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AVIFAUNAL RESPONSES TO FIRE IN SOUTHWESTERN MONTANE FORESTS ALONG A BURN SEVERITY GRADIENT

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Abstract. The effects of burn severity on avian communities are poorly understood, yet this information is crucial to fire management programs. To quantify avian response patterns along a burn severity gradient, we sampled 49 random plots (2001–2002) at the 17 351-ha Cerro Grande Fire (2000) in New Mexico, USA. Additionally, pre-fire avian surveys (1986–1988, 1990) created a unique opportunity to quantify avifaunal changes in 13 pre-fire transects (resampled in 2002) and to compare two designs for analyzing the effects of unplanned disturbances: after-only analysis and before–after comparisons. Distance analysis was used to calculate densities. We analyzed after-only densities for 21 species using gradient analysis, which detected a broad range of responses to increasing burn severity: (I) large significant declines, (II) weak, but significant declines, (III) no significant density changes, (IV) peak densities in low- or moderate-severity patches, (V) weak, but significant increases, and (VI) large significant increases. Overall, 71% of the species included in the after-only gradient analysis exhibited either positive or neutral density responses to fire effects across all or portions of the severity gradient (responses III–VI). We used pre/post pairs analysis to quantify density changes for 15 species using before–after comparisons; spatiotemporal variation in densities was large and confounded fire effects for most species. Only four species demonstrated significant effects of burn severity, and their densities were all higher in burned compared to unburned forests. Pre- and post-fire community similarity was high except in high-severity areas. Species richness was similar pre- and post-fire across all burn severities. Thus, ecosystem restoration programs based on the assumption that recent severe fires in Southwestern ponderosa pine forests have overriding negative ecological effects are not supported by our study of post-fire avian communities. This study illustrates the importance of quantifying burn severity and controlling confounding sources of spatiotemporal variation in studies of fire effects. After-only gradient analysis can be an efficient tool for quantifying fire effects. This analysis can also augment historical data sets that have small samples sizes coupled with high non-process variation, which limits the power of before–after comparisons.

Key words: after-only, before–after comparisons; bird communities; breeding densities; Cerro Grande, New Mexico, USA; distance sampling; fire effects; gradient analysis; historical data.

Introduction

In May of 2000, the Cerro Grande fire in New Mexico, USA, made national headlines (e.g., Janofsky 2000) when it burned over 17 000 ha, threatened Los Alamos National Laboratory, and destroyed 235 homes (information *available online*).[4] Beginning as a prescribed fire at Bandelier National Monument, the Cerro Grande fire was a harbinger of a particularly severe fire season; 3.4 million ha burned in 2000, exceeding the 10-year average (1992–2002) by >1.5 million ha (information *available online*).[5] The severity of the 2000 and 2002 fire seasons (collectively 6.8 million ha burned) has been used as evidence to support the assertion that decades of fire suppression, logging, and grazing practices have led to increased size and severity of wildland fires and prompted major fuel reduction initiatives including the National Fire Plan and Healthy Forest Restoration Act (Graham et al. 2004, Schoennagel et al. 2004). Primary targets of such programs are montane forests that historically burned frequently, but with low severity (Keane et al. 2002, Graham et al. 2004). In particular, Southwestern ponderosa pine forests (like those that burned in the Cerro Grande fire) have been characterized as unnaturally dense due to fire exclusion since Euro-American settlement (Moore et al. 1999, Allen et al. 2002). Consequently, open, park-like forests maintained by frequent surface fires have been replaced in many areas by dense stands capable of supporting crown fires (Allen et al. 2002, Schoennagel et al. 2004). A primary goal of many ecosystem restoration pro-

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grams is to reduce tree densities, thereby reducing the risk of severe wildland fire and allowing the reintroduction of prescribed understory fire (Covington et al. 1997).

Recent research, however, has begun to challenge the generality of the "Southwest paradigm," and an alternative view is beginning to emerge of more variable historical fire regimes, which included crown fire in low-elevation montane forests (Baker and Ehle 2001, Schoennagel et al. 2004). Yet, this variation is often ignored in ecosystem restoration programs (Schoennagel et al. 2004). There is historical precedence for severe fires in montane systems (Pierce et al. 2004), consequently, the relatively limited time frame used as a reference for restoration of historical fire regimes may not adequately reflect current climatic conditions (Tiedemann et al. 2000, Wagner et al. 2000, Pierce et al. 2004). Thus, the relative importance of climate and fuels in dictating recent fire activity is uncertain (Veblen et al. 2000).

A corollary of the Southwest paradigm is the assumption that both fire exclusion and the greater severity of recent fires have predominantly negative ecological effects. This assumption, although largely untested, is a fundamental justification for ecosystem restoration programs (e.g., Covington et al. 1997, Fulé et al. 1997, Moore et al. 1999, Keane et al. 2002, Graham et al. 2004). Because fire ecology has focused on vegetation structure and dynamics, our current understanding of fire effects on avifauna in western forests is quite limited. Recent reviews found a limited number of studies comparing burned and unburned forests, most of which sampled single burns and lacked suitable replication (Hutto 1995, Finch et al. 1997, Kotliar et al. 2002, Saab and Powell 2005); in the Rocky Mountains, many of the studies sampled burns <500 ha and burn severity was not quantified (Kotliar et al. 2002, Saab et al. 2005). Thus, the general avifaunal response patterns suggested by such qualitative reviews are preliminary and oversimplified because burn severity has typically been treated as a binomial variable.

Wildfires are unplanned events; consequently, pre-fire data rarely exist and fire effects are typically evaluated using an impact–reference approach (Wiens and Parker 1995; also called "after-only," Osenberg et al. 1994) in which burned sites are compared to unburned reference areas. We used this approach by conducting post-fire surveys at Cerro Grande. In addition, the existence of pre-fire data on avian populations and forest types from the area of the Cerro Grande fire created a unique opportunity to evaluate post-fire changes in avian communities by resampling the pre-fire study area. The comparison of before and after data in burned and unburned sites approximates a Before After Control Impact (BACI) design for planned impacts (Stewart-Oaten et al. 1986, Wiens and Parker 1995). Before–after comparisons have advantages over impact–reference designs because temporal and pre-impact spatial variation in populations can be quantified, whereas randomly located samples using the impact–reference approach avoids pseudoreplication problems inherent in before–after comparisons (Wiens and Parker 1995).

Our primary objective was to characterize avifaunal responses to fire by examining how densities changed along a burn severity gradient and by comparing community composition pre- and post-fire. We also characterized the spectrum of observed avian response patterns, which we present as a comparative framework for studies on the effects of burn severity. Our second objective was to compare the advantages and disadvantages of after-only and before–after designs in characterizing avifaunal response to fire. We include a recent study of fire effects using the before–after design for a mixed-severity regime in the northern Rocky Mountains (Smucker et al. 2005) as a part of this evaluation. We discuss the implications of our results for fire research and management practices.

METHODS

Study area

The study area is in the Jemez Mountains and adjacent Pajarito Plateau in north-central New Mexico, ranging in elevation from 1645 m to 3200 m (Fig. 1). The Jemez Mountains were formed by volcanic activity and are dissected by steep-walled canyons (Allen 1989). Mean annual precipitation is 45 cm. Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*) are the most prevalent forest cover types found over the study area. Engelmann spruce–subalpine fir (*Picea engelmanni–A. lasiocarpa*), pinyon–juniper (*Pinus edulis–Juniperus* spp.), juniper–grassland, and riparian habitats are also present (Siders and Kennedy 1996).

Pre-fire sampling

Pre-fire sampling of montane forests (1901–2493 m elevation) included areas that subsequently burned, as well as nearby areas that did not burn and served as reference areas. In 1986–1988 and 1990, Kennedy conducted avian surveys and qualitatively classified the vegetation in canyon bottoms and adjacent upland forests in 23 transects on the Los Alamos National Laboratory, Santa Fe National Forest, Bandelier National Monument, San Ildefonso Pueblo, and Santa Clara Pueblo (Fig. 1, and Fig. A1 in Appendix A). The nonrandom sampling design was developed to estimate prey availability within the home range of radio-tagged accipiters nesting in the area (Morrison and Kennedy 1989, Kennedy 1991). Sampling points were located at 200-m intervals along these transects; the number of points surveyed in these transects varied from 12 to 48. In all four years, one observer surveyed birds using 50-m radius point counts of six-minute duration. In 1988 and 1990, each detection was assigned to a distance category (0–25 m, 26–50 m). Sampling periods varied across years; in 1986–1988 there were three sampling periods (May/June, July, Aug/Sept), whereas in 1990 sampling

