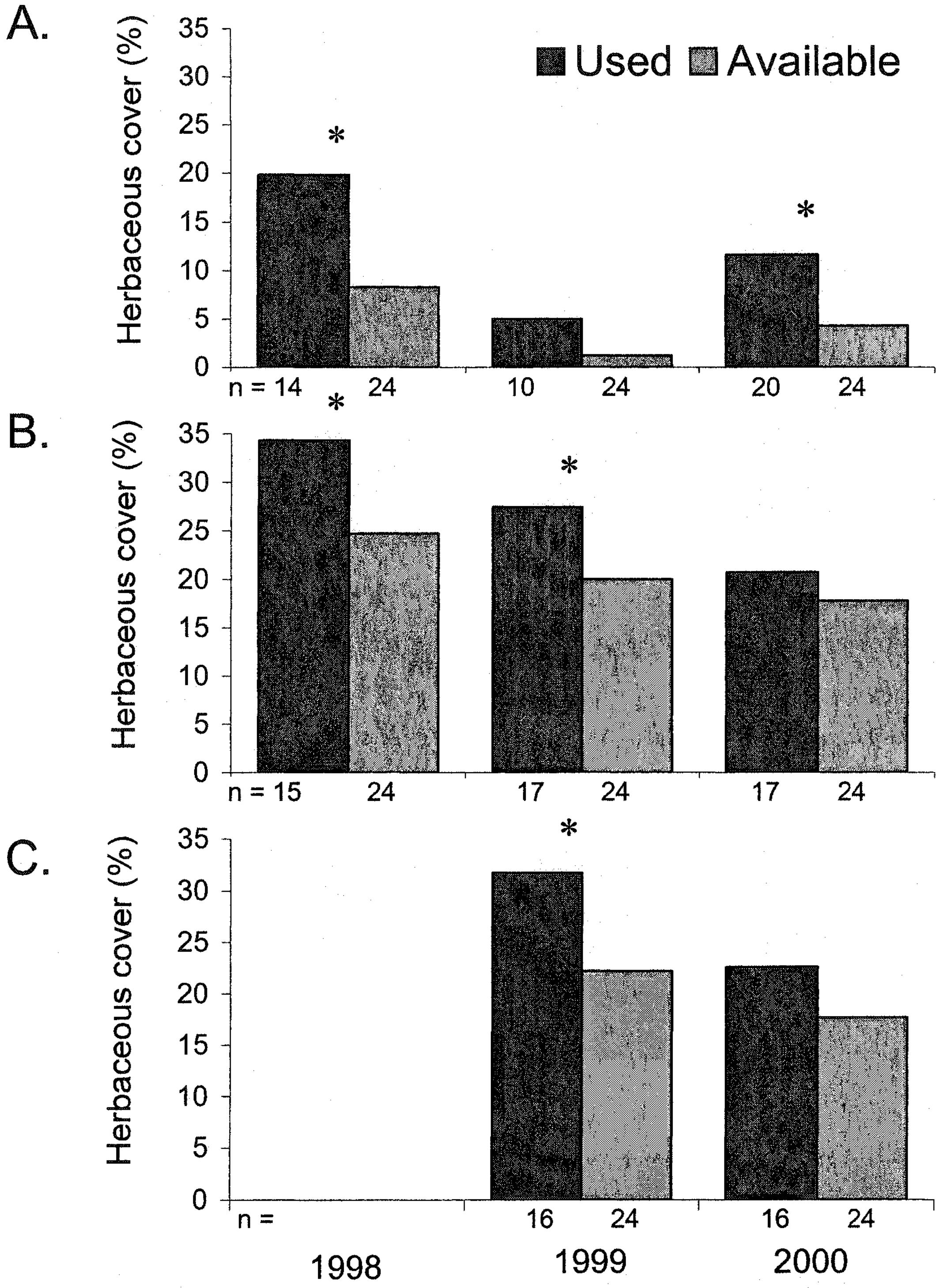


Figure 3.03. Mean herbaceous cover (%) within 11 m of Yellow-eyed Junco nests ("used") versus that within 11 m of systematic sampling points ("available") on (A) Treatment, (B) Control 1, and (C) Control 2 from 1998-2000. Asterisks denote statistically significant differences between "used" and "available" locations at $P \leq 0.05$ after Bonferroni corrections for multiple tests within each plot.

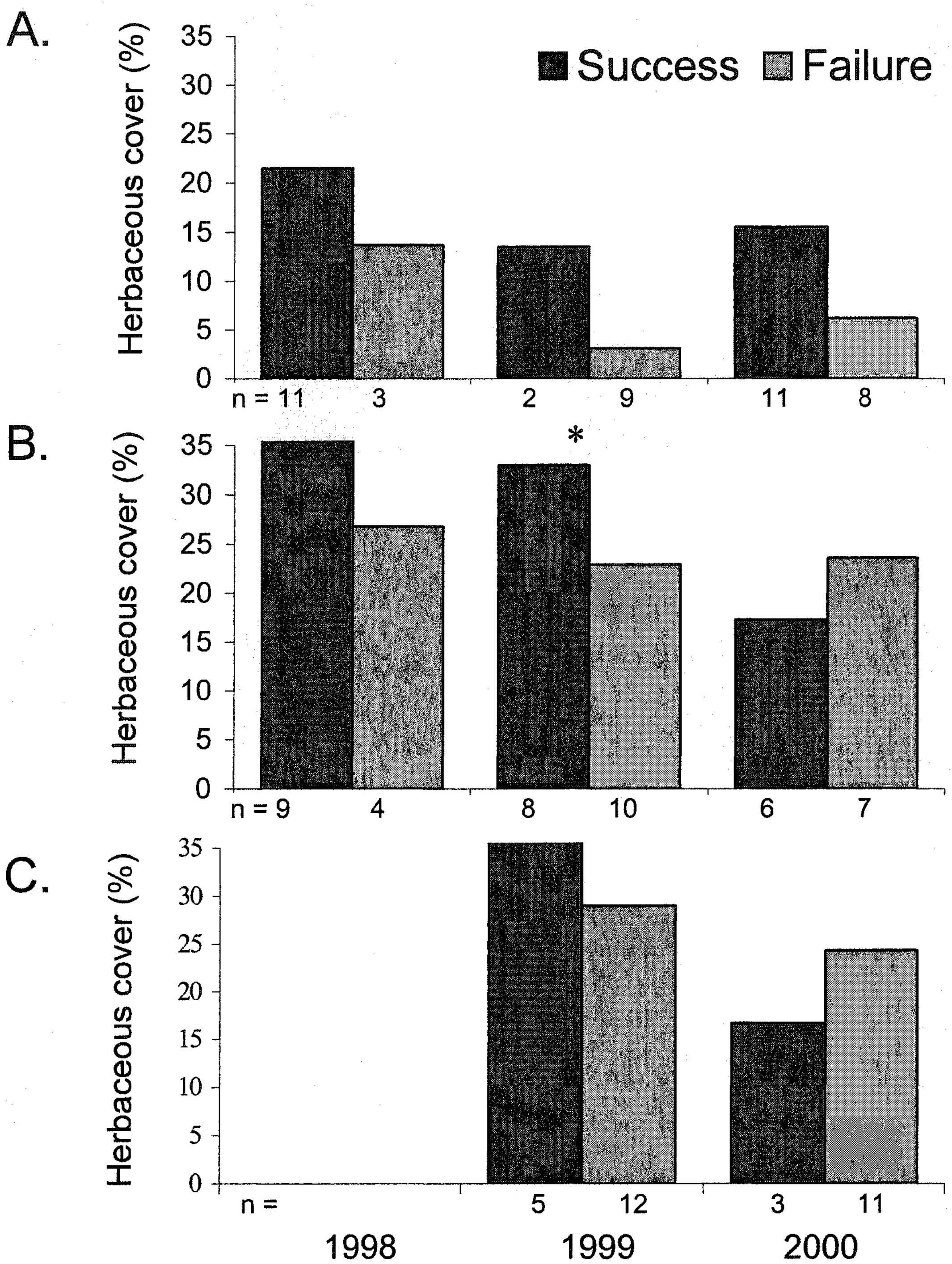


Figure 3.04. Mean herbaceous cover (%) within 11 m of Yellow-eyed Junco nests of known fate on (A) Treatment, (B) Control 1, and (C) Control 2 from 1998-2000. Successful nests fledged at least one young. Failed nests included those abandoned before eggs were laid. Only the difference on Control B in 1999 was statistically significant after correcting for multiple tests (*P = 0.005).

df, $P = 0.105$). In 2000, however, only the Treatment difference was statistically significant ($U = 141.5$, 43 df, $P = 0.033$). Again, in 1999, successful nests were surrounded by greater cover from grasses, forbs, and ferns than failed nests. In this year, these differences were statistically significant on both Control 1 and Treatment, but not on Control 2. On Control 1, mean herbaceous cover (± 1SD) around the eight successful nests (33.0 ± 5.6) was nearly 50% higher than that within 11 m of failed nests (22.9 ± 14.1) ($U = 8.5$, 18 df, $P = 0.005$). This difference was most remarkable on Treatment during this first breeding season post-fire, where cover surrounding the two successful nests (13.5 ± 9.2) was more than four times that within 11 m of failed nests (3.1 ± 6.5). This difference was nearly statistically significant despite the small sample size ($U = 1.5$, 11 df, $P = 0.062$). The apparent advantage of nesting amidst heavy herbaceous cover seemed to wane or even reverse in 2000, when average cover about failed nests tended to exceed that surrounding successful nests on both controls (Figure 3.04). Neither of these latter differences were statistically significant ($P > 0.31$), however.

The SAGU fire effected an 83% reduction in herbaceous cover during year 1 (Table 3.01, Figure 3.05). Then, in year 2, herbaceous cover increased more than threefold (Table 3.01, Figure 3.05). The flush of herbaceous growth continued into year 3, when cover from grasses, forbs, and ferns rose by another 74% (Table 3.01, Figure 2.13). Accordingly, the fire caused the probability of classification of vegetation surrounding systematic sampling points as potential nesting microhabitat to fall significantly on the Treatment relative to Control 1 in year 1 ($U = 144$, 48 df, $P = 0.0029$) but then to rise in year 2 ($U = 57$, 48 df, $P < 0.0001$) and again in year 3 ($U = 132$, 48 df, $P = 0.0013$).

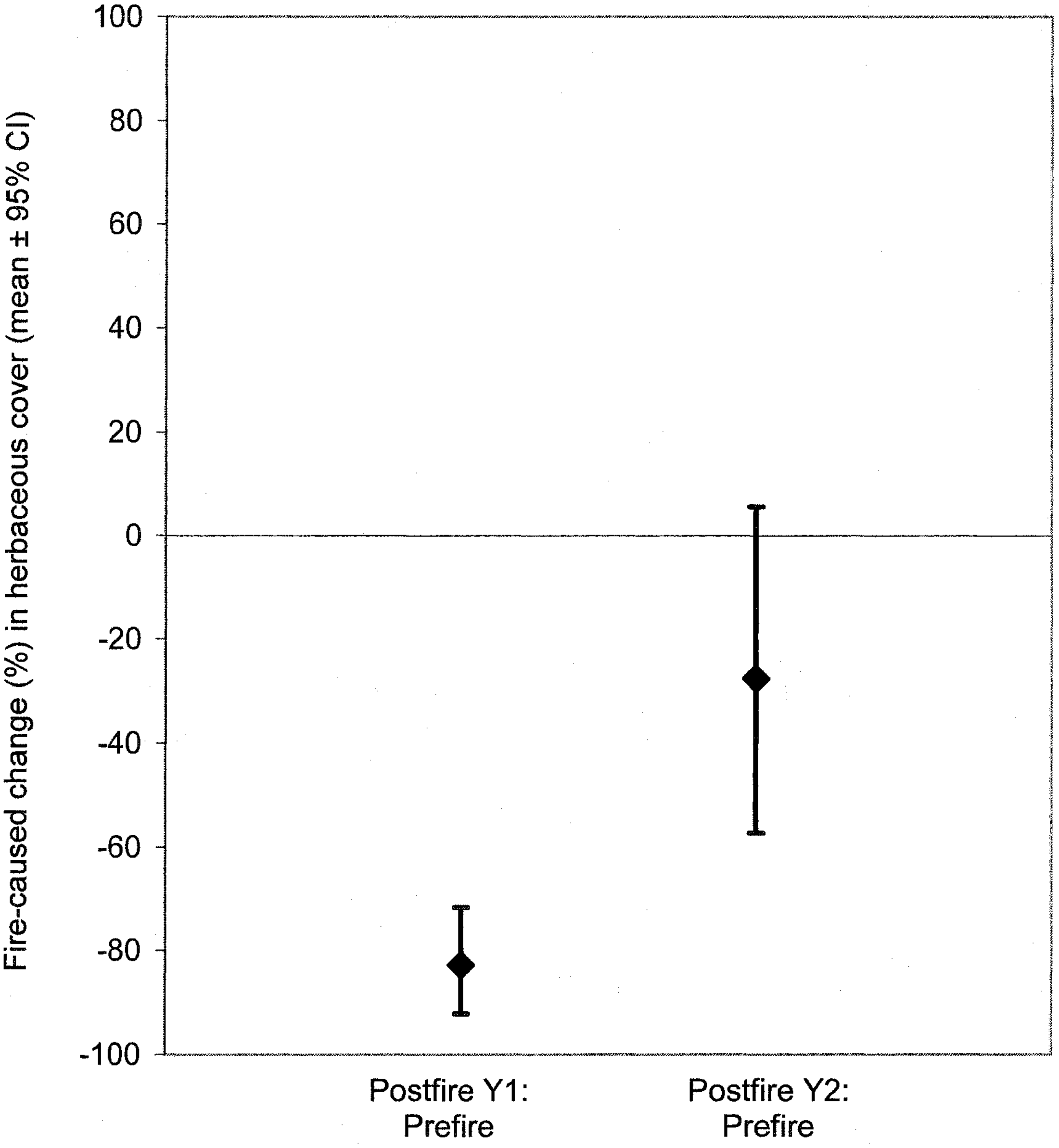


Figure 3.05. Fire-caused change (%) in cover of herbaceous vegetation from the summer before to the first and second summers after fall burning at SAGU.

In addition to herbaceous cover, low woody stems (< 1 m tall) and coarse woody debris (CWD) were commonly used by juncos to directly conceal their nests (Table 3.03). The SAGU fire also significantly affected these habitat attributes. This treatment caused an average 44% net loss of low woody cover during year 1 (Figure 2.12), largely via consumption of low oak foliage, and a 65% reduction in cover from CWD (Figure 2.14), presumably due to direct consumption of these fuels during the fires. In year 2, new growth overcompensated for first-year losses from leaf shed, and woody cover below 1m increased by 148% (Figure 2.12). The fire effected trivial change in CWD after year 1 (Figure 2.14).

The other two fire treatments likewise effected latent flushes in production of grasses, forbs, and ferns (Table 3.01, Figure 2.13). Although the first-year decline and second-year increase in herbaceous cover attributable to the WACA burn were strong and consistent enough to be statistically significant, the second-year effect was modest in comparison to that of the SAGU fire. The GRCA fire, however, had no significant effect on herbaceous cover in year 1, and the second-year increase was only nearly significant (Figure 2.13). Both fires caused cover from coarse woody debris (CWD) to decline significantly in Year 1 (Figure 2.14). Cover from CWD fell by 64% at WACA and 30% at GRCA, with little change thereafter (Figure 2.14).

Changes in low woody vegetation were less consistent among the three fire treatments. At GRCA, there was little change in cover from low vegetation due to fire in year 1 (Figure 2.12). In year 2, cover in this stratum rose on the treatment relative to the control, however the 51% increase was only nearly statistically significant (Figure 2.12). The WACA fire actually effected in a 27% rise in mean cover during year 1, probably

Table 3.03. Percent of total nests dependent upon each habitat attribute for primary concealment on each plot at SAGU by year.

	Treatment 1			**Control 1**			**Control 2**	
Nest Placement	Prefire (n = 14)	Postfire Y1 (15)	Postfire Y2 (22)	Prefire (16)	Postfire Y1 (19)	Postfire Y2 (18)	Postfire Y1 (19)	Postfire Y2 (16)
Grass/fern	29	40	32	56	58	22	74	62
Woody stems	36	7	9	31	16	56	5	18
Coarse woody debris	21	13	27	0	5	11	10	6
Rock	7	13	27	6	10	6	0	6
Litter	7	0	4	6	0	0	0	0
Root hole[a]	0	7	0	0	0	0	0	0
Tree branch/ cavity	0	20	0	0	10	6	10	6

[a] Nest placed in hole left by tree root that was consumed by fire

due to treefall and sagging branches (Figure 2.12). At GRCA, the fire effected trivial change in total cover from low woody vegetation (Figure 2.12). The 27% increase in cover at GRCA during the second interval, albeit statistically insignificant, was also largely due to the rise in sprout numbers (mostly aspen suckers). At WACA, there was little change in total numbers of sprouts or seedlings during year 2 to offset the loss of scorched foliage, and cover from low woody vegetation apparently fell by 14%, although this change was not statistically significant.

Change in prey capture rate due to the SAGU fire

Prey capture rates of adult Yellow-eyed Juncos averaged between four and five items per minute on all study plots in every year (Figure 3.06). Mean capture rates (± 1SD) on the treatment plot were 4.5 ± 1.3, 4.2 ± 0.9, and 4.9 ± 1.9 in 1998, 1999, and 2000, respectively. Values during these same periods on Control 1 were 5.0 ± 2.1, 4.7 ± 2.6, and 4.1 ± 1.9. In 1999 and 2000, prey capture rates (± 1SD) on Control 2 were 4.2 ± 2.8 and 4.6 ± 2.6, respectively. Notably, the grand mean for my total of 100 observations at SAGU over three years was equivalent to the average capture rate of 4.6 insects/minute (n = 253 observations averaging 61 J/insect) reported by Weathers and Sullivan (1991b) for adult Yellow-eyed Juncos in comparable ponderosa pine forest in southeastern Arizona. The rate of prey acquisition by adult juncos was affected little by fire in Year 1. In Year 2, there was a 33% increase, but this change was not statistically significant (Figures 3.06, 3.07).

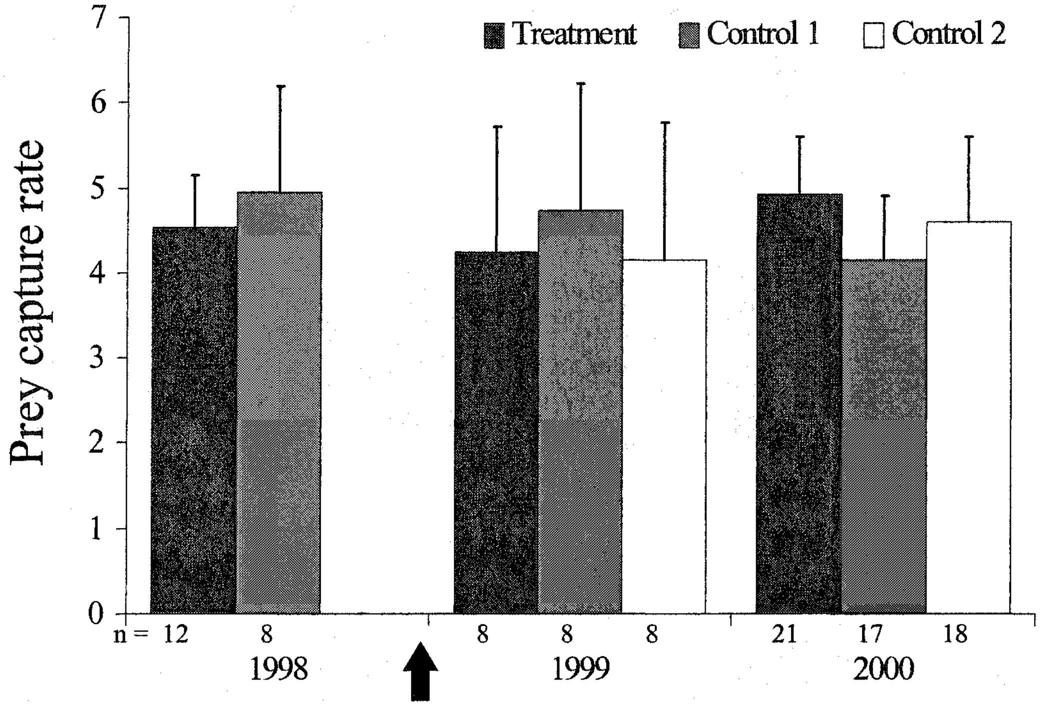


Figure 3.06. Prey capture rates (+ 95% CI) for adult Yellow-eyed Juncos on control and treatment plots at SAGU before and after burning in the fall of 1998 (arrow). Sample size is listed below each bar. Capture rates differed little among plots or years. Prey captures increased by 33% from 1999 to 2000 on the treatment plot relative to Control 1. Although this change was not statistically significant, it coincided with a notably similar 31% increase in trap rates of junco prey on the burned plot relative to Control 1.

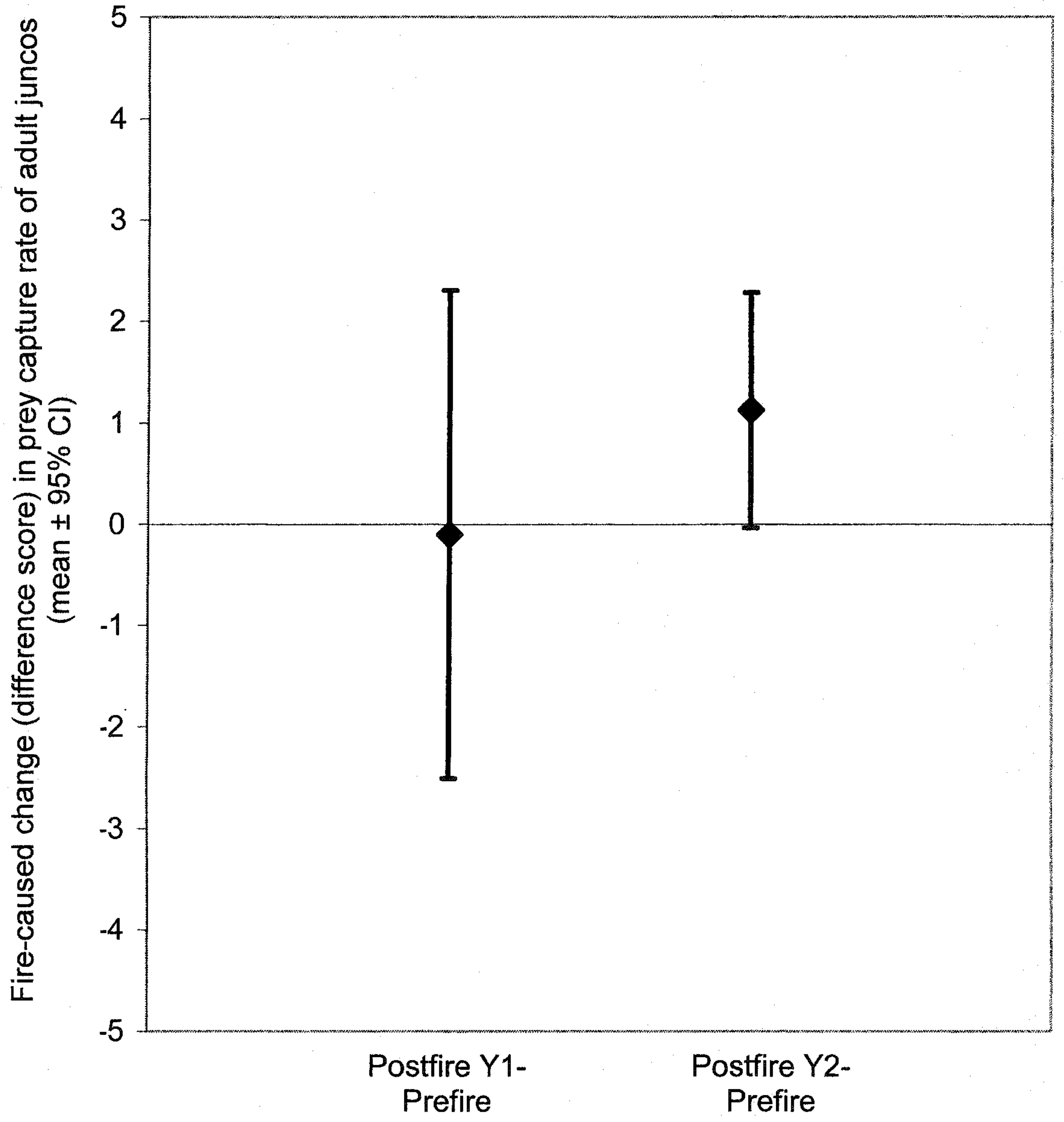


Figure 3.07. Fire-caused change (difference score) in prey capture rate of adult juncos from the summer before to the first and second summers after fall burning at SAGU.

Changes in activity-density of arthropod prey due to three fires

The effect of fire on activity-density of arthropods known to be eaten by juncos varied by treatment (Table 3.01, Figure 3.08). In year 1, trap rates were affected little by the fires at SAGU and WACA, while the GRCA fire caused captures to fall by 18%. In year 2, the WACA and GRCA fires effected declines of 43% and 25%, respectively. At SAGU, the mean trap rate of junco prey increased by 31% on the burned plot relative to the control, but this change was not statistically significant.

Population growth functions

In the absence of density-dependent influences on vital rates taken from unburned forest, a hypothetical population, starting with 100 individuals, exceeds 300 by year 77 and peaks at 1863 individuals in year 100 (Figure 3.09a). This model illustrates the potential for exponential population growth in a static environment wherein the average nesting success (46%) exceeds that necessary for $\lambda = 1$ (43%) as estimated with Sullivan's (1988) estimates of juvenile and adult survival for Yellow-eyed Juncos in unburned ponderosa pine forests. After accounting for the short-term influence of fires with a mean return interval (± 1SD) of 6.3 ± 2.5 years on nesting success of Yellow-eyed Juncos, population size reaches a low of 14 individuals in year 82 (Figure 3.09b). By year 100, however, that number has risen to 49. These data suggest that the influence of chronic fire on reproductive success alone could bound a population of Yellow-eyed Juncos. After the influence of nine of the 15 fires was removed from the model used to generate Figure 3.09b, the resulting mean fire return interval (± 1SD) was 16.3 ± 11.8 years (Figure 3.09c). This third model produced population oscillations of intermediate

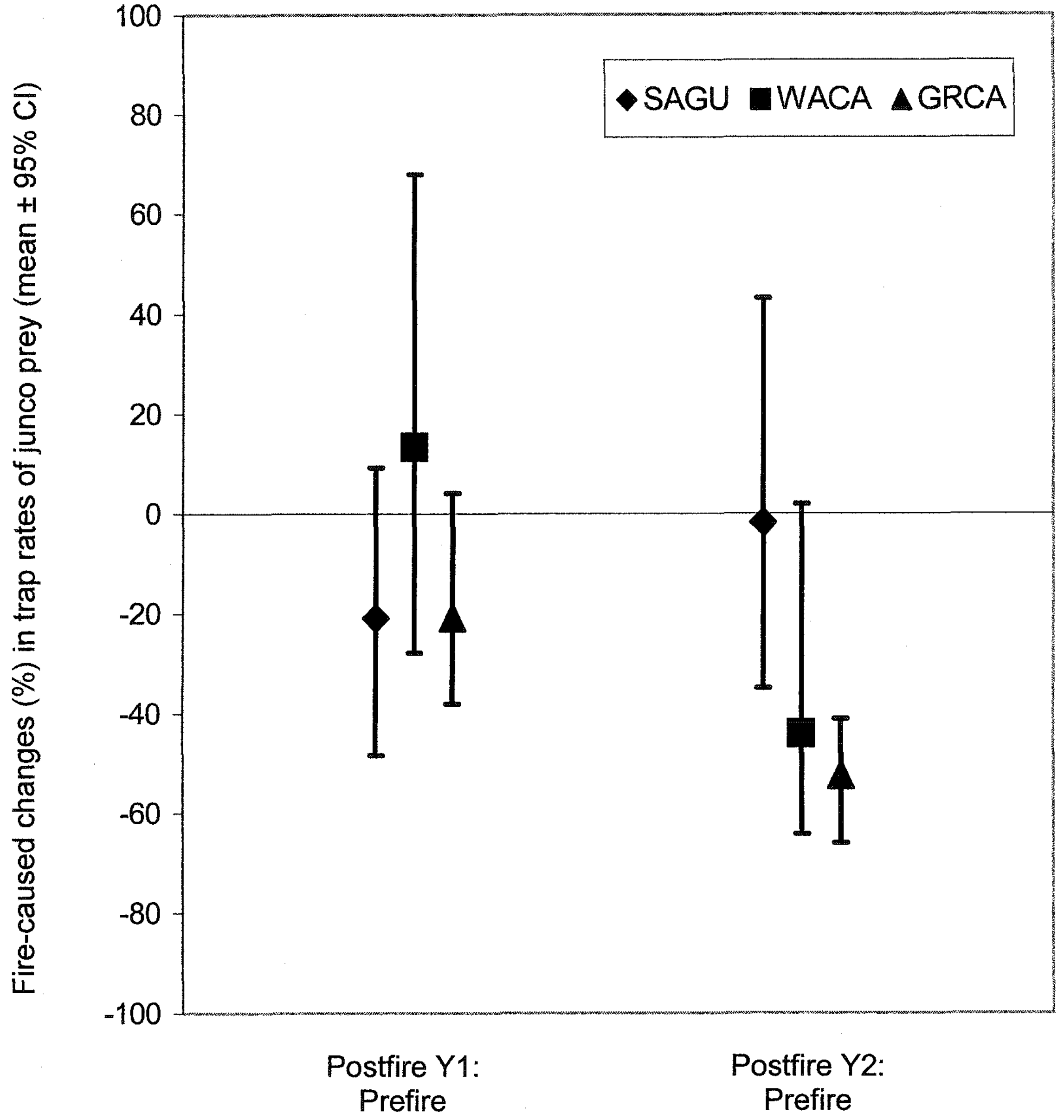
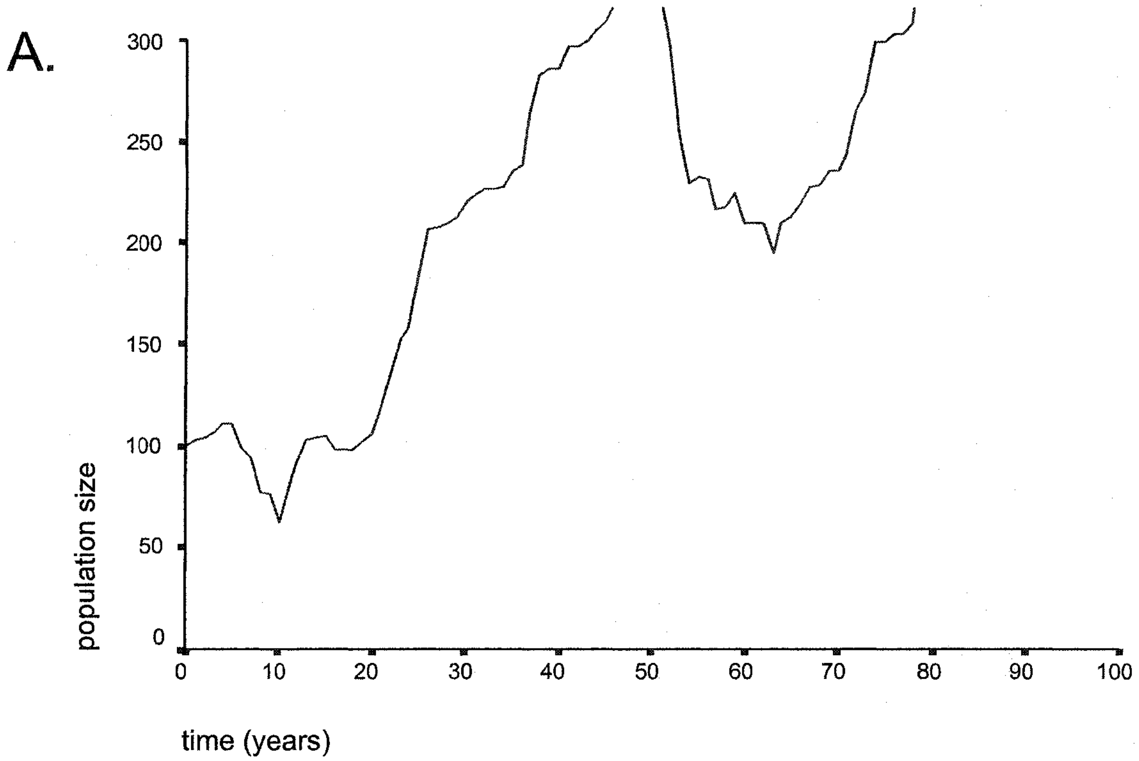


Figure 3.08. Fire-caused change (%) trap rates of junco prey from the summer before to the first and second summers after fall burning.



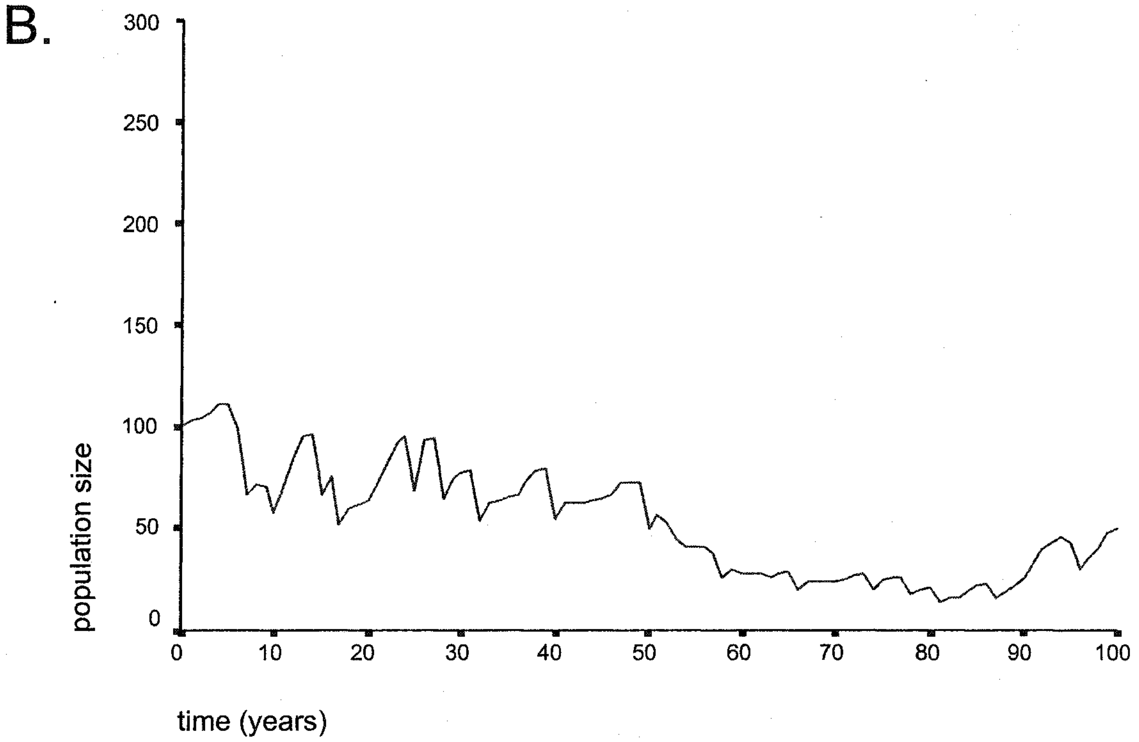


Figure 3.09. Models of Yellow-eyed Junco population change over 100 years in Southwestern ponderosa pine forest (A) without disturbance from fire and with mean fire return intervals of (B) 6.3 and (C) 16.3 years.

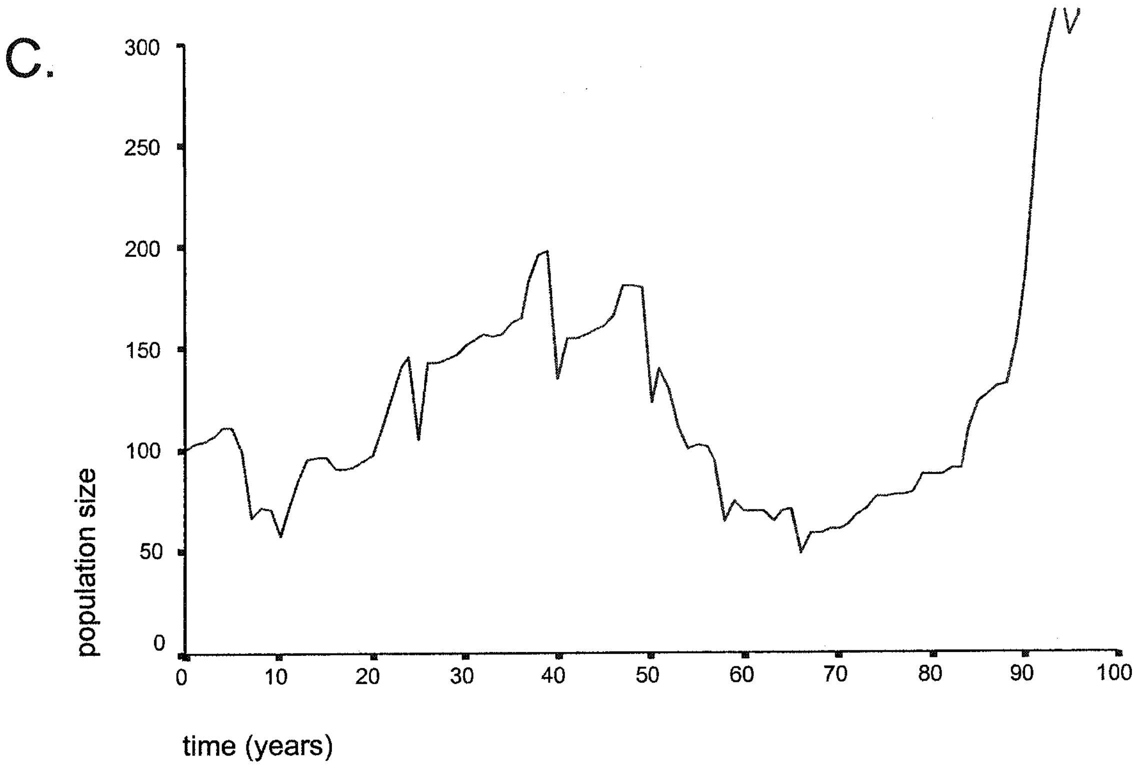


Figure 3.09. Cont.

amplitude, until numbers increased dramatically over the 39-year fire-free interval from year 68-97 (which I included to mimic the absence of widespread fire in SAGU from 1955-1994). Comparison of all three models illustrates the weakening influence of fire on junco populations with decreased fire frequency.

DISCUSSION

Like those of most breeding passerines, junco populations generally consist of territorial breeders and surplus, unmated birds, or floaters, during the spring and summer months (Hensley and Cope 1951, Sherry and Holmes 1989, Newton 1992, Peer et al. 2000, Bayne and Hobson 2001). In the absence of discernable changes in territory numbers, changes in encounter rates of adult juncos were likely due to movement by floaters or divorcées (*sensu* Choudhury 1995) into and out of my study plots. Although encounter rates were affected little by the GRCA fire — I detected only trivial declines in both years — junco numbers apparently fell and then rose on burned plots relative to controls in the first two postfire breeding seasons at SAGU and WACA. However, only the second-year increase (283%) at SAGU was statistically significant. Given the poor reproduction on the SAGU treatment plot during the first postfire breeding season, I assume that this second-year effect was due to immigration.

In the only other quasi-experimental study of the effects of understory burning on breeding bird abundances in Southwestern ponderosa pine forest, Horton (1987) reported a modest, and statistically insignificant, first-year reduction in junco encounters attributable to the fire treatments. These data and my own finding of first-year declines in junco encounters after all three fires suggest at least a weak aversion by the birds to recently burned ponderosa pine forest. The response may have been weak because it was a function of aversions by only a subset of the junco population (i.e., floaters) or due to patchy effects of fire on important resources, or both. Moreover, my data indicate that, although prescribed burning can effect a significant latent increase in junco numbers, replicated fire treatments will not necessarily have similar effects.

The rebound in junco numbers at SAGU coincided with a rise in herbaceous production, the vigorous sprouting of top-killed oaks, and an increased trap rate of arthropod prey. Increases in these foraging and nesting resources may have attracted unpaired males and females to the burned forest and allowed territory owners and subordinates to share space (Davies and Houston 1981; Stamps and Krishnan 1997, 1999). Regardless of whether the newcomers could reproduce via extra-pair copulations (Ewen et al. 1999), occupancy of favorable habitat should have immediate benefits in terms of food acquisition and protection from predation, while knowledge of the area and its inhabitants should increase the likelihood of territory acquisition and successful reproduction in subsequent years (Stamps and Krishnan 1999).

While encounter rates fluctuated annually at all sites, the number of territories held by adult male juncos was essentially static on all plots at SAGU throughout the study. Others have reported similar breeding densities of juncos in Arizona ponderosa pine forest (i.e., 23 Dark-eyed Junco pairs per 40 ha, Carothers et al. 1973). These numbers are consistent with territory size estimates (0.7-1.2 ha) of Eaton (1965), Moore (1972) and Sullivan (1999). Stability of these numbers in the face of fire suggests that territorial juncos at SAGU are extremely tenacious or that habitat quality was not compromised by burning such that it could support fewer territories, or both.

Strong site fidelity is pervasive in breeding passerines (Greenwood 1980), even in the face of habitat alteration caused by burning (Best 1979, Petersen and Best 1987, O'Neal et al. 1996). Juncos appear to be no exception to this veritable rule. Preemptive site occupancy by territorial males is common among breeding Yellow-eyed Juncos, and individuals are "extremely site faithful" within and among years (Sullivan 1999). Birds even remain on breeding territories year round when weather permits (Moore 1972; Horvath and Sullivan 1988; M. Olker, *pers. comm.*). Benefits of local familiarity and fidelity include enhanced predator evasion (Metzgar 1967, Ambrose 1972, Snyder et al. 1976, Renner 1988, Clarke et al. 1993) and resource exploitation (Hinde 1956, Greenwood 1980, Davies and Houston 1981, Healy and Hurly 1995, Douglas 1996, Tobias 1997) by residents versus newcomers. However, the reproductive costs of site fidelity may outweigh such benefits when territory quality is compromised by changing environmental conditions.

Martin (2001) and Moore (1972) noted fluctuations in the density of junco territories among and within years, respectively, in Arizona forests. Both pointed to the level of precipitation during the breeding season as a key determinant of territory numbers. In high-elevation forests of northern Arizona, Martin (2001) found that the number of Dark-eyed Junco territories within his study area was strongly correlated ($r = -0.72$, $P = 0.008$) with May + June precipitation over a 13-year period. Because "shifts in abundance were correlated with weather during the period of settling and nesting and not with weather in the prior year," he reasoned that such changes reflected an annual "redistribution of birds, possibly during the migratory settling period." Moore (1972) reported steady increases in territory size and concomitant attrition of territorial Yellow-eyed Juncos in montane forests of southeastern Arizona within breeding seasons and attributed these changes to displacement of males via intraspecific contests and to wholesale territory desertion. However, the juncos in Moore's (1972) study were particularly prone to nest disturbance by both humans and nest predators (i.e., jays, squirrels) because his study plots were located in heavily trafficked campgrounds and picnic areas in the Santa Catalina Mountains just north of Tucson, Arizona. Accordingly, he attributed territory desertion, in large part, to "the disruptive influence of large numbers of picnickers in the areas where territories had been established," but also hypothesized that low food levels during the arid foresummer contributed to this movement (Moore 1972).

At SAGU, juncos probably remain on or near their breeding territories for much of the year, migrating to lower elevations only during periods of severe cold and heavy snow (Moore 1972, Horvath and Sullivan 1988). During the non-breeding seasons of 1997-98 and 1998-99, snowfall was probably sufficient to cause the birds to move to lower elevations, at least from November through January (WRCC 2002). Dominant males likely (re-)established breeding territories in ponderosa pine forest in March of 1998 and 1999 (Moore 1972, *pers. obs.*). During early nesting stages in April through mid-June, cumulative precipitation differed little from 1998 to 1999 (2.3 vs. 1.6 cm, respectively), as did May + June rainfall (0.1 vs. 0.4 cm) (WRCC 2002). Therefore, from 1998 to 1999 at SAGU, there may have been little annual "redistribution" of junco territories as described by Martin (2001). From 27 October 1999 to 22 June 2000, there was *no* precipitation recorded in the Rincon Mountains (WRCC 2002). Accordingly, at least some juncos appeared to have overwintered on or near their breeding territories on my SAGU study plots (M. Olker, *pers. comm.*). Thus, it is not surprising that territory numbers were similar in 1999 and 2000.

Although site tenacity is common in birds, the population consequences of strong site attachments by individuals in the face of habitat alteration have seldom been described (Petersen and Best 1987, O'Neal et al. 1996). I estimated that Yellow-eyed Juncos can achieve $\lambda = 1$ with a 43% mean nesting success, or a daily survival rate of approximately 0.966. However, nest success of the juncos on the treatment plot was a mere 7% during the first breeding season after an autumn fire—a 77% decline relative to the first-year change observed on Control 1. By the following year, the success rate had returned to the prefire level of 48%. This variation in nesting success over three years of study (daily survival rates among years were 0.970, 0.897, 0.970) far exceeded that documented by Sullivan et al. (1988) for Yellow-eyed Juncos within a single study plot within another southeastern Arizona mountain range. In their study, nest success ranged from 30-65% over six breeding seasons, with an average of 49% (daily survival rates were 0.982, 0.979, 0.975, 0.973, 0.957, 0.951; Sullivan et al. 1988). Productivity estimates from Control 1, however, stayed within this range (daily survival among years: 0.970, 0.953, 0.958). Therefore my data suggest that fire can effect substantial temporal variation in junco productivity, with a patch of forest fluctuating between source and sink habitat (*sensu* Pulliam 1988) during the first few years postfire. Nest success on Control 2 was significantly lower than the critical 43% in both years of study (daily survival was 0.911, 0.909), further suggesting that Yellow-eyed Juncos occupy both source and sink habitat across the mountain within any given year.

Fire affects nesting success of birds largely via its influence on nest predation and food availability. The former is thought to be particularly important, as predation generally accounts for > 90% of nesting mortality in passerine birds (Martin 1995). Indeed, Sullivan (1999) noted that within her study site in the Chiricahua Mountains, Arizona, "low [Yellow-eyed Junco] fledging rates occurred in drought years when nest predation rates were high." The nest-site preferences of bird species have surely been shaped by natural selection to reduce nest predation (Li and Martin 1991, Martin 1998). Birds that continue to nest within an area after much of the preferred nesting microhabitat has disappeared may incur heavy reproductive losses from predation (Martin 2001). Therefore it is not surprising that birds breeding in recently burned areas often position their nests in patches of vegetation relatively undisturbed by fire (Aquilani et al. 2000). Yet if burned areas support only sparse remnants of preferred nesting microhabitat, predators may have to search fewer potential nest locations before finding an occupied site (Best 1979, Martin 1988, Martin and Roper 1988, Li and Martin 1991). In this way, nest placed within the unburned islands in a sea of burned vegetation may still be subject to heavy predation.

Mammals, snakes, and jays all prey on junco nests and nestlings, and the success of a junco nest largely depends on how well concealed from predators it is (Sullivan 1988, 1989). In addition, young juncos are weak flyers for the first few weeks post-fledging and seek refuge from predators beneath cover from grass and dense brush thickets near the nest (Moore 1972, Sullivan 1989, *pers. obs.*). Heavy cover from low vegetation within the vicinity of the nest may reduce the probability of predation on both nests and recently fledged young. Indeed, prior to the fall burn, juncos tended to place their nests in patches of forest with relatively high cover from grasses, ferns, or forbs

(Figure 3.03), and nests that fledged at least one young tended to have more herbaceous cover within an 11-m radius than those that were abandoned or lost to predation (Figure 3.04). Notably, the first-year reduction and subsequent flush of herbaceous production caused by the SAGU fire was accompanied by similar changes in Yellow-eyed Junco nesting success.

In addition to reducing herbaceous cover, the SAGU fire also caused a first-year decline in cover from low woody vegetation and coarse woody debris, which juncos often use to conceal nests (Table 3.03). In the absence of preferred nesting microhabitat, juncos may have attempted to nest in suboptimal locations. For example, both Kilgore (1971) and I found juncos attempting to nest in holes left by burned-out roots during the first breeding season after fire. Although they may be attractive to juncos looking for a place to tuck away a nest, these holes can be physically unstable in the first post-fire nesting season. On my site, the root-hole in which one junco built her nest collapsed shortly thereafter. The nest was filled with debris before the bird had laid her first egg. This nest was one of five abandoned prior to egg-laying on the treatment plot in 1999. Of all nests found in all plot-year combinations, those on the treatment plot during the first season postfire had the highest rate of early abandonment and placement in trees (Table 3.04). Although juncos are predominately ground-nesters, they may place their nests in trees (up to 20 m in ponderosa pine reported by Moore [1972]) when risk of predation on ground nests is high (i.e., Smith 1936).

Comparison of the growth curves in Figure 3.09 illustrates the damping effect that fire can have on junco population oscillations solely via its influence on nesting success. In the absence of fire, junco numbers are clearly subject to strong density-dependent

Table 3.04. Percent of all nests in each fate category.

	Treatment 1			Control 1			Control 2	
	Prefire	Postfire Y1	Postfire Y2	Prefire	Postfire Y1	Postfire Y2	Postfire Y1	Postfire Y2
Nest fate	(n = 14)	(15)	(22)	(16)	(19)	(18)	(19)	(16)
Abandoned[a]	0	33	9	0	0	0	10	0
Fledged[b]	79	20	59	56	42	33	27	19
Failed	21	40	27	25	58	45	53	75
Unknown[c]	0	7	4	19	0	22	10	6

[a] Nest deserted before eggs laid

[b] ≥1 young junco fledged from nest

[c] I was unable to monitor nest to completion

influences of predation, starvation, and disease, for which neither model accounts. Certainly the unbounded growth illustrated in Figure 3.09a (population size approaches 2000 in year 100) is not to be observed in nature. Moreover, none of the models make any allowance for movement. I do not expect these growth functions to emulate real-world population dynamics. Instead they simply illustrate how strongly fire may impinge as a density-independent influence on populations of Yellow-eyed Juncos. In addition, Figure 3.05b suggests that populations of these birds can persist in the face of chronic fire disturbance without augmentation via immigration, which is not surprising given that birds of Southwestern ponderosa pine forests have long been subject to such a regime (Finch et al. 1997). It is likewise not surprising that the influence of fire on junco populations appears to wane (i.e., relative to that of density-dependent factors) with decreased fire frequency. Figure 3.09c emphasizes how important relatively long fire-free intervals can be in this regard. Although knowledge of the average frequency of fires in this forest type may provide insight into the role of fire in the dynamics of populations over a given time, variation in fire intervals about this mean may shed even more light on the cumulative influence of burning on wildlife numbers.

My estimates of the population consequences of understory burning for Yellow-eyed Juncos assume that the first-year survival of birds fledged during the first two breeding seasons postfire was comparable to that in unburned forest. If, in either year, fledgling or juvenile survival was compromised by burning, I likely underestimated the nesting success necessary for reproduction to balance adult mortality during that interval. Predation is the primary cause of death in nestling and recently fledged juncos, whereas starvation accounts for most mortality in recently independent young, or juveniles

(Sullivan 1989). Again, the first-year reduction of cover from low vegetation caused by the SAGU fire may have left young juncos more vulnerable to predation during the first postfire breeding season. The second-year flush in understory production may have had the opposite effect, however, by providing increased protective cover for recently fledged birds. Those who escape predation during this early post-fledging period are generally evicted from their natal territories by parents at about 4 weeks. Recently independent birds tend to join local juvenile flocks and remain in the vicinity of natal territories until late August, when they move downslope for winter (Sullivan 1999). As juveniles, Yellow-eyed Juncos are inefficient foragers, spending over 90% of the daylight hours foraging while still losing weight, and are thus prone to starvation (Weathers and Sullivan 1989b). If fire's effects on prey levels exacerbated the problem of food acquisition for recently independent young, then burning could have effected lower survival of juveniles who remained within the burned area upon independence. However, I found no evidence that food availability was further compromised by burning based on trap rates and prey capture rates of adult birds in either year (Figures 3.07, 3.08). In fact, food availability may have even increased in year 2 due to fire (Figures 3.07, 3.08) . If juvenile survival was compromised in year 1 by higher predation and but enhanced in year 2 by reduced starvation, I likely underestimated the negative first-year and positive second-year population consequences for Yellow-eyed Juncos based on fire's effects on nesting success.

Because these models are based on estimates of the effects of a single fire on one group of Yellow-eyed Juncos in the Rincon Mountains of Arizona, they have little predictive power. Their purpose was entirely exploratory, enabling me to assess the potential long-term influence fire on junco populations after assuming that repeated fires would affect reproductive success in a manner similar to that of the SAGU fire. However, the effects of nominally similar fire treatments may vary considerably in their effects on resources important to juncos and other forest animals (see Chapter 2). The SAGU fire effected significant changes in nesting microhabitat associated with successful junco nests. The availability of arthropod prey was affected little, or possibly enhanced in year 2, by this fire. Changes in abundance and productivity of juncos attributable to the SAGU burn mirrored these changes in key resources. The effects of burning on junco nesting microhabitat were patchier or weaker (or both) at WACA and GRCA, as were their numeric responses as indexed by encounter rates. In addition, these fires cause activity-densities of junco prey to fall significantly in year 1 at GRCA and in year 2 on both sites. A second-year reduction in prey availability may have compromised juvenile survival, offsetting some of the benefits of the increased herbaceous production due to burning. In this light, the short-term effects of these fires on junco populations at WACA and GRCA may have been considerably weaker than those evinced by the SAGU burn.

CONCLUSION

Understory fires may have a marked, short-term effect on habitat quality for Yellow-eyed Juncos via its effects on low forest vegetation, which provides cover as well as nesting and foraging substrates for these birds. Fire at SAGU caused nesting success to fall and then rise in the first two breeding seasons postfire, presumably due to changes in availability of preferred nesting microhabitat. Despite changes in habitat quality, territory density was not affected by burning, although the encounter rate of juncos fell and rose in concert with cover from low vegetation and nesting success. The availability of arthropod prey may have increased in year 2 with the flush in understory production.

I developed models in which demography was closely linked to disturbance over a 100-year period. My simulations show how a population of Yellow-eyed Juncos can persist in the face of disturbance from fire on the order of every decade with variance of population density tightly bounded by the frequent fires. According to Turchin (1995), "it is generally accepted that population regulation cannot occur in the absence of density dependence." While this may be true, strictly speaking, my data suggest that the chronic disturbance of forest fire alone can set bounds to populations of these birds. Density-dependent factors should increasingly impinge on populations, however, as fire frequency departs from the historic precedent in Southwestern ponderosa pine forest.

My models of population dynamics assume that the effects of fire on Yellow-eyed Junco productivity are typical. If no two fires are alike, however, my estimates of effects may not be typical of replicated treatments. Only by identifying the mechanisms behind observed demographic responses of juncos to understory burning, may we fully understand and reliably predict the short-term effects of individual fires and the long-term influence of chronic disturbance, or lack thereof, on junco populations (Marzluff et al. 2000). If the change in cover from low vegetation is the primary driver of the effects of fire on junco populations, and different fire causes different herbaceous response, fire's influence on nesting success may vary widely among treatments. As Aquiliani et al. (2000) concluded, "given the complex nature of fire effects on ecological communities, we believe the best path toward understanding these effects will be a progressive accumulation of knowledge from case studies across a range of sites." Every prescribed fire should be viewed as a means to this end.

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