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Interactive Effects of Fire and Nonnative Plants on Small Mammals in Grasslands

Andrea R. Litt and Robert J. Steidl

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Cover Image: With the help of professional firefighters, we set 36 fires to assess interactive effects of fire and dominance of nonnative grass on small mammals. Between 2000 and 2004, we captured 11,226 individual mammals from 24 species, 3 of which are pictured: Sigmodon fulviventer, Perognathus hispidus, and Dipodomys merriami. In the grasslands we studied, fires often burn uniformly, eliminating nearly all above-ground plant biomass. Photos by the authors and by Danielle O'Dell.

Contrast in vegetation composition and structure between 2 nearby areas of semi-desert grassland, 1 dominated by native grasses (top) and 1 dominated by a nonnative grass, *Eragrostis lehmanniana* (bottom). Photo by our friend and colleague, Eric Albrecht, who studied songbirds on these grasslands as part of his M.S. degree, and who died in 2004.

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Interactive Effects of Fire and Nonnative Plants on Small Mammals in Grasslands

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ABSTRACT Invasions by nonnative plants have changed the structure of many terrestrial ecosystems and altered important ecological processes such as fire, the dominant driver in grassland ecosystems. Reestablishing fire has been proposed as a mechanism to restore dominance of native plants in grasslands invaded by nonnative plants, yet fire may function differently in these altered systems, potentially affecting animals in novel ways. To assess whether invasions by nonnative plants alter the effects of fire on animals, we performed a manipulative experiment in semi-desert grasslands of southeastern Arizona that have been invaded by a perennial, nonnative grass from Africa, Lehmann lovegrass (*Eragrostis lehmanniana*). We applied fire to 36 of 54 1-ha plots established along an invasion gradient where dominance of *E. lehmanniana* ranged from 0% to 91% of total live plant biomass. Over the 5-year period from 2000 to 2004, we used mark-recapture methods to assess how population and community attributes of small mammals varied along the gradient of nonnative grass and in response to fire. We quantified changes in presence of 17 species, abundance of 9 species, total abundance of all species combined, species richness, and species composition. Based on 11,226 individual mammals from 24 species, we found that effects of nonnative-grass dominance varied with habitat preferences of each species, resulting in composition of the small-mammal community changing predictably along the invasion gradient. As dominance of nonnative grass increased, presence and abundance of granivorous heteromyids and insectivores (e.g., *Chaetodipus*, *Perognathus*, *Onychomys*; pocket mice and grasshopper mice) decreased, whereas presence and abundance of omnivorous and herbivorous murids (e.g., *Reithrodontomys*, *Sigmodon*; harvest mice and cotton rats) increased. Species richness of the small-mammal community averaged 8.4 species per plot and was highest at intermediate levels of nonnative-grass dominance where vegetation heterogeneity was greatest. Abundance of all small mammals combined averaged 26.9 individuals per plot and did not vary appreciably with nonnative-grass dominance. During the 4- to 8-week period immediately after fire, abundance of 6 of the 9 most common species changed, with 5 species decreasing and 1 species increasing on burned plots relative to unburned plots. During this same time period, species richness of small mammals decreased by an average of 3 species (38%) and total abundance of all species combined decreased by an average of 16 individuals (61%) on burned plots relative to unburned plots. Effects of fire on vegetation biomass, on presence of 9 of 17 mammalian species, and on abundance of 4 of 9 mammalian species remained evident ≥2 years after fire. Effects of fire on most small-mammal species varied with the degree of nonnative-grass dominance, suggesting that fire functioned differently in areas invaded by nonnative plants relative to areas dominated by native plants. Specifically, effects of fire on presence of 12 of 14 species and abundance of 7 of 9 species varied along the gradient of *E. lehmanniana*. During this post-fire period, however, composition of the small-mammal community in areas dominated by nonnative grass transitioned towards composition of areas dominated by native grasses, suggesting that fires had some restorative effect on habitat for small mammals. The relative strength of this effect will likely depend in general on the structural and compositional contrasts between invaded and native plant communities. Despite the reported ineffectiveness of fire at reducing dominance of nonnative plants, restoring fire to grasslands invaded by nonnative plants can help maintain the mosaic of vegetation conditions necessary to support the diverse assemblage of animals that inhabit these fire-governed ecosystems. © 2011 The Wildlife Society.

KEY WORDS community composition, *Eragrostis lehmanniana*, fire, gradient, grasslands, heterogeneity, invasion, Lehmann lovegrass, nonnative species, populations, restoration, small mammals.