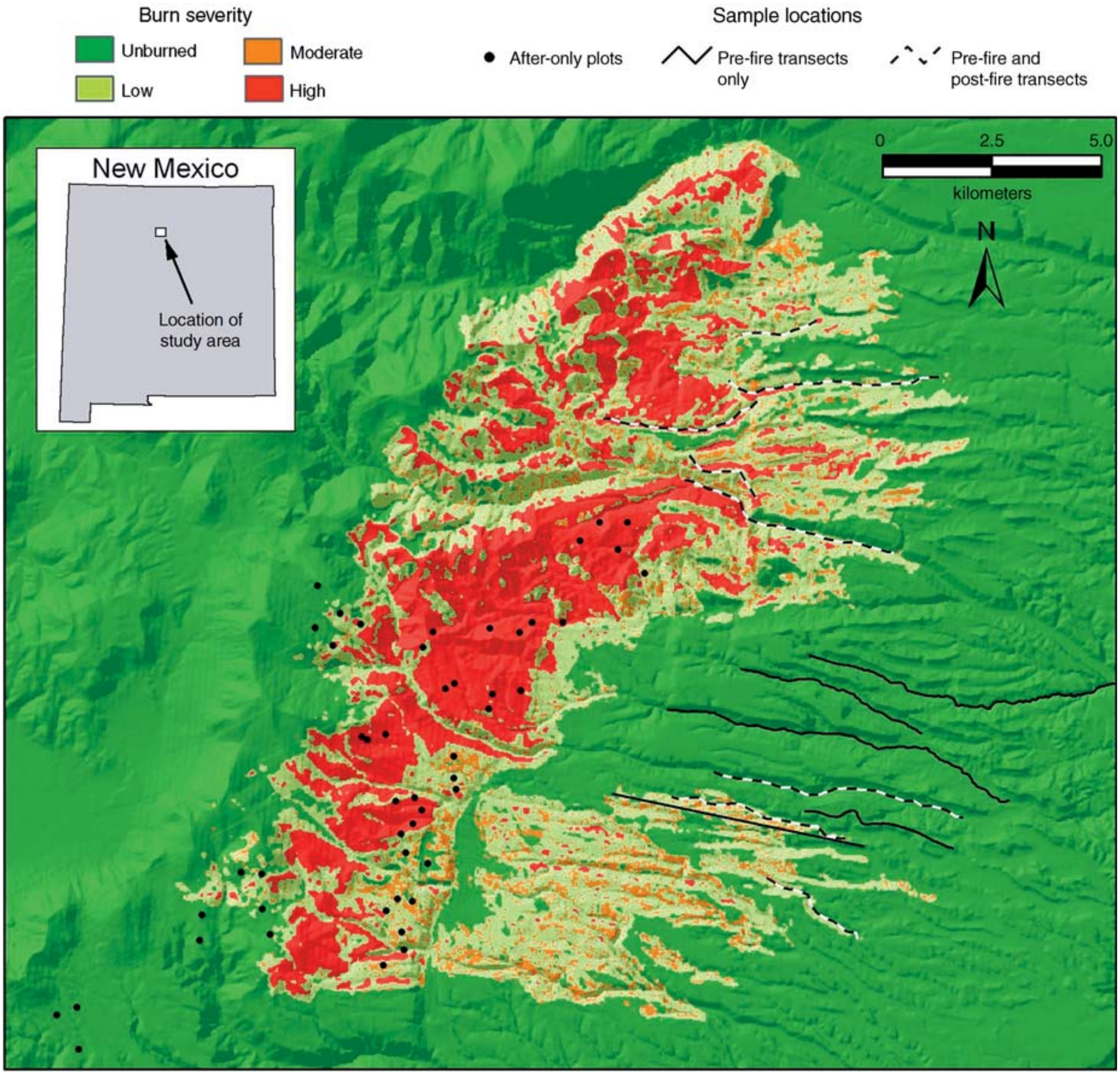

FIG. 1. Sampling locations in relation to the burn-severity map based on the Δ Normalized Burn Ratio. Only plots and transects <1 km from the burn perimeter are shown (see Fig. A1 in Appendix A for unburned transects >1 km from burn perimeter).

occurred in July. Cover type at each point was classified as canyon bottom [(1) ephemeral stream with a ponderosa pine overstory, (2) ephemeral stream with a mixed-conifer overstory, or (3) perennial stream with a mixed-coniferous and deciduous overstory] or upland forest [(1) ponderosa pine or (2) mixed coniferous].

Post-fire sampling

Hand-drawn maps of the pre-fire transects were digitized from USGS topographic maps at 1:24 000. In 2001, the starting point of each transect was located and marked using a GPS. All subsequent post-fire sample points were spaced ~200 m from the initial point. Due to access restrictions at Los Alamos National Laboratory, San Ildefonso Pueblo, and Santa Clara Pueblo, four of the 23 pre-fire transects were not resampled. Three unburned transects at considerable distances from the Cerro Grande Fire and three transects that had been altered by anthropogenic activities were also not resampled. The remaining 13 transects were surveyed by two observers in June 2002 (hereafter "before–after"; Fig. 1; Appendix A). Each point was surveyed for six minutes. To enhance the precision of the density estimates using distance sampling, we expanded the number of distance categories sampled from two to five: 0–10 m, 11–25 m, 26–50 m, 51–75 m, 76–100 m (Buckland et al. 2001).

In June 2001 and 2002, bird surveys were conducted at 49 plots at Cerro Grande (hereafter "after-only"). Plots were randomly located on burned and nearby unburned areas within Santa Fe National Forest and Bandelier National Monument (Fig. 1, Fig. A1). Plot elevations ranged from 2270 m to 2970 m. Each 200 m × 500 m plot contained four overlapping 100-m radius survey points, with centers spaced 100 m apart. All plots were visited twice each year; during the first visit, the first and third points were surveyed by one observer, during the second visit the second and fourth points were surveyed by a second observer (four observers total over two years). Each after-only point was surveyed for 10 minutes and used the same distance categories as the post-fire transects. Cover type (upland only) was classified as ponderosa or mixed-coniferous.

Canopy and understory burn severity was ranked in 15-m radius plots centered at each before–after (2002) and after-only (2001) survey point (canopy ranks, 0 = no crown scorch, 1 = some trees partial crown scorch, 1.5 = all trees partial scorch, 2 = all trees complete scorch, 2.5 = all needles consumed, 3 = all needles and small branches consumed; understory ranks, 0 = no burn, 1 = needles scorched, 2 = needles consumed, 3 = needles and small branches consumed). Intermediate values were assigned if conditions included characteristics of adjacent ranks. Field ranks were used to categorize burn severity into four levels: unburned (canopy 0, understory 0), low (canopy 0–1.50, understory 1–1.75), moderate (canopy 1.51–2.50, understory >1.75), and high (canopy >2.50, understory >1.75). Burn severity levels were used for categorical summaries and analysis, whereas burn severity ranks were used in the analysis of a continuous gradient.

To quantify differences in burn severity among the before–after and after-only sampling areas and to compare burn severity across spatial scales, we used a burn severity map (Fig. 1) developed using the Normalized Burn Ratio (ΔNBR; Kotliar et al. 2003, Key and Benson 2005). The average ΔNBR score was quantified within 90-m radius plots centered on survey points. Burn severity ranks for 15-m plots and ΔNBR scores for 90-m buffers were highly correlated (Pearson correlation = 0.912). To quantify burn severity at larger scales, we classified ΔNBR scores into four severity classes using a *K* means clustering algorithm called ISODATA (using ERDAS Imagine; Leica Geosystems 2004); canopy burn severity ranks were used to classify clusters created by the ISODATA algorithm (N. B. Kotliar, *unpublished data*). The proportion in each NBR severity class within 500-m buffers surrounding a center line running the length of each transect or plot was used to compare burn severity among sampling locations.

Statistical analysis

Density estimation by burn severity and cover type.—Sample units varied by study design. For after-only densities, plots were used as sample units and canopy burn severity rank was averaged by plot. Before–after densities were calculated by transect, stratified by burn severity level and cover type. We classified each point within transects by burn severity level. Because fire behavior varied within transects, more than one burn severity level was represented in each burned transect (Fig. 1, Table A1 in Appendix A). To eliminate undue emphasis on very small samples when estimating densities, a minimum of four points per severity level for each transect was established. Isolated points within transects were switched to the burn severity level of adjacent points; all nine (3%) points that switched levels fell along the breakpoint between levels.

We used distance analysis to estimate densities while controlling for variation in detectability among species, cover types, and observers (Buckland et al. 2001). In studies of fire effects, it is critical to test the assumption of constant detectability because removal of the forest canopy may increase the probability of detecting birds and potentially inflate abundance estimates in unadjusted counts. Likewise, in before–after comparisons, it is necessary to control for pre- and post-perturbation observer differences (Wiens and Parker 1995).

We used all visual and aural observations of adult birds. Birds designated as family groups were counted as a single detection, where distance was estimated to the center of the group, and birds detected as flocks or flying over the canopy were eliminated from analysis (Buckland et al. 2001). To increase the number of species with adequate sample sizes (>40; Buckland et al. 2001) for calculating detection probabilities, we augmented the Cerro Grande data set with detections from 40 plots in a companion study at the 2000 Pumpkin fire in Arizona (see Appendix B for details and number of detections). Density estimates, log-normal confidence intervals, and detection probabilities were obtained for pre- and post-fire data using program DISTANCE, version 4.0 (Thomas et al. 2002). Detection probabilities were generated for pre-fire and post-fire data separately (see Appendix B for details on calculation of detection probabilities). For all detection probabilities, comparisons of Akaike's Information Criterion corrected for small sample sizes (AIC_c), chi-square goodness-of-fit statistics, and visual inspections of probability density and detection probability plots were used to select the most parsimonious model and assess overall model fit (Appendix B; Buckland et al. 2001, Buckland and Anderson 2002). Because the lowest AIC_c values were obtained with the half-normal cosine model, this model was used to estimate densities.

We conducted preliminary statistical analyses on the pre-fire data (three-way ANOVA, PROC GLM) to determine if densities could be pooled over covariates that might cause significant heterogeneity in the data (sampling period, year, and cover type). We applied pre-fire detection probabilities to the full pre-fire data set (23 transects) to test the null hypothesis that mean densities for each covariate level were equal; we used a significance level of $P = 0.05$ for this analysis. Four transects with pre-fire sampling solely in August/September were dropped because densities differed significantly from the other two sampling periods and we lacked a corresponding sampling period post-fire. Thus, only nine transects could be used to calculate before–after densities (Appendix A). Because seven of the remaining transects were sampled only one year pre-fire and two were sampled two years pre-fire, we pooled samples across years for all species except Steller's Jays (see Appendix C for scientific names) and Western Bluebirds, which had significant year effects. Finally, we tested for differences in densities among cover types for each species and pooled cover types within transects if densities were not significantly different. We performed pairwise multiple comparisons (Fisher's least significant difference [LSD]; PROC LSD) to determine if densities could be calculated for broader cover type groups.

Statistical comparison of densities by burn severity.—There are several techniques to analyze the effects of perturbations using after-only and before–after data sets, depending on the study design and objectives (Wiens and Parker 1995). We used gradient analysis for the after-only data, which provides greater power when time series data are not available (Wiens and Parker 1995, Day et al. 1997). For the before–after data, we used the pre/post pairs analysis to quantify and control potential sources of temporal and spatial variation, which can confound or obscure differential responses to burn severity (Wiens and Parker 1995, Murphy et al. 1997). Densities were log transformed prior to analyses.

For the gradient analysis, we tested for the effects of burn severity on avian densities by treating mean burn severity rank per plot as a continuous variable (values ranged from 0 to 3). We also tested for the effects of annual variation, cover type (upland ponderosa pine or mixed coniferous), and all two-way interactions on transformed densities using a general linear model (PROC GLM; Appendix D) with repeated measures. A quadratic term, $(\text{burn severity})^2$, was included in the model to test for threshold effects and other nonlinear response patterns. The general form of the model for the gradient analysis was

$$\begin{aligned}\ln(\text{density}) = {} & \beta_0 + \beta_1(\text{burn severity}) + \beta_2(\text{burn severity})^2 \\ & + \beta_3(\text{year}) + \beta_4(\text{cover type}) \\ & + \beta_5(\text{burn severity} \times \text{year}) \\ & + \beta_6(\text{burn severity} \times \text{cover type}) \\ & + \beta_7(\text{year} \times \text{cover type}). \qquad (1)\end{aligned}$$

For the pre/post pairs analysis, we evaluated differences in densities by burn severity level while controlling for cover type variation using a two-way analysis of variance (ANOVA) with fixed effects (Type III sums-of-squares F test; PROC MIXED; Appendix E). Burn severity was treated as a categorical variable because of sample size limitations. For each species, we used differences in densities among pre-post pairs (i.e., Eq. 1 in Murphy et al. 1997) at each burn severity level. The general form of the model for the pre/post pairs analysis was

$$\begin{aligned}\ln(\text{density}_{\text{post-fire}}) - \ln(\text{density}_{\text{pre-fire}}) & \\ = \beta_0 + \beta_1(\text{burn severity}) + \beta_2(\text{cover type}) & \\ + \beta_3(\text{burn severity} \times \text{cover type}). & \qquad (2)\end{aligned}$$

To compare each level of burn severity, we performed post hoc, pairwise multiple comparisons tests (Fisher's LSD) for species with significant main effects. This allowed us to examine the sources of variation in more detail. All statistical tests were conducted using SAS 8.02 (SAS Institute 2001) and SYSTAT 10 (SPSS 2002). The significance level of all tests of burn severity main effects and interactions were set a priori at $P = 0.1$ to better balance the probabilities of committing Type I and Type II error. Burn severity was retained in the final models, while all other covariates were dropped when $P \geq 0.10$.

Community patterns.—To evaluate the assumption that recent severe fires like Cerro Grande have negative effects on avian communities, we compared pre- and post-fire species richness and community similarity based on the before–after data. To include all species in this analysis, we used frequency of occurrence (i.e., percentage of points occupied) for all 13 transects (Appendix F). Because richness is strongly dependent on sample size, which varied among burn severity levels, we restricted comparisons within levels. To standardize sampling efforts, we used only one pre- and one post-fire visit for each point, and truncated all samples at 50 m. Pre- and post-fire community similarity was evaluated by comparing the percentage of species occurring: (1) both pre- and post-fire, (2) pre-fire only, and (3) post-fire only.

RESULTS

Post-fire density patterns across a burn severity gradient

Collectively, the 21 species analyzed using gradient analysis represent a continuum of positive and negative responses across the burn severity gradient (Table 1). We classified these into six potential response patterns based on parameter estimates of slopes from the gradient analysis (Table 2, Fig. 2). In both years, densities of Cordilleran Flycatchers, Warbling Vireos, Mountain Chickadees, Hermit Thrushes, Yellow-rumped Warblers, and Dark-eyed Juncos decreased significantly with increasing burn severity (Tables 1, 2, and Fig. 2a). In 2002 only, American Robins and Chipping Sparrows demonstrated smaller, but significant, decreases in density with increasing burn severity (Tables 1, 2, and Fig. 2b). Mourning Doves, Northern Flickers, White-breasted Nuthatches, American Robins (2001), Western Tanagers, and Virginia's Warblers

TABLE 1. Density (means, with SE in parentheses) by burn severity level for after-only data the first year (2001) and the second year (2002) post-fire at the Cerro Grande Fire, New Mexico, USA.

	Density (no. birds/ha)							
	2001				2002			
Species†	Unburned [$n = 7$]	Low [$n = 12$]	Moderate [$n = 13$]	High [$n = 17$]	Unburned [$n = 7$]	Low [$n = 12$]	Moderate [$n = 13$]	High [$n = 17$]
Mourning Dove	0.00	0.14 (0.10)	0.00	0.25 (0.12)	1.23 (0.59)	0.57 (0.22)	0.93 (0.33)	1.67 (0.41)
Broad-tailed Hummingbird	0.27 (0.17)	0.55 (0.14)	0.58 (0.20)	0.83 (0.19)	0.94 (0.29)	1.25 (0.39)	1.37 (0.38)	2.04 (0.27)
Hairy Woodpecker	0.35 (0.24)	0.61 (0.29)	1.07 (0.23)	1.10 (0.27)	1.52 (0.45)	1.70 (0.39)	2.01 (0.38)	2.26 (0.50)
Northern Flicker	0.85 (0.24)	0.00	0.20 (0.09)	0.27 (0.10)	0.47 (0.19)	0.44 (0.12)	0.66 (0.17)	0.62 (0.12)
Western Wood-Pewee	0.00	0.07 (0.07)	0.34 (0.16)	2.03 (0.37)	0.00	0.66 (0.29)	0.95 (0.38)	1.98 (0.40)
Cordilleran Flycatcher	2.44 (0.63)	0.85 (0.25)	0.17 (0.12)	0.40 (0.24)	2.11 (0.68)	1.14 (0.42)	0.26 (0.14)	0.27 (0.12)
Warbling Vireo	3.82 (0.79)	2.65 (0.73)	1.57 (0.52)	0.07 (0.07)	7.64 (1.47)	3.61 (0.77)	2.25 (0.83)	1.20 (0.56)
Steller's Jay	0.99 (0.69)	1.66 (0.22)	0.99 (0.28)	0.53 (0.15)	0.43 (0.20)	1.66 (0.41)	1.53 (0.52)	0.53 (0.19)
Mountain Chickadee	2.81 (0.76)	0.94 (0.30)	0.58 (0.27)	0.00	2.01 (0.88)	1.64 (0.38)	1.22 (0.42)	0.00
White-breasted Nuthatch	0.32 (0.21)	0.19 (0.19)	0.61 (0.21)	0.40 (0.22)	1.14 (0.00)	0.85 (0.32)	0.79 (0.30)	1.07 (0.30)
House Wren	0.31 (0.16)	0.23 (0.14)	0.17 (0.10)	0.65 (0.21)	0.71 (0.31)	0.50 (0.24)	0.34 (0.22)	1.19 (0.35)
Western Bluebird	0.00	0.00	0.00	1.08 (0.25)	0.12 (0.12)	0.21 (0.21)	0.26 (0.15)	2.41 (0.32)
Hermit Thrush	1.73 (0.26)	0.82 (0.14)	0.43 (0.19)	0.08 (0.03)	1.17 (0.28)	1.07 (0.21)	0.73 (0.19)	0.04 (0.04)
American Robin	0.91 (0.40)	0.68 (0.28)	1.26 (0.30)	0.59 (0.25)	1.30 (0.65)	0.61 (0.26)	0.49 (0.22)	0.21 (0.12)
Virginia's Warbler	0.00	0.27 (0.27)	0.12 (0.12)	0.00	0.91 (0.32)	2.52 (0.69)	2.08 (0.71)	0.28 (0.15)
Yellow-rumped Warbler	5.17 (1.22)	4.70 (1.11)	3.12 (0.67)	0.68 (0.31)	5.37 (0.75)	5.31 (0.90)	3.78 (0.67)	0.94 (0.30)
Western Tanager	0.56 (0.21)	0.29 (0.15)	0.74 (0.23)	0.41 (0.10)	0.81 (0.22)	1.27 (0.25)	1.27 (0.15)	0.67 (0.19)
Spotted Towhee	0.24 (0.24)	0.70 (0.48)	0.77 (0.65)	0.00	0.00	0.84 (0.56)	3.61 (1.31)	0.69 (0.35)
Chipping Sparrow	1.04 (0.70)	0.15 (0.15)	0.07 (0.07)	0.11 (0.07)	1.04 (0.37)	0.76 (0.19)	0.84 (0.30)	0.32 (0.15)
Dark-eyed Junco	2.81 (0.76)	2.03 (0.47)	1.08 (0.35)	0.83 (0.26)	2.41 (0.53)	3.04 (0.55)	1.94 (0.49)	0.88 (0.36)
Black-headed Grosbeak	0.00	0.50 (0.20)	0.53 (0.18)	0.30 (0.13)	0.49 (0.26)	1.15 (0.34)	0.53 (0.25)	0.30 (0.15)

Notes: Plot densities are stratified by burn severity and pooled over cover type.

† See Appendix C for scientific names and list of species.

(2001) had similar, but often variable, densities across the burn severity gradient (Tables 1, 2, and Fig. 2c). Many species exhibited peak densities in low- or moderate-severity patches, as indicated by a significant quadratic term, including Steller's Jays, Virginia's Warblers (2002), Spotted Towhees (2002), and Black-headed Grosbeaks (Tables 1, 2, and Fig. 2d). Broad-tailed Hummingbirds (2002), Hairy Woodpeckers (2001), and House Wrens (2001) increased moderately with increasing burn severity (Tables 1, 2, and Fig. 2e). Western Wood-Pewees and Western Bluebirds were uncommon in all but the highest burn severity level (Tables 1, 2, and Fig. 2f). In total, 18 species exhibited significant burn severity or (burn severity)^2 effects (Table 2; Appendix D).

The gradient analysis also detected significant temporal variation (i.e., year main effects or interactions) for 13 species (Table 2; Appendix D). In several cases, the overall direction of changes was the same across years, but the magnitude was different. House Wrens shifted from weak to strong positive responses (Table 2, and Fig. 2e, f). Broad-tailed Hummingbirds exhibited more pronounced increases in 2002 compared to 2001, whereas Hairy Woodpeckers showed the reverse pattern (Tables 1, 2). Several species exhibited significant patterns for one year only. Virginia's Warblers and

TABLE 2. Parameter estimates from the repeated-measures GLM for after-only data at the Cerro Grande fire, New Mexico.

Species†	Significant burn severity effects (P)	Year	Burn severity	(Burn severity)^2	r^2	Response class#
Cordilleran Flycatcher‡	<0.01	pooled	−0.23	NS	0.21	I
Warbling Vireo‡	<0.001	2001	−0.51	NS	0.5	I
		2002	−0.52	NS	0.36	I
Mountain Chickadee	<0.001	pooled	−0.34	NS	0.37	I
Hermit Thrush	<0.001	pooled	−0.28	NS	0.56	I
Yellow-rumped Warbler	<0.001	pooled	−0.49	NS	0.39	I
Dark-eyed Junco	<0.001	pooled	−0.29	NS	0.23	I
Chipping Sparrow	<0.05	2001	−0.07	NS	0.03	III
		2002	−0.12	NS	0.05	II
American Robin	<0.1	2001	−0.04	NS	−0.01	III
		2002	−0.13	NS	0.08	II
Steller's Jay	<0.05	pooled	0.44	−0.17	0.10	IV
Virginia's Warbler	<0.05	2001	0.12	−0.04	−0.01	III
		2002	0.60	−0.27	0.25	IV
Spotted Towhee	NS	2001	0.07	−0.05	0.01	III
		2002	0.92	−0.27	0.06	IV
Black-headed Grosbeak‡	<0.05	pooled	0.25	−0.10	0.04	IV
Mourning Dove	<0.1	2001	0.05	NS	0.04	III
		2002	0.11	NS	0.02	III
Northern Flicker	NS	2001	−0.06	NS	0.02	III
		2002	0.04	NS	−0.00	III
White-breasted Nuthatch‡	NS	2001	0.05	NS	−0.00	III
		2002	−0.004	NS	−0.02	III
Western Tanager	NS	2001	−0.002	NS	−0.02	III
		2002	−0.09	NS	0.04	III
Broad-tailed Hummingbird	<0.01	2001	0.08	NS	0.02	III
		2002	0.19	NS	0.14	V
Hairy Woodpecker	<0.05	2001	0.15	NS	0.10	V
		2002	0.10	NS	0.02	III
House Wren‡§	<0.001	2001	0.14	NS	0.10	V
		2002	0.26	NS	0.24	VI
Western Wood-Pewee	<0.001	pooled	0.32	NS	0.34	VI
Western Bluebird	<0.001	2001	0.22	NS	0.32	VI
		2002	0.42	NS	0.58	VI

Notes: Estimates and adjusted r^2 are provided by year if there was a significant ($P < 0.1$) year or year × burn severity effect; otherwise, estimates are pooled across years. Only significant ($P < 0.1$) terms for (burn severity)^2 are provided; NS denotes not significant. For species with a nonsignificant ($P > 0.1$) quadratic term, burn severity represents the slope. For species with a significant ($P < 0.1$) term for (burn severity)^2, negative quadratic terms indicate a concave downward curve.

† See Appendix C for scientific names and list of species.

‡ Significant ($P < 0.1$) cover type effects in overall model.

§ Mixed-coniferous cover type only.

Response classes were based on slopes and significant quadratic terms. Response class I, slope ≤ -0.2; response class II, $-0.2 <$ slope < -0.1; response class III, slopes not significantly different from 0; response class IV, significant quadratic term; response class V, $0.1 <$ slope < 0.2; response class VI, slope ≥ 0.2.

Spotted Towhees exhibited significant density peaks in low/moderate severity in 2002 only (Table 2). Chipping Sparrows and American Robins shifted from no significant trends in 2001 to a weak negative response in 2002 (Table 2).

Spatial variation, as indicated by significant cover type main effects or interactions, was exhibited by six species (Table 2; Appendix D). For example, Cordilleran Flycatchers and Warbling Vireos exhibited more pronounced declines in upland mixed-coniferous stands than in upland ponderosa pine stands. Significant increasing slopes for House Wrens were demonstrated for upland mixed-coniferous stands, but not ponderosa pine stands.

Pre- and post-fire changes in density

The pre/post pairs design allowed us to analyze density patterns for 15 species. Only four species exhibited significant burn severity effects based on this analysis (Table 3; Appendix E). Mourning Doves had significantly higher densities across all burn severities compared to unburned forest, reflecting significant increases from pre-fire densities ($F_{3,17} = 2.64$, $P = 0.083$; Table 3). American Robins were highly variable pre-fire, but nevertheless exhibited significant post-fire declines in unburned forest and significant post-fire increases in high-severity patches ($F_{3,17} = 6.39$, $P = 0.004$; Table 3). However, post-fire densities were similar among burn severity levels, as reflected by a lack of

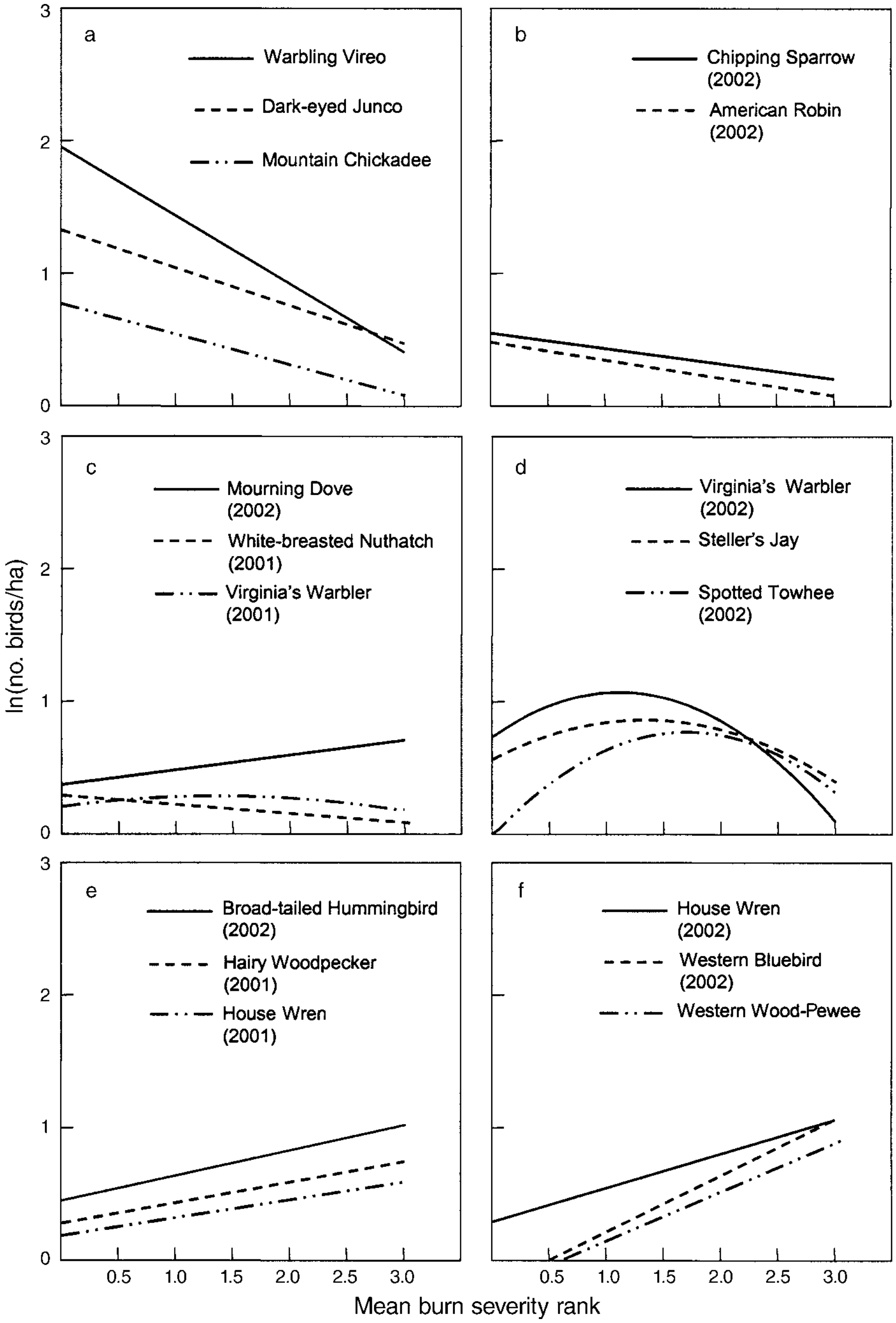

FIG. 2. Representative species for each response class corresponding to variation in density patterns along the burn severity gradient: (a) response class I represents species with strong declines in density with increasing burn severity; (b) response class II represents species with weak declines; (c) response class III represents species that show no significant differences in densities across the burn severity gradient; (d) response class IV represents species that reach peak densities at low or moderate severity; (e) response class V represents species with weak positive responses across the burn severity gradient; (f) response class VI represents species with strong increases in density with increasing burn severity (see Table 2 for the full set of species within each response class).

significant post-fire contrasts (Table 3). Post-fire densities of Broad-tailed Hummingbirds and Western Bluebirds increased with increasing burn severity and were significantly higher in high-severity patches compared to unburned patches ($F_{3,18} = 3.33$, $P = 0.043$; $F_{3,18} = 3.49$, $P = 0.037$, respectively; Table 3). Thus, all significant differences in densities indicated a positive numerical response to burned forests.

Although fewer significant differences in densities were detected with the pre/post pairs, many nonsignif-

Table 3. Density (means, with SE in parentheses) for species for pre- and for post-fire (before–after transects) by burn severity level at the Cerro Grande Fire, New Mexico.

	Density (no. birds/ha)							
	Pre-fire				Post-fire			
Species†	Unburned [$n = 7$]	Low [$n = 6$]	Moderate [$n = 4$]	High [$n = 5$]	Unburned [$n = 7$]	Low [$n = 6$]	Moderate [$n = 4$]	High [$n = 5$]
Mourning Dove‡	0.54	0.19	0.59	0.17	0.49^{a}	1.82^{ab}	2.04^{ab}	2.26^{b}
	(0.41)	(0.14)	(0.37)	(0.17)	(0.19)	(0.84)	(1.44)	(0.75)
Broad-tailed Hummingbird‡	4.07	7.18	4.67	4.40	0.76^{a}	2.08^{a}	3.26^{ab}	5.52^{b}
	(1.59)	(1.73)	(0.89)	(1.89)	(0.35)	(0.93)	(1.39)	(0.87)
Hairy Woodpecker	0.75	0.81	0.76	2.59	0.00	0.33	0.56	1.18
	(0.35)	(0.43)	(0.76)	(2.06)		(0.18)	(0.38)	(0.47)
Northern Flicker	1.57	0.58	1.78	3.32	0.33	0.07	0.29	0.10
	(0.38)	(0.29)	(0.93)	(1.71)	(0.17)	(0.07)	(0.19)	(0.06)
Western Wood-Pewee	3.91	2.27	2.02	2.17	0.36	0.53	1.01	1.06
	(1.16)	(0.71)	(0.85)	(0.90)	(0.14)	(0.27)	(0.39)	(0.44)
Steller’s Jay	1.16	0.62	0.74	1.15	0.10	0.38	0.70	0.10
	(0.56)	(0.45)	(0.27)	(0.69)	(0.10)	(0.20)	(0.48)	(0.10)
Mountain Chickadee	1.32	0.40	1.17	0.57	0.51	0.55	0.50	0.00
	(0.43)	(0.26)	(0.99)	(0.23)	(0.19)	(0.25)	(0.50)	
Pygmy Nuthatch	1.13	1.22	1.43	2.41	0.55	0.50	0.85	0.18
	(0.41)	(0.46)	(0.22)	(1.96)	(0.37)	(0.26)	(0.52)	(0.18)
Western Bluebird‡	0.62	1.62	1.69	0.29	0.30^{a}	0.51^{a}	1.14^{b}	3.44^{c}
	(0.44)	(0.83)	(0.99)	(1.38)	(0.23)	(0.22)	(0.6)	(1.31)
American Robin‡	1.77^{a}	0.66^{b}	1.36^{b}	0.15^{c}	0.47	0.88	0.76	1.09
	(0.67)	(0.36)	(1.06)	(0.15)	(0.17)	(0.32)	(0.50)	(0.45)
Virginia’s Warbler	3.07^{a}	2.27^{a}	0.53^{b}	0.00^{b}	0.42	0.41	0.41	0.00
	(1.16)	(0.75)	(0.53)		(0.16)	(0.28)	(0.41)	
Western Tanager	0.47	0.42	0.66	0.09	0.32	1.33	0.59	0.91
	(0.13)	(0.27)	(0.47)	(0.09)	(0.13)	(0.42)	(0.30)	(0.33)
Spotted Towhee	3.74^{a}	3.11^{a}	3.21^{a}	0.65^{b}	1.69	2.94	2.04	0.56
	(0.58)	(1.15)	(1.92)	(0.65)	(0.69)	(0.71)	(1.03)	(0.56)
Chipping Sparrow	1.47^{a}	2.66^{a}	5.20^{b}	1.31^{a}	0.47	1.02	0.59	0.33
	(0.90)	(1.64)	(1.51)	(0.90)	(0.14)	(0.38)	(0.36)	(0.24)
Black-headed Grosbeak	1.03	0.46	0.51	0.09	0.24	0.54	0.31	0.00
	(0.51)	(0.29)	(0.51)	(0.09)	(0.16)	(0.29)	(0.31)	

Notes: Transect densities are stratified by burn severity and pooled over cover type (Table A1 in Appendix A). Significantly different densities (based on post hoc contrasts) among burn severity levels (based on post-fire classifications) are designated by different superscript letters.

† See Appendix C for scientific names and list of species.

‡ Significant burn severity effects (ANOVA; see Appendix E for details).

icant post-fire trends (Table 3) were consistent with the patterns detected by the after-only gradient results (Table 1). Mountain Chickadee and Virginia’s Warbler exhibited density declines with increasing burn severity; Black-headed Grosbeak, Chipping Sparrow, and Spotted Towhee exhibited peak densities at low severity; and Hairy Woodpecker and Western Wood-Pewee exhibited increasing densities with increasing burn severity. For several of the species (Hairy Woodpecker, Virginia’s Warbler, Western Tanager, and Chipping Sparrow) showing nonsignificant trends; treatment effect P values were between 0.1 and 0.2, which is sometimes used as evidence of impacts in pre/post pairs analysis (e.g., Murphy et al. 1997). There were two exceptions: Mourning Doves and American Robins exhibited significantly higher densities post-fire based on before–after data, but were similar or slightly lower based on after-only data (Tables 1, 3). Thus, the response patterns for these species remain equivocal.

Our ability to detect significant fire effects was limited by underlying spatiotemporal variation. Five species had significant cover type effects (Appendix E), although our power to test for cover type effects was low. In addition, densities of many species were much higher in unburned reference areas pre-fire as compared to post-fire (Table 3). Although pre/post pairs analysis can help to control these sources of variation, low sample sizes prevented adequate partitioning of such confounding variation.

Community patterns

A total of 49 species was observed with the before–after data. Species richness was similar pre- vs. post-fire in unburned (46 vs. 41 species), low- (42 vs. 49), moderate- (35 vs. 33), and high-severity patches (27 vs. 28). Likewise, community similarity (represented by species occurring both pre- and post-fire) was relatively high and consistent across unburned, low-, and moderate-severity patches (Fig. 3). Community similarity was lowest in high-severity areas, yet richness remained

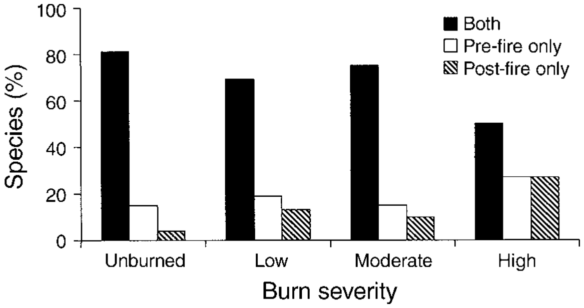

FIG. 3. Community similarity pre- and post-fire across a burn severity gradient at the Cerro Grande fire. Pre- and post-fire community similarity was evaluated by comparing the percentage of species detected pre-fire only, post-fire only, and both pre- and post-fire. The number of species for each burn severity class are as follows: unburned, $n = 75$; low, $n = 50$; moderate, $n = 20$; and high, $n = 27$.

unchanged. This was because the number of species only observed pre-fire in areas that subsequently burned at high severity (e.g., Brown Creeper, Grace's Warbler, Hermit Thrush) was similar to the number of species observed only post-fire in these areas (e.g., Green-tailed Towhee, Rock Wren, Western Tanager; Appendix F).

Burn severity patterns among sampling locations

Burn characteristics of landscapes sampled by before–after and after-only designs differed in several respects. Before–after samples were located in an area of moderate fire behavior, whereas after-only samples were distributed in an area dominated by a wind-driven crown fire (Fig. 1). The distribution of after-only samples corresponded to that of the entire burn, whereas severely burned areas were under represented by the before–after design (Fig. 4). Many before–after samples fell along the burn perimeter in proximity to large contiguous areas of unburned forest (Fig. 1). Crown fire patches were generally small in the area sampled by before–after transects, whereas most after-only plots were within or near large patches of severely burned forest where unburned or less severely burned areas were often small and isolated (Fig. 1).

DISCUSSION

Species response patterns

A broad spectrum of responses to the burn severity gradient was evident in the after-only density patterns (Fig. 2). Although these responses represent a continuum of positive and negative responses, the separation of this continuum into discrete response classes provides a framework for comparing past and future studies, as well as proposing mechanisms for the observed patterns.

Negative response patterns are represented by response classes I and II. Species in response class I generally demonstrated pronounced declines over the entire severity gradient, including low-severity patches. This group included sub-canopy aerial insectivores (Cordilleran Flycatcher), ground foragers (Hermit Thrush), and foliage gleaners (Mountain Chickadee, also a cavity nester; Jones and Donovan 1996, McCallum et al. 1999, Lowther 2000), which were likely sensitive to foliar volume in the understory and canopy. Within this response class, there was variation in the magnitude of response at high severity. Mountain Chickadees were not observed in high-severity patches, whereas Yellow-rumped Warblers and Dark-eyed Juncos were occasionally detected (Table 1). Some of the variation among species may correspond to differential sensitivity to the size of forest gaps (Kotliar et al. 2002). For example, Yellow-rumped Warblers and Dark-eyed Juncos may use small forest openings or edges, but avoid expansive areas of crown fires where most trees have died. Because these species prefer a mixed-open canopy (Hunt and Flaspohler 1998, Nolan et al. 2002), the spatial patterning of burn severity may play a role in the magnitude of their response (Kotliar et al. 2002). Response class II represents a weak negative response and both species (American Robin, Chipping Sparrow) exhibited significant declines with increasing severity in 2002, but no significant trends in 2001 (Tables 1, 2, and Fig. 2b).

Response class III (Fig. 2c) included species that were common across the entire burn severity gradient and, thus, represent species that do not respond to fire in terms of abundance. Species in this group prefer mixed-open canopies (Pravosudov and Grubb 1993, Mirarchi and Baskett 1994, Moore 1995, Hudon 1999, Sallabanks and James 1999) and include cavity-nesting species (Northern Flicker, White-breasted Nuthatch), aerial insectivores (Western Tanager), and ground foragers (Mourning Dove, American Robin). Two species (Mourning Dove, American Robin) exhibited significantly higher densities in burned forests with the before–after data. The conflicting results between the before–after and after-only datasets for these species illustrate the limitations of both sampling approaches. Uncontrolled pre-fire variation potentially masks post-fire

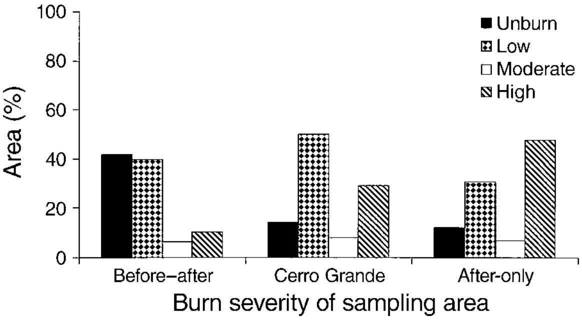

FIG. 4. Burn severity based on the Δ Normalized Burn Ratio within 500-m buffers surrounding each transect (before–after) or plot (after-only) located within the burn perimeter and for the entire Cerro Grande fire.

density changes. Alternatively, the lack of significant post-fire differences across the severity gradient may derive from the overriding re-structuring of forests by fire, which may swamp pre-fire variation.

Response classes IV, V, and VI represent species that demonstrated a positive response to burns. Species in response class IV exhibited peak densities at low or moderate severities, whereas densities in high-severity patches were similar to unburned areas (Tables 1, 2, and Fig. 2d). Most species in this group, such as Spotted Towhees and Virginia's Warbler, are associated with the shrub layer (Greenlaw 1996, Olson and Martin 1999), which may resprout vigorously following fire. Additionally, Steller's Jay is a relatively wide-ranging species characteristic of open-canopy forests (Greene et al. 1998). Response class V included species that were common across the entire burn severity gradient, but reached peak densities in high-severity patches. This class includes species associated with snags (Hairy Woodpecker, House Wren; Johnson 1998, Jackson et al. 2002) or vegetation, such as aspen and flowering plants (Broad-tailed Hummingbirds; Calder and Calder 1992), which may rapidly increase immediately post-fire. Indeed, the magnitude of response for House Wrens, a secondary cavity nester associated with the shrub layer, was greater in 2002 (mixed-conifer stands), presumably in response to aspen resprouting and increased availability of nest cavities excavated by primary cavity nesters. Response class VI includes two aerial insectivores (Western Wood-Pewee and Western Bluebird, also a cavity nester; Bemis and Rising 1999, Guinan et al. 2000). These species exhibited the strongest positive response to burned forest and were largely restricted to high-severity patches (Table 1). Although the responses for all three classes were positive, there were markedly different responses across the burn severity gradient (Fig. 2d–f).

Temporal variation suggested additional distinctions between positive and negative responders. Strong negative responses were immediate and consistent across the first two years post-fire, whereas the magnitude of the positive response increased in 2002 for many species (Tables 1, 2, and Fig. 2). However, such changes in density are difficult to interpret for two years of data. Likewise, Smucker et al. (2005) observed an increase in abundance for many positive responders in the first three years post-fire. They did not test this statistically, however, and the third year coincided with the use of an untrained observer, confounding the interpretation of their patterns because they only present abundance data unadjusted for detection probabilities. Thus, the temporal dynamics of avian populations post-fire needs additional study (Kotliar et. al. 2002).

Overall, 71% of the species in the gradient analysis exhibited either positive or neutral density responses to fire effects in at least one year post-fire (response classes III–VI). Two additional species (Yellow-rumped Warbler and Hermit Thrushes) showed minimal differences in low-burn compared to unburned reference areas in 2002 (Table 1). This suggests that the majority of species may tolerate or benefit from many of the ecological changes that occur across the severity gradient immediately post-fire. Most species occurred across all burn severities, consequently, pre- and post-fire species richness was similar. The greatest species turnover occurred in the high-severity patches, but the number of species absent post-fire was balanced by the number of species that only occurred post-fire. Community changes in high-severity patches also derived from pronounced density declines in response classes I and II that were offset by density peaks in response classes V and VI. Thus, positive effects of fire essentially balanced the negative effects for this species pool. Because approximately two-thirds of Cerro Grande burned at low or moderate severity (Kotliar et al. 2003), our results suggest the avifaunal community composition was largely unchanged over much of the burn.

Most studies of avifaunal response to burns in western forests have not quantified burn severity but simply compared severe burns to nearby unburned reference areas (but see Smucker et al. 2005). In a recent review (Kotliar et al. 2002), 11 studies (<10 years post-fire) were used to classify the abundance patterns of 41 species into three response classes: 22% of species were more abundant in burned forests, 32% were more abundant in unburned forests, and 44% were similar in burned and unburned forests, or the responses varied among burns (i.e., mixed/neutral). Because severe burns contain complex mixtures of burn severities (Turner et al. 1994, Kotliar et al. 2003), these studies undoubtedly included more than just severely burned patches (Kotliar et al. 2002). Our study, in conjunction with the recent results of Smucker et al. (2005), illustrates how diverse post-fire density patterns may be exhibited when burn severity is quantified and included in the analysis. For most species that exhibited clear positive or negative associations with burned forests, the patterns we observed are consistent with past studies. This includes Warbling Vireos, Mountain Chickadees, Hermit Thrushes, Hairy Woodpeckers, Western Wood-Pewees, and House Wrens (Table 2). Many species categorized by Kotliar et al. (2002) as mixed/neutral responses (e.g., Mourning Dove, White-breasted Nuthatch, American Robin, Chipping Sparrow) also exhibited highly variable densities, weak responses, and lack of significant differences in our study (Table 2). The consistency of our density patterns with more qualitative assessments of fire effects suggests that many previously reported response patterns are fairly robust, especially for species falling into our response classes I, III, and VI.

There are important distinctions between our results and past studies that may reflect, in part, the influence of burn severity on avian response patterns. For example, Steller's Jay was previously classified as having a primarily negative association with burned forest (Kotliar et al. 2002), but we observed peak densities at low- and moderate-severity patches (Table 2, Fig. 2d). Yellow-rumped Warblers and Dark-eyed Juncos were previously classified as having mixed/neutral responses (Kotliar et al. 2002), whereas we found pronounced declines with increasing burn severity (Table 2), although both of these species were observed in high-severity areas (Table 1). Because Cerro Grande was much larger than most of the burns reviewed in Kotliar et al. (2002), spatial patterning of burn severity may contribute to differences observed across studies.

Even when burn severity is quantified, design differences among studies can hinder comparisons. For example, Smucker et al. (2005) compared avifaunal response one to five years before, and one to three years after, a 55 000-ha fire in a mixed-coniferous forest in the northern Rocky Mountains. Several species (Hairy Woodpecker, Northern Flicker, Yellow-rumped Warbler) exhibited similar response patterns as observed in this study. There were several species that exhibited significant differences in our after-only design (Warbling Vireo, Mountain Chickadee, House Wren) that showed nonsignificant trends with their before–after design. Finally, several species exhibiting peak abundances at low or moderate severity in Smucker et al.'s study (2005), exhibited either a decline in abundance with increasing severity (e.g., Hermit Thrush, Chipping Sparrow, Dark-eyed Junco), and/or a mixed response (e.g., American Robin, Western Tanager) in our after-only data. Because Smucker et al. (2005) used a different burn severity classification, unadjusted counts, smaller size of sample units (individual points within transects), and did not stratify by cover type (ponderosa pine–Douglas-fir, mixed-coniferous, and lodgepole pine stands), design differences as well as geographic and landscape differences, may have contributed to the varied results among our studies.

Study design considerations

The variation among studies illustrates the importance of quantifying burn severity, cover type variation, and adjusting counts for detection probabilities so that results among studies can be more readily compared. In particular, responses of species that consistently exhibit both positive and negative responses across the severity gradient could be misinterpreted when severity is not evaluated (Kotliar et al. 2002, Smucker et al. 2005). In addition, the relative magnitude of negative or positive responses is more difficult to assess if comparisons are not made across the full range of severities. Thus, differential responses across the severity gradient cannot be quantified with simple burn vs. unburned forest comparisons (Kotliar et al. 2002, Smucker et al. 2005).

Burns vary widely in size and spatial patterning of burn severity, which can affect species response patterns (Kotliar et al. 2002). Because standards for quantifying burn severity are lacking (Key and Benson 2005), we provide some guidelines for quantifying burn severity to facilitate future comparisons among studies. Arbitrary breakpoints between burn severity levels can hinder gradient analysis and inter-burn comparisons. For example, moderate-severity burns have been variously classified as 0–10% crown fire (Dwyer 2000), 20–80% tree mortality (Smucker et al. 2005), and all trees partial to complete needle scorch (as in this study). Ideally, field measurement of burn severity should be continuous to prevent such discrepancies. This is particularly critical for the detection of nonlinear responses to burn severity, which we observed in this study.

Because severity patterns are strongly scale dependent (Cocke et al. 2005) and species can respond differentially across scales, measurement scale can affect results. Likewise, within-plot variation in burn severity can contribute to variation among studies. In our study, moderate severity plots could be comprised of uniformly burned survey points or a combination of low- and high-severity points. Within-plot variation was less pronounced for low- or high-severity plots. Similarly, variation in burn severity across 1-km transects likely contributed to the relatively high proportion (69%) of 32 species (summarized by Kotliar et al. 2002) that exhibited a mixed/neutral response to the La Mesa fire (this 6250-ha fire occurred in 1977 near the area subsequently burned by Cerro Grande; Johnson and Wauer 1996). Remotely sensed characterizations of burn severity, like ΔNBR (Cocke et al. 2005, Key and Benson 2005), can facilitate comparisons among studies and be used to quantify burn severity and spatial attributes of burn patches at multiples scales.

The before–after comparisons and after-only gradient analysis we employed at Cerro Grande provided an unprecedented opportunity to evaluate the relative usefulness of these sampling designs for quantifying avifaunal response to burns. Further, our ability to employ distance analysis to quantify both observer effects and detection differences among burn severity levels is a unique but important aspect of our study design. Although there was general correspondence in trends for species common to both data sets, fewer significant patterns were detected by the pre/post pairs analysis. This is likely due in part to lower power resulting from smaller sample sizes, particularly at high burn severity, which is typical of historical data sets associated with unplanned disturbances (Wiens and Parker 1995). Smucker et al. (2005) also had limited power to detect significant responses (50% of 32 species at $P < 0.05$) using before–after comparisons. In comparison, the gradient analysis at Cerro Grande detected significant patterns for 81% (71% at $P < 0.05$) of the species. The after-only data had sufficient samples to treat burn severity as a continuous rather than categorical variable, thereby increasing our ability to detect significant trends. In general, low sample sizes and high underlying variation in the before–after data resulted in weak inferences because only very large changes could be detected. Likewise, in a study of the Exxon Valdez oil spill, Murphy et al. (1997) detected only large effects of oiling using pre/post pairs analysis because of high population variability and small sample sizes.

Several other factors likely contributed to the discrepancies in results. Because the time elapsed between pre- and post-fire surveys was >10 years, temporal variation in populations may derive from long-term trends in the landscape that are not related to fire (e.g., successional changes within cover types, expansion of human developments). Densities in unburned reference areas were much higher pre-fire than post-fire for many species, suggesting potential long-term trends or unresolved sampling differences that masked short-term response to fire. Pre-fire sampling occurred during relatively wet conditions compared to the drought conditions during post-fire sampling (based on Palmer Drought Index, *available online*).[6] Some of the discrepancies among data sets may also be due to differences between species pools; the pre/post analysis included a higher proportion of species exhibiting neutral or positive responses, but did not include five species classified as response class I (after-only). Finally, the larger size of sample units and/or more moderate fire conditions surrounding the before–after transects compared to after-only plots (Figs. 1 and 4) may also account for lack of significant negative responses to burns in the pre/post analysis. Indeed, the magnitude of differences between burned and unburned areas in the before–after data was sometimes much less than that observed with the after-only data (e.g., Mountain Chickadee; Tables 1 and 3). Likewise, many before–after transects were in more mesic conditions of canyon bottoms, which can moderate fire behavior and facilitate post-fire regrowth (Dwire and Kauffman 2003). Consequently, post-fire forest conditions for before–after transects may be more similar to pre-fire conditions compared to after-only plots. As a result of the design limitations in the before–after data, we have greater confidence in the results from the gradient analysis.

Despite inherent difficulties in analyzing and interpreting the historical data set, our results demonstrated significant spatiotemporal variation and the importance of controlling such potentially confounding sources of variation in before–after and after-only designs (Wiens and Parker 1995). Ideally, before–after designs should include a minimum of three years pre- and post-fire sampling to quantify non-process, temporal population variation (Stewart-Oaten et al. 1986). Controlling temporal variation is especially critical for planned BACI and after-only designs (Stewart-Oaten et al. 1986, Hewitt et al. 2001, Stewart-Oaten and Bence 2001), used to study the effects of prescribed fire or other fuels treatments, because uncontrolled population variation will increase the difficulty of detecting fire effects under more moderate conditions characteristic of understory prescribed fire.

The greatest value of our before–after data set was quantifying post-fire changes in community composition, which cannot be evaluated with after-only data. Design limitations of our pre/post pairs analysis underscore the challenges of using historical data to evaluate the effects of unplanned disturbances. Although often viewed as an ideal study design because of its use of "controls" (e.g., Smucker et al. 2005), in practice, the use of BACI designs is problematic even for well-planned experiments. Resampling of historical data sets with limited sample sizes will inevitably lack sufficient power to detect population changes (Murphy et al. 1997), and such unplanned studies rarely meet the strict requirements for sound statistical design (Stewart-Oaten et al. 1986, Hewitt et al. 2001, Weiss and Reice 2005). The inclusion of after-only data that spatially overlap before–after samples can provide independent tests of avifaunal response patterns. Careful consideration of the statistical constraints imposed by historical data sets should be evaluated prior to resampling post-fire. Gradient analysis (Wiens and Parker 1995, Day et al. 1997), particularly if cofactors and a time series component are included, may be a more powerful and efficient technique for quantifying response to burns than control–impact studies (Ellis and Schneider 1997).

Neither design can fully resolve the inherent statistical challenges in quantifying fire effects at a single wildland fire (Kotliar et al. 2002). Further, true replication of burns cannot exist because of the large scales at which they occur (van Mantgem et al. 2001, Weiss and Reice 2005) and the variation among burns in spatial patterning of burn severity. Thus, multiple studies are needed to fully characterize species response patterns. To facilitate cross-study comparisons and maximize the power of the individual data sets, a priori development of study protocols are necessary (Anderson et al. 1999, Franklin et al. 2004). We have highlighted several important design considerations, such as collecting continuous, quantitative measures of burn severity and controlling sources of spatiotemporal variation. In addition, avian abundance responses should be based on densities, rather than unadjusted counts, to control for observer and cover type variability among studies. Because species responses vary, even over short time frames, short- and long-term studies across a broad range of fire conditions, including areas of fire exclusion, are essential to our understanding of fire effects (Kotliar et al. 2002).

Management implications

Our results demonstrated that many species tolerate or capitalize on the ecological changes resulting from severe fires; thus, assumptions about overriding negative ecological effects of recent crown fires in Southwest ponderosa pine forests (e.g., Allen et al. 2002) are invalid for the avifauna at Cerro Grande. The diverse response

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patterns and the high level of species turnover in high-severity patches illustrate the importance of severe fires to landscape and habitat dynamics in fire prone systems. Although there is increasing evidence that crown fires occurred historically even in montane forests, the role of severe fires cannot be fully resolved given limitations of the historical record (Baker and Ehle 2001). To develop sound fire management programs and policies, it is important to quantify the ecological consequences of fire regime dynamics across a broad range of temporal and spatial scales, regardless of whether changes are anthropogenic, climate driven, or a combination of both.

The paradigm that recent large fires are beyond the range of historical variability gives rise to additional untested assumptions that influence fire management decisions. The extent to which ecosystem restoration programs targeting forest conditions and fire regimes characteristic of a specific location and time period provides for a diverse avifauna has been poorly tested. Yet, the validity of this assumption is fundamental to the success of such restoration programs. Although many species, particularly those preferring low-severity burns or mixed-open canopies (e.g., response classes II, III, IV) may benefit from, or tolerate, ecosystem restoration programs, severe fires create forest structures and ecological elements that cannot be readily created by forest thinning and understory prescribed fire (Hutto 1995, Kotliar et al. 2002). Species preferring closed-canopy forests (including species in response class I) may benefit from fire exclusion (Bock and Block 2005). Our results demonstrated that even in Southwest ponderosa pine forests, high-severity patches, like those that resulted from the Cerro Grande fire, can create ecological conditions that benefit many species thereby increasing species diversity at landscape scales.

Increasing evidence from other disciplines indicates that even in montane systems, severe fires provide additional ecological functions (e.g., Bisson et al. 2003, Fulé et al. 2004). The tendency to focus on total area burned rather than more detailed reporting by burn severity (Stephens and Ruth 2005) further obfuscates the broad range of ecological changes that can occur following severe fires. In conclusion, the current management emphasis on low-severity fires (e.g., prescribed burns) and a narrow range of stand densities in montane forests may negatively impact species associated with high-severity burns, as well as species associated with dense forests. Fire management that includes a broad range of natural variability (Allen et al. 2002), including areas of severe fire, is more likely to preserve a broad range of ecological functions than restoration objectives based on narrowly defined historic fire regimes (Schoennagel et al. 2004).

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Literature Cited

Allen, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Dissertation. University of California, Berkeley, California, USA.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. Klingel. 2002. Ecological restoration of Southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.

Anderson, D. R., K. P. Burnham, A. B. Franklin, R. J. Gutierrez, E. D. Formsan, R. G. Anthony, G. C. White, and T. M. Shenk. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resource controversies. Wildlife Society Bulletin 27:1050–1058.

Baker, W. L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Canadian Journal of Forest Research 31: 1205–1226.

Bemis, C., and J. D. Rising. 1999. Western Wood-Pewee (*Contopus sordidulus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 451. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessburg, D. C. Lee, J. L Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178:213–229.

Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. Studies in Avian Biology 30:14–32.

Buckland, S. T., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Estimating abundance of biological populations. Oxford University Press, London, UK.

Calder, W. A., and L. L. Calder. 1992. Broad-tailed Hummingbird (*Selasphorus platycercus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 16. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA. American Ornithologists' Union, Washington, D.C., USA.

Cocke, A. E., P. Z. Fulé, and J. E. Crouse. 2005. Comparison of burn severity assessments using differenced Normalized Burn Ratio and ground data. International Journal of Wildland Fire 14:189–198.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 97:23–29.

Day, R. H., S. M. Murphy, J. A. Wiens, and G. C. Hayward. 1997. Effects of the Exxon Valdez oil spill on habitat use by birds in Prince William Sound, Alaska. Ecological Applications 7:593–613.

Dwire, K. A., and J. B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management 178:61–74.

Dwyer, J. K. 2000. Response of secondary cavity-nesting birds to wildfire in ponderosa pine forests of northern Arizona. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.

Ellis, J. I., and D. C. Schneider. 1997. Evaluation of a gradient sampling design for environmental impact assessment. Environmental Monitoring and Assessment 48:157–72.

Finch, D. M., J. L. Ganey, W. Yong, R. T. Kimball, and R. Sallabanks. 1997. Effects and interactions of fire, logging, and grazing. Pages 103–136 *in* W. M. Block and D. M. Finch, editors. Songbird ecology in Southwestern ponderosa pine forests: a literature review. USDA Forest Service General Technical Report RMRS-GTR-292. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Franklin, A. B., et al. 2004. Population dynamics of the California Spotted Owl (*Strix occidentalis occidentalis*): a meta-analysis. Ornithological Monographs 54:1–54.

Fulé, P. Z., A. E. Cocke, T. A. Heinlein, and W. W. Covington. 2004. Effects of an intense prescribed forest fire: Is it ecological restoration? Restoration Ecology 12:220–230.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of Southwestern ponderosa pine forests. Ecological Applications 7:895–908.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. USDA Forest Service General Technical Report RMRS-GTR-120. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Greene, E., W. Davison, and V. R. Muehter. 1998. Steller's Jay (*Cyancitta stellarri*). *In* A. Poole and F. Gill, editors. The birds of North America, number 343. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Greenlaw, J. S. 1996. Spotted Towhee (*Pipilo maculatus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 263. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Guinan, J. A., P. A. Gowaty, and E. K. Eltzroth. 2000. Western Bluebird (*Sialia mexicana*). *In* A. Poole and F. Gill, editors. The birds of North America, number 510. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Hewitt, J. E., S. E. Thrush, and V. J. Cummings. 2001. Assessing environmental impacts: effects of temporal variability at likely impact scales. Ecological Applications 11: 1502–1516.

Hudon, J. 1999. Western Tanager (*Piranga ludoviciana*). *In* A. Poole and F. Gill, editors. The birds of North America, number 432. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Hunt, P. D., and D. J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *In* A. Poole and F. Gill, editors. The birds of North America, number 376. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

Jackson, J. A., H. R. Ouellet, and B. J. S. Jackson. 2002. Hairy Woodpecker (*Picoides villosus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 702. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Janofsky, M. 2000. Citing poor plan, U.S. takes blame in Los Alamos fire. New York Times, 19 May 200, Section A1:3.

Johnson, L. S. 1998. House Wren (*Troglodytes aedon*). *In* A. Poole and F. Gill, editors. The birds of North America, number 380. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Johnson, T. H., and R. H. Wauer. 1996. Avifaunal response to the 1977 La Mesa fire. Pages 70–94 *in* C. D. Allen, editor. Fire effects in Southwestern forests: proceedings of the second La Mesa Fire Symposium, Los Alamos, NM, March 29–31, 1994. USDA Forest Service General Technical Report RMRS-GTR-286. Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, USA.

Jones, P. W., and T. M. Donovan. 1996. Hermit Thrush (*Catharus guttatus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 271. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. USDA Forest Service General Technical Report RMRS-GTR-91. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Kennedy, P. L. 1991. Reproductive strategies of northern Goshawks and Cooper's hawks in north-central New Mexico. Dissertation. Utah State University, Logan, Utah, USA.

Key, C. H., and N. C. Benson. 2005. Landscape assessment: ground measure of severity, the Composite Burn Index; and remote sensing of severity, the Normalized Burn Ratio. *In* D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, and L. J. Gangi, editors. FIREMON: Fire effects monitoring and inventory system. USDA Forest Service General Technical Report RMRS-GTR-164-CD:LA1–LA51, Rocky Mountain Forest and Range Experiment Station, Ogden, Utah, USA.

Kotliar, N. B., S. L. Haire, and C. H. Key. 2003. Lessons from the fires of 2000: post-fire heterogeneity in ponderosa pine forests. Pages 277–279 *in* P. Omi and L. Joyce, editors. Fire, fuel treatments, and ecological restoration: USDA Forest Service Conference proceedings April 16–18, 2002, Fort Collins, Colorado. RMRS-P-29. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Kotliar, N. B., S. J. Heijl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

Leica Geosystems. 2004. ERDAS Imagine. Version 8.3. Leica Geosystems, Norcross, Georgia, USA.

Lowther, P. E. 2000. Pacific-slope Flycatcher (*Empidonax difficilis*) and Cordilleran Flycatcher (*Empidonax occidentalis*). *In* A. Poole and F. Gill, editors. The birds of North America, number 556. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

McCallum, D. A., R. Grundel, and D. L. Dahlsten. 1999. Mountain Chickadee (*Poecile gambeli*). *In* A. Poole and F. Gill, editors. The birds of North America, number 453. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Mirarchi, R. E., and T. S. Baskett. 1994. Mourning Dove (*Zenaida macroura*). *In* A. Poole and F. Gill, editors. The birds of North America, number 117. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: a Southwestern ponderosa pine perspective. Ecological Applications 9:1266–1277.

Moore, W. S. 1995. Northern Flicker (*Colaptes auratus*). *In* A. Poole and F. Gill, editors. The birds of North America, number 166. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Morrison, J. L., and P. L. Kennedy. 1989. The use of line transect to evaluate the abundance of diurnal mammalian prey. Journal of Raptor Research 23:172–175.

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the Exxon Valdez oil spill on birds: comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299–313.

Nolan, V., Jr., E. D. Ketterson, D. A. Cristol, C. M. Rogers, E. D. Clotfelter, R. C. Titus, S. J. Schoech, and E. Snajdr. 2002. Dark-eyed Junco (*Junco hyemalis*). *In* A. Poole and F. Gill, editors. The birds of North America, number 716. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Olson, C. R., and T. E. Martin. 1999. Virginia's Warbler (*Vermivora virginiae*). *In* A. Poole and F. Gill, editors. The birds of North America, number 477. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, K. E. Abu-Saba, and A. R. Flegal. 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. Ecological Applications 4:16–30.

Pierce, J. L., G. A. Meyer A., and J. T. Jull. 2004. Fire-induced erosion and millennial scale climate change in northern ponderosa pine forests. Nature 432:87–90.

Pravosudov, V. V., and T. C. Grubb, Jr.. 1993. White-breasted Nuthatch (*Sitta carolinensis*). *In* A. Poole and F. Gill, editors. The birds of North America, number 54. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

Saab, V. A., and H. D. W. Powell. 2005. Fire and avian ecology in North America. Studies in Avian Biology No. 30. Cooper Ornithological Society, Ephrata, Pennsylvania, USA.

Saab, V. A., H. D. W. Powell, N. B. Kotliar, and K. R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: implications for avian communities and fire management. Studies in Avian Biology 30:76–90.

Sallabanks, R., and F. C. James. 1999. American Robin (*Turdus migratorius*). *In* A. Poole and F. Gill, editors. The birds of North America, number 462. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; American Ornithologists' Union, Washington, D.C., USA.

SAS Institute. 2001. SAS/STAT guide for personal computer. Version 6.12. SAS Institute, Cary, North Carolina, USA.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 54:661–676.

Siders, M. S., and P. L. Kennedy. 1996. Forest structural characteristics of accipiter nesting habitat: Is there an allometric relationship? Condor 98:123–132.

Smucker, K. M., R. L. Hutto, and B. M Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

SPSS. 2002. SPSS for Windows, release 11.5.0. SPSS, Chicago, Illinois, USA.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stewart-Oaten, A., and J. R. Bence. 2001. Temporal and spatial variation in environmental impact assessment. Ecological Monographs 71:305–339.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology 67:929–940.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, and J. H. Pollard. 2002. DISTANCE 4.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, UK.

Tiedemann, A. R., J. O. Klemmedson, and E. L. Bull. 2000. Solution of forest health problems with prescribed fire: Are forest productivity and wildlife at risk? Forest Ecology and Management 127:1–18.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Fire effects on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal Vegetation Science 5:731–742.

van Mantgem, P., M. Schwartz, and M. B. Keifer. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Natural Areas Journal 21:266–273.

Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado front range. Ecological Applications 10:1178–1195.

Wagner, M. R., W. M. Block, B. W. Geils, and K. F. Wenger. 2000. Restoration ecology: a new forest management paradigm or another merit badge for foresters. Journal of Forestry 98:22–27.

Weiss, J. M., and S. R. Reice. 2005. The aggregation of impacts: using species-specific effects to infer community-level disturbances. Ecological Applications 15:599–617.

Wiens, J. A., and K. R. Parker. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecological Applications 5:1069–1083.

APPENDIX A

Sampling locations at the Cerro Grande fire, New Mexico (*Ecological Archives* A017-018-A1).

APPENDIX B

Calculation of detection probabilities (*Ecological Archives* A017-018-A2).

APPENDIX C

Scientific and common names (*Ecological Archives* A017-018-A3).

APPENDIX D

Results of after-only gradient analysis at the Cerro Grande fire, New Mexico (*Ecological Archives* A017-018-A4).

APPENDIX E

ANOVA results for pre/post pairs analysis at the Cerro Grande fire, New Mexico (*Ecological Archives* A017-018-A5).

APPENDIX F

Frequency of occurrence for before–after transects at the Cerro Grande fire, New Mexico (*Ecological Archives* A017-018-A6).