Efectos Interactivos del Fuego y Plantas No Nativas Sobre Pequeños Mamíferos en Pastizales

RESUMEN Invasiones por plantas no nativas han cambiado la estructura de muchos ecosistemas terrestres y alterado procesos ecológicos importantes tales como el fuego, el conductor dominante en ecosistemas de pastizales. El restablecimiento del fuego ha sido propuesto como un mecanismo para restaurar la dominancia de plantas nativas en pastizales invadidos por plantas no nativas, aun el fuego puede funcionar en forma distinta en esos sistemas alterados, potencialmente afectando a los animales en forma distinta. Para evaluar si las invasiones de plantas no nativas alteran los efectos del fuego sobre los animales, realizamos un experimento manipulativo en pastizales del semidesierto del sureste de Arizona que han sido invadidos por un pasto perene no nativo procedente de África, Lehmann lovegrass (*Eragrostis lehmanniana*). Aplicamos fuego a 36 de 54 parcelas de 1 ha establecidos a lo largo de un gradiente de invasión donde la dominancia de *E. lehmanniana* oscilo de 0 a 91% del total de la biomasa de plantas vivas. Sobre un periodo de 5 años desde 2000 hasta 2004, usamos métodos de marcaje-recaptura para evaluar como los atributos de la población y comunidad de pequeños mamíferos variaron a lo largo del gradiente de pastos no nativos y en respuesta al fuego. Cuantificamos cambios en la presencia de 17 especies, abundancia de 9 especies, abundancia total, riqueza de especies y composición de especies. Basado en 11,226 mamíferos individuales de 24 especies, encontramos que los efectos de la dominancia de pastos no nativos variaron con las preferencias de hábitat de cada especie, resultando en un cambio predecible de la composición de la comunidad de pequeños mamíferos a lo largo del gradiente de invasión. Conforme la dominancia de los pastos no nativos incremento, la presencia y abundancia de heterómidos granívoros e insectívoros (e.g., *Chaetodipus*, *Perognathus*, *Onychomys*) declinó, mientras que la presencia y abundancia de omnívoros y herbívoros múridos (e.g., *Reithrodontomys*, *Sigmodon*) incremento. La riqueza de especies de la comunidad de pequeños mamíferos promediaron 8.4 especies por parcela y fue la más alta a niveles intermedios de dominancia de pastos no nativos donde la heterogeneidad de la vegetación fue mayor. La abundancia de todo los pequeños mamíferos combinados promediaron 26.9 individuos por parcela y no varía apreciablemente con la dominancia de pastos no nativos. Durante el periodo de 4 a 8 semanas inmediatamente después del fuego, la abundancia de 6 de 9 de las especies más comunes cambiaron, con 5 especies declinando y una especie incrementando sobre las parcelas quemadas en relación a las parcelas no quemadas. Durante este mismo periodo de tiempo, la riqueza de especies de pequeños mamíferos declino por un promedio de 3 especies (-38%) y el total de la abundancia de

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todas las especies combinadas por un promedio de 16 individuos (-61%) sobre las parcelas quemadas en relación a las parcelas no quemadas. Los efectos del fuego sobre la biomasa de la vegetación, presencia de 9 de 17 especies de mamíferos, y abundancia de 4 de 9 especies de mamíferos permanecieron evidentes 2 ≥ años después del fuego. Los efectos del fuego sobre la mayoría de especies de pequeños mamíferos variaron con el grado de dominancia de pastos no nativos, sugiriendo que el fuego funcionó en forma distinta en áreas invadidas por plantas no nativas en relación a las áreas dominadas por plantas nativas. Específicamente, los efectos del fuego sobre la presencia de 12 de 14 especies y la abundancia de 7 de 9 especies variaron a lo largo del gradiente de *E. lehmanniana*. Durante este periodo después de la quema, sin embargo, la composición de la comunidad de pequeños mamíferos en áreas dominadas por pastos no nativos se convirtieron hacia la composición de áreas dominadas por pastos nativos, sugiriendo que el fuego tuvo algo de efecto de restauración sobre el hábitat para pequeños mamíferos. La fortaleza relativa de este efecto probablemente dependerá en general sobre los contrastes de estructura y composición entre comunidades de plantas invadidas y nativas. A pesar de la inefectividad reportada del fuego para reducir la dominancia de plantas no nativas, restaurando el fuego a pastizales invadidos por plantas no nativas pueden ayudar a mantener mosaicos de condiciones de vegetación necesarias para soportar la diversidad de grupos de animales que habitan esos ecosistemas gobernados por el fuego.

Effets Interactifs du Feu et des Plantes Non Indigènes sur les Petits Mammifères dans les Prairies

RÉSUMÉ L'invasion des plantes exotiques modifie la structure de nombreux écosystèmes terrestres et d'importants processus écologiques, tel le régime d'incendies qui façonne les écosystèmes des prairies. Le rétablissement des régimes d'incendies a été proposé pour restaurer la dominance des plantes indigènes dans les prairies envahies par des plantes exotiques, mais les incendies peuvent fonctionner différemment dans ces systèmes altérés et potentiellement affecter les animaux de nouvelles façons. Afin d'évaluer si les invasions de plantes exotiques modifient les effets du feu sur les animaux, nous avons effectué une étude expérimentale dans les prairies semi-désertiques du Sud-est de l'Arizona, qui ont été envahies par une graminée vivace exotique Africaine, *Eragrostis lehmanniana*. Nous avons incendié 36 des 54 parcelles de 1-ha établies le long d'un gradient où la dominance d'E. *lehmanniana* variait de 0 à 91% de la biomasse totale des plantes. Au cours de la période de 5 ans de 2000 à 2004, nous avons utilisé des méthodes de marquage-recapture pour évaluer comment les attributs des populations et communautés de petits mammifères variaient en fonction de l'abondance d'E. *lehmanniana* et en réponse au feu. Nous avons quantifié la variabilité de la présence de 17 espèces, de l'abondance de 9 espèces, de l'abondance totale, et de la richesse et composition des espèces. Basé sur 11,226 mammifères provenant de 24 espèces, nous avons trouvé que les effets de la dominance d'E. *lehmanniana* dépendait du choix d'habitat de chaque espèce, entraînant des changements prévisibles dans la composition de la communauté de petits mammifères. L'accroissement de la dominance de la graminée exotique entraîna une réduction de la présence et de l'abondance des hétéromyides granivores et insectivores (p. ex., *Chaetodipus*, *Perognathus*, *Onychomys*) et un accroissement de la présence et de l'abondance des muridés omnivores et herbivores (p. ex., *Reithrodontomys*, *Sigmodon*). La richesse des espèces de la communauté de petits mammifères était en moyenne de 8,4 espèces par parcelle, et était plus élevée aux niveaux intermédiaires de dominance d'E. *lehmanniana*, lorsque l'hétérogénéité de la végétation était la plus grande. L'abondance de tous les petits mammifères combinés était en moyenne de 26,9 individus par parcelle et n'était pas affectée de façon importante par la dominance de la graminée exotique. Au cours de la période de 4 à 8 semaines immédiatement après l'incendie, l'abondance de 6 des 9 espèces les plus abondantes changea, avec 5 espèces moins abondantes et 1 espèce plus abondante dans les parcelles brûlées que dans les parcelles non brûlées. Pendant cette même période, la richesse des espèces de petits mammifères diminua en moyenne de 3 espèces (38%) et l'abondance totale combinée de toutes les espèces diminua en moyenne de 16 individus (61%) dans les parcelles brûlés par rapport aux parcelles non brûlés. Les effets du feu sur la biomasse de la végétation, la présence de 9 des 17 espèces de mammifères et l'abondance de 4 de 9 espèces de mammifères sont restés évident ≥2 ans après l'incendie. Les effets du feu sur la plupart des espèces de petits mammifères variaient en fonction du degré de dominance d'E. *lehmanniana*, suggérant que le feu fonctionne différemment dans les zones envahis par des plantes exotiques comparé aux zones dominées par les plantes indigènes. En particulier, les effets du feu sur la présence de 12 de 14 espèces et l'abondance de 7 de 9 espèces ont varié sur le gradient d'E. *lehmanniana*. Cependant, au cours de cette période après-feu, la composition de la communauté de petits mammifères dans les zones dominées par la graminée exotique a convergée vers la composition des zones dominées par les graminées indigènes, suggérant que les incendies ont un effet restaurateur sur l'habitat pour les petits mammifères. La force relative de cet effet dépendra probablement en général des différences structurelles et compositionnelles entre communautés végétales envahies et indigenes. Malgré l'inefficacité signalée du feu pour réduire la dominance des plantes exotiques, le rétablissement des régimes d'incendies dans les prairies envahis par des plantes exotiques peut aider à maintenir la mosaÿque des conditions végétales nécessaire pour supporter un assemblage diversifié des animaux qui peuplent les écosystèmes régis par les incendies.

Contents

INTRODUCTION

Invasions by nonnative species have altered the structure and function of nearly all ecosystems, illustrating the role of biological invasions as a central process in global change (Vitousek et al. 1996). Invasions by nonnative plants can simplify native plant communities by reducing floristic diversity, structural heterogeneity, and space among plants, while typically increasing vegetation biomass (Brooks et al. 2004, Geiger 2006). Changes to the plant community resulting from invasions by nonnative plants can affect the quantity and quality of habitat for native animals by altering vegetation structure, food resources, and other important habitat features (Wilson and Belcher 1989, Levine et al. 2003, Ostoja and Schupp 2009, Steidl and Litt 2009). Effects of plant invasions on animals are likely to be especially strong in areas where nonnative plants have reduced vegetation heterogeneity markedly, as high vegetation heterogeneity tends to support a greater diversity of plants and animals (Fuhlendorf et al. 2006). Communities dominated by nonnative plants can differ markedly from those dominated by native plants in their ability to function as habitat for a wide array of organisms (Wilson and Belcher 1989, Fuhlendorf et al. 2006, Ostoja and Schupp 2009, Litt and Steidl 2010*b*).

Although invasions by nonnative plants generally are thought to reduce habitat quality for animals (Bock et al. 1986), habitat quality can increase for species that prefer characteristics of the invading plant, such as areas of dense vegetation and high cover (Litt 2007, Litt and Steidl 2010*b*). If areas dominated by dense nonnative plants increase habitat quality for herbivores, foraging pressure on their preferred native food plants might increase, potentially conferring an advantage to nonnative plants and facilitating their spread (Callaway and Maron 2006, Orrock et al. 2008).

Structural changes in the plant community resulting from nonnative plants also can drive important functional changes to numerous ecosystem processes, including fire (Brooks et al. 2004). In many plant communities, fire is the principal process governing vegetation structure and composition (Wright and Bailey 1982, Bahre 1991, Whelan 1995, DeBano et al. 1998, Bredenkamp et al. 2002); in turn, the structure and composition of the plant community influences the frequency, intensity, and severity of fire (McPherson 1995). The fire regime also affects many other important physical and chemical processes, such as soil erosion, water infiltration, and nutrient cycling (Hendricks 1985, Kozlowski 1999, Dukes and Mooney 2004). Consequently, by altering the composition and structure of vegetation communities, invasions by nonnative plants can alter fire regimes and other ecological processes relative to ecosystems dominated by native plants (Mack and D'Antonio 1998, Brooks et al. 2004).

Animals that inhabit fire-governed ecosystems often have adaptations to cope with fire and the resulting habitat changes initiated by fire (Lawrence 1966; Komarek 1969, Fox 1982, 1990; Fox et al. 2003, Letnic et al. 2004). After fires, some species respond positively to changes in vegetation, which can include increases in plant and arthropod food resources (Buckner and Landers 1979, Fox 1982, Vieira 1999, Tietje et al. 2008). Areas that support a natural fire regime typically develop a mosaic of seral conditions resulting from fires of varying intensities and coverages that provide habitat conditions for a wide range of species (Fuhlendorf et al. 2006). In areas where nonnative plants are dominant and have changed the fire regime, however, the altered intensity, frequency, and timing of fires can create novel conditions to which native species may not be well-adapted (D'Antonio et al. 1999). When changes to the fire regime exceed the natural range of variation, they have the potential to eliminate native plant and animal species (Brooks et al. 2004).

In ecosystems where fire was once a dominant process but has been suppressed for many years, efforts to restore this important ecosystem driver can be plagued by a series of novel complications that could yield unexpected or undesired effects (Paine et al. 1998), including the inability to recreate a previous system state, a goal of many restoration efforts (Westoby et al. 1989, McPherson and Weltzin 2000). In grassland ecosystems, for example, increases in dominance of nonnative grasses are thought to initiate a positive feedback grass-fire cycle that might facilitate further increases in dominance of nonnative grass and fire frequency (Anable et al. 1992, D'Antonio and Vitousek 1992, Mack and D'Antonio 1998). Therefore, invasions by nonnative grasses can drive important functional changes to grassland ecosystems (Richardson et al. 2000). Because nonnative grasses are now dominant components in many grassland and savanna ecosystems throughout the world (D'Antonio and Vitousek 1992, Lonsdale 1994, Pivello et al. 1999, Richardson and van Wilgen 2004), the potential for wildfires to occur or management fires to be set in areas invaded by nonnative grasses is increasingly likely, creating an array of novel impacts for animals as well as unique management and conservation challenges (Paine et al. 1998, Levine et al. 2003).

Historically, in semi-desert grasslands of the southwestern United States, fire had a return interval of about 10 years and governed major ecological patterns in this plant community (McPherson 1995). Fires were ignited by dry lightning that preceded the onset of summer monsoon rains (Humphrey

1949, Bahre 1991), were often patchy and wide-ranging, sometimes extending hundreds of square kilometers, and were limited only by continuity of fine fuels (Dick-Peddie 1993, McPherson 1995). Many plant communities in this region have been invaded by nonnative plants, specifically several species of African grasses. One such species, Lehmann lovegrass (*Eragrostis lehmanniana*), was introduced to Arizona in the 1930s to reduce soil erosion and revegetate areas degraded by intense livestock grazing during a period of extreme drought (Crider 1945). Since its introduction, *E. lehmanniana* has increased in dominance and distribution, spreading throughout the southwestern United States and northern Mexico (Cox and Ruyle 1986, Anable et al. 1992, Schussman et al. 2006). This perennial bunchgrass produces more litter and up to 4 times more biomass than native grass species (Cable 1971, Cox et al. 1990, Anable et al. 1992, Geiger 2006), altering fuel loads, fuel continuity, and moisture conditions. *E. lehmanniana* is well adapted to fire, with germination rates and dominance sometimes increasing after fire (Cable 1965, Ruyle et al. 1988, Sumrall et al. 1991, Bock and Bock 1992).

Invasion of *E. lehmanniana* has altered the structure and composition of these grassland plant communities appreciably, resulting in concomitant changes to habitat for animals and the structure of animal communities (Bock et al. 1986, Flanders et al. 2006, Litt 2007, Litt and Steidl 2010*b*). Because fire has been suppressed in many of these grasslands for decades, reintroducing fire has been proposed as a strategy to reduce dominance of this nonnative grass despite potential changes in the function of fire that might result from increased biomass and fuel loads. Driven principally by concerns about controlling prescribed fires, management fires typically are prescribed during spring because of cooler ambient temperatures, higher humidity, and increased fuel and soil moisture, instead of during summer when wildfires ignited historically.

Animal populations and communities are affected by both fire (e.g., Ream 1981, Smith 2000) and invasions by nonnative plants (e.g., Bock et al. 1986, Scheiman et al. 2003, Flanders et al. 2006). What is unclear, however, is whether fire and nonnative plants affect animal populations and communities independently or whether they function interactively (Paine et al. 1998, Richardson et al. 2000). That is, do effects of fire on animals increase, decrease, or change completely in areas invaded by nonnative plants relative to effects of fire in areas dominated by native plants (Steidl and Litt 2009)? Our overarching goal was to evaluate the interaction between fire and plant invasions and the consequences of those compounded effects on animals. Therefore, we designed a manipulative experiment to quantify responses of small mammals to fire at both population and community scales along a gradient of invasion by nonnative grass. We selected small mammals for study because they are sensitive to changes in vegetation structure and heterogeneity and because of their important functional roles in the ecology of grasslands (Rosenzweig 1973, Brown and Heske 1990, Brown and Harney 1993, Williams et al. 2002*b*). We sought to quantify the independent effects of fire and nonnative-grass invasion on small mammals but focused especially on assessing potential interactions between fire and nonnative-grass invasion by investigating 6 interrelated questions: 1) How do attributes of small-mammal populations and the small-mammal community change with dominance of nonnative grass? 2) How do small mammals respond immediately after fire? 3) How long do fire effects on small mammals persist? 4) Does changing the timing of prescribed fire from summer to spring influence fire effects on small mammals? 5) Does dominance of nonnative grass influence the presence, magnitude, and duration of fire effects on small mammals? 6) Does reintroducing fire restore structure of the small-mammal community in areas invaded by nonnative grass?

STUDY AREA

We studied semi-desert grasslands in southeastern Arizona between elevations of 1,420 m and 1,645 m on Fort Huachuca Military Reservation (31° N, 110° W), where vegetation communities that included a grassland component comprised an area of approximately 15,000 ha. Annual precipitation in this area averaged 391 mm (SE = 17 mm, $n = 39$ years, 1955–1998; Air Force Combat Climatology Center 2001), 2/3 of which falls typically during a monsoonal period between July and October that is preceded by frequent lightning storms, the historical source of wildfire ignition. Fire history has been recorded since 1977 and none of the areas we studied had burned for ≥ 9 years before the study began. Livestock have been excluded since 1950. Common native grasses included *Aristida* spp. (three-awn grasses), *Bothriochloa barbinodis* (cane bluestem), *Bouteloua* spp. (grama grasses), *Digitaria californica* (Arizona cottontop), *Eragrostis intermedia* (plains lovegrass), and *Panicum* spp. (panicum grasses). Common shrubs included *Baccharis pteronioides* (yerba de pasmo), *Baccharis sarothroides* (desert broom), *Dasylirion wheeleri* (sotol), *Isocoma tenuisecta* (burroweed), *Mimosa culeaticarpa* var. *biuncifera* (wait-a-minute bush), and *Mimosa dysocarpa* (velvetpod catclaw).

METHODS

Experimental Design

We employed a field experiment with 2 factors: degree of dominance by nonnative grass (a continuous effect) and fire treatment (a fixed effect with 3 levels: spring fire, summer fire, and unburned control). To examine effects of nonnative grass, we established 54 1-ha plots (100 m × 100 m) across a gradient of dominance by *E. lehmanniana* that ranged from 0% to 91% of total live biomass ($\bar{x} = 44.2\%$, SE = 2.8), allowing us to draw inferences across the entire range of nonnative-grass dominance (Whittaker 1967, Ter Braak and Prentice 1988). To examine simple and interactive effects of fire, we arranged plots in groups of 3, assigning a treatment level at random to each plot within a group. Plots within each group were relatively close in space (separated by 100–200 m), which minimized the influence of nontreatment variation (e.g., soils, vegetation) and allowed us to contrast fire treatments among plots that were similar in ecological character but far enough apart to ensure that mammal populations on adjacent plots were independent. We did not treat these groups of plots as blocks in our analysis because one of the grouping factors, the degree of invasion by nonnative grass, was of direct interest.

We chose a plot size of 1 ha to balance a series of sampling objectives: 1) to ensure that resident populations of small mammals within a plot were of sufficient size (estimated abundance of common species sometimes exceeded 50 individuals per ha; Litt 2007); 2) to create a fire patch large enough to influence the local small-mammal community yet small enough to ensure that the plot burned as completely as possible; 3) to ensure sufficient replication of the treatment structure; 4) to ensure that all plots could be treated and sampled efficiently; and 5) to reduce the possibility that fire would escape the plot perimeter.

Timing of spring fires (Mar) was consistent with management fires and timing of summer fires (Jun and Jul) was consistent with historic lightning-ignited wildfires, allowing us to quantify variation in fire effects based on season of ignition. Because weather conditions, especially precipitation, vary substantially among years in semi-desert grasslands (Hidy and Klieforth 1990) and can affect fire behavior and severity, we replicated the entire treatment structure in each of 2 years to assess annual variation in treatment effects. This combination of 2 fire seasons and 2 fire years resulted in 4 fire treatments (spring and summer 2001, spring and summer 2002) plus their respective controls, which we evaluated on 9 plots for each fire year. Therefore, during spring 2000 we began sampling on 27 plots in 9 groups of 3 plots that we treated in 2001, and during spring 2001 we began sampling on an additional 27 plots that we treated in 2002, for a total of 54 1-ha plots.

For each fire treatment, prescribed fires on all 9 plots were completed within 5–12 days, except in spring 2001 when fires on 2 plots were completed 1 month after the others. Prescription for the 36 experimental fires involved burning a 10- to 15-m strip around the outside of the plot perimeter, setting a head fire to burn the plot, then spot-igniting any unburned patches to burn as much vegetation as possible.

Sampling

Small mammals.— We sampled small mammals each spring (May–Jun), summer (Jul–Aug), and winter (Feb–Mar) from spring 2000 through spring 2004. On each plot, we established an 8 × 8 grid of Sherman live traps spaced 12.5 m apart. We set traps at dusk, baited with wild bird seed, mainly millet and sunflower seeds, and a mixture of peanut butter and oats, and checked them at dawn every day for 5 consecutive days. We completed trapping on all plots in a season within a 3- to 4-week period that we defined as a sampling period. We sampled small mammals on each plot for $\geq$1 year prior to fire treatment (3 sampling periods), and for either 2 years (6 sampling periods, 2002 fires) or 3 years (9 sampling periods, 2001 fires) after fire treatment.

We identified all captured animals to species and individually double-marked them with a numbered ear tag (Monel tag 1005-1, National Band and Tag Co., Newport, KY) and with ink from permanent felt-tipped markers. We individually double-marked species with small ears (*Chaetodipus*, *Perognathus*, *Spermophilus* spp.; pocket mice and ground squirrels) with ink only. We released individuals at the point of capture (University of Arizona Institutional Animal Care and Use Committee Protocols 99-121, 02-109).

Vegetation.— We used biomass (g/m^2) of *E. lehmanniana* as a continuous explanatory variable to characterize dominance of nonnative grass on each plot. All vegetation was clipped on 25 0.5-m^2 quadrats established at random on each plot each March and September from September 1999 to September 2003 (details in Geiger 2006). Samples were oven-dried and dry weights recorded by species for each quadrat then averaged over all quadrats in each plot. Because *E. lehmanniana* grows mainly during summer, we used vegetation data collected in fall to estimate peak biomass (Cox et al. 1990). We used data from each fall to characterize vegetation from summer of the sampling year through winter and spring of the subsequent year (e.g., vegetation sampling from fall 2001 corresponded to small-mammal sampling from summer 2001, winter 2002, and spring 2002).

Although we were focused principally on the influence of nonnative grass, habitat for small mammals was affected by other plot-level characteristics. Therefore, we quantified additional vegetation and soil attributes on each plot to use as covariates to increase efficiency of our analyses. Using the sampling strategy described above for *E. lehmanniana*, we quantified biomass of litter, native grasses, woody vegetation, and herbaceous vegetation averaged over all quadrats on each plot for each vegetation-sampling period. After all vegetation was clipped and collected, percent cover of gravel ($<$7.5 cm diam) and cobble ($\geq$7.5 cm diam) was estimated visually on each quadrat and averaged over all quadrats and vegetation sampling periods.

We estimated shrub density on plots by counting all plants with multiple woody stems in a 1-m-wide transect established diagonally across each plot. We estimated density of shrubs $>$30-cm tall and small trees, which were uncommon, using point-centered quarter sampling, measuring the distance to the nearest shrub or tree $>$30-cm tall in each of 4 quadrants at 4 points located at random on each plot. We performed both measures in summer 2004 and combined all species for analysis as we were interested in accounting for variation in vegetation structure rather than composition; we converted counts to density (no./m^2; Thompson 2002). These 2 measures captured different structural aspects that might be important for small-mammal species: woody species that provided cover near the ground and woody species that provided cover in the canopy.

Fuel load and burn completeness.— We calculated average total biomass (all standing biomass [g/m^2]) for each plot before fires as a measure of fuel load. For spring fires, we used biomass data collected in September of the year before fires (e.g., Sep 2000 for spring fires in 2001); for summer fires, we used biomass data collected in March of the same year as fires (e.g., Mar 2001 for summer fires in 2001). Immediately after each prescribed fire, we walked 2 transects established diagonally across each plot, recording for each step whether the immediate area was burned or unburned, and used the percentage of transect areas that were burned as a measure of how completely fires burned vegetation on plots. We computed the percentage change in total vegetation biomass for each fall following fire (3–6 months post-fire and 15–18 months post-fire) relative to pre-fire values.

Small-Mammal Populations and Communities

On each plot and for each sampling period, we quantified characteristics of small mammals at population and community scales, as each scale provided a different perspective on how small mammals respond to nonnative grass, fire, and their interaction. At the population scale, we quantified species presence, which we defined as having captured ≥ 1 individual of a species on a plot during a 5-day sampling period, and abundance. We used presence to indicate that an area provided habitat for a species and abundance as a gauge of habitat quality. Presence and abundance provide complementary information about habitat for a species and examining both metrics allow for a more complete understanding of patterns within a study system (Fletcher et al. 2005). At the community scale, we quantified species richness, community composition, and total abundance, which we defined as the sum of abundances for the 9 most common species. We used species richness and total abundance to evaluate coarse-grained changes in the small-mammal community and we used community composition to evaluate changes in the assemblage of species inhabiting a plot.

On plots where we classified a species as present, we generated an estimate of abundance with closed-capture Huggins models in Program MARK (version 4.3, White and Burnham 1999) for the 9 most common species: *Baiomys taylori*, *Chaetodipus hispidus*, *Chaetodipus penicillatus*, *Dipodomys merriami*, *Onychomys leucogaster*, *Perognathus flavus*, *Reithrodontomys fulvescens*, *Sigmodon arizonae*, and *Sigmodon ochrognathus* (all common names listed in Table 1). We generated estimates of abundance in lieu of using relative abundance values because of the fundamental importance of accounting for imperfect detection to make inferences reliable (Williams et al. 2002*a*). To increase the amount of information available by which to evaluate alternative models to estimate abundance, we aggregated data across plots and years for each season (spring, summer, or winter) and each species separately (Litt and Steidl 2010*a*). We aggregated data solely to estimate abundance, which allowed us to adjust for variation in detection probability and generate plot-specific estimates of abundance for each species and each sampling period. We used a model-selection framework (Burnham and Anderson 2002) to evaluate candidate models for detection probability that included classification terms for year, fire treatment (combination of fire season and fire year), and dominance of nonnative grass. We generated model-averaged estimates of abundance for each species, plot, and sampling period. We then used individual plot-based estimates of abundance within a hypothesis-testing framework for subsequent analyses because of the advantages over a model-selection approach for randomized experiments (Burnham and Anderson 2002).

Accounting for variation in detection probability among species also allowed us to make reliable comparisons at the community scale (Nichols 1986, Slade and Blair 2000). We estimated species richness with the first-order jackknife estimator (Burnham and Overton 1979) to account for variation in detection probability among species. We quantified changes in community composition with multivariate analyses of presence and abundance of small-mammal species (see below).

Statistical Analyses

We divided analyses into 4 parts to address our questions of interest. First, we quantified effects of dominance of *E. lehmanniana* on small mammals. Second, we examined the immediate effects of fire on small mammals. Third, we quantified persistence of fire effects, determined whether fire effects varied with season or year when fires were applied, and, most importantly, assessed the degree to which dominance of *E. lehmanniana* influenced the effects of fire on small mammals (i.e., fire × nonnative grass interaction). Fourth, we examined whether fire functioned to restore community composition of small mammals in areas dominated by nonnative grass, where we defined restoration as shifting community composition toward composition in areas dominated by native grasses. In general, we used univariate analyses to evaluate responses at the population scale and both univariate and multivariate analyses to evaluate responses at the community scale.

Given the staggered entry of plots into the study and the range of questions we explored, sample sizes varied by analysis. Therefore, we report the number of plot samples used for each analysis, which we define as the number of plots multiplied by the number of sampling periods. Across the entire study, there were 621 plot samples (27 plots in each of the first 3 sampling periods, 54 plots in each of the subsequent 10 sampling periods). Although we present complete results from all analyses, given the large number of species we captured, we provide a subset of figures selected from these analyses to illustrate the range of responses.

We used a generalized linear mixed-model approach for all univariate analyses at both population and community scales and

Table 1. Species of small mammals and the number and percentage of the 11,226 total individuals captured in grasslands of southeastern Arizona, 2000–2004.

		Individuals	
Scientific name	**Common name**	**No.**	**%**
Order insectivora			
Soricidae			
Notiosorex crawfordi	Desert shrew	1	0.01
Order Rodentia			
Geomyidae			
Thomomys spp.	Pocket gopher	1	0.01
Heteromyidae			
Chaetodipus baileyi	Bailey's pocket mouse	61	0.54
Chaetodipus hispidus[a,b,c]	Hispid pocket mouse	1,219	10.86
Chaetodipus intermedius[b,c]	Rock pocket mouse	200	1.78
Chaetodipus penicillatus[a,b,c]	Desert pocket mouse	533	4.75
Dipodomys merriami[a,b,c]	Merriam's kangaroo rat	952	8.48
Dipodomys ordii[c]	Ord's kangaroo rat	175	1.56
Perognathus flavus[a,b,c]	Silky pocket mouse	1,412	12.58
Muridae			
Baiomys taylori[a,b,c]	Northern pygmy mouse	843	7.51
Neotoma albigula[b,c]	White-throated wood rat	238	2.12
Onychomys leucogaster[a,b,c]	Northern grasshopper mouse	942	8.39
Onychomys torridus[b,c]	Southern grasshopper mouse	326	2.90
Peromyscus boylii[c]	Brush mouse	16	0.14
Peromyscus eremicus[c]	Cactus mouse	55	0.49
Peromyscus leucopus[b,c]	White-footed mouse	217	1.93
Peromyscus maniculatus[b,c]	Deer mouse	320	2.85
Reithrodontomys fulvescens[a,b,c]	Fulvous harvest mouse	863	7.69
Reithrodontomys megalotis[b,c]	Western harvest mouse	309	2.75
Reithrodontomys montanus[b,c]	Plains harvest mouse	265	2.31
Sigmodon arizonae[a,b,c]	Arizona cotton rat	1,561	13.91
Sigmodon fulviventer[b,c]	Fulvous cotton rat	158	1.41
Sigmodon ochrognathus[a,b,c]	Yellow-nosed cotton rat	480	4.28
Sciuridae			
Spermophilus spilosoma[c]	Spotted ground squirrel	79	0.70

[a] Species considered when assessing changes in abundance across the gradient of nonnative grass and after fire.

[b] Species considered when assessing changes in presence across the gradient of nonnative grass.

[c] Species considered when assessing changes in presence after fire.

selected an appropriate link function for each continuous, binary, or multinomial response variable (Littell et al. 2006). When appropriate, we treated plots as subjects to account for repeated measurements taken on the same plots over time, and for each analysis we evaluated 4 possible covariance structures (compound symmetric, first-order autoregressive, first-order autoregressive moving average, and toeplitz), and selected one based on values of Akaike's information criterion adjusted for small sample bias ($\mathrm{AIC_c}$) and the Bayesian information criterion (BIC; Littell et al. 2006).

We used principal components analysis (PCA) for all multivariate analyses and based each PCA on a centered correlation matrix. We ordinated presence and log-transformed estimates of abundance separately and used Pearson correlations to identify the species of small mammals whose presence or abundance was associated most closely with a small subset of the principal components. As with univariate analyses, presence and abundance provide complementary views of changes in community composition.

Effects of nonnative grass.— For these analyses, we included data collected from plots only before they were burned, analyzed variation in presence of a species only if the species was present on $\geq$10% of plot samples, and analyzed abundance only for plots where the species was present. Before we assessed the influence of nonnative grass on presence or abundance of each species, we first accounted for variation explained by plot-level covariates: biomass of litter, woody species, and herbaceous species; density of all shrubs; density of shrubs >30-cm tall; and cover of cobble, as well as season and year of sampling. We excluded biomass of native grasses and gravel cover as potential covariates because they were correlated with biomass of nonnative grass ($r = -0.61$ and $r = -0.67$, respectively), the explanatory variable of interest. Other covariates were not highly correlated ($|r| < 0.5$) with each other, except for woody biomass and cobble cover ($r = 0.62$). For each response variable, we first chose a subset of important covariates that we identified using stepwise variable selection with $P = 0.15$ to enter and $P = 0.05$ to remain (Ramsey and Schafer 2002:338). We then fit a model that included important covariates and biomass of nonnative grass, removed covariates that no longer explained a significant amount of variation ($P > 0.10$), and fit a final model for inference. We log-transformed cobble cover and estimates of abundance for small mammals to better meet assumptions of parametric tests.

We expressed the effect of nonnative-grass dominance on response variables as the multiplicative percentage change in each response for every 100 $\mathrm{g/m^2}$ increase in average biomass of nonnative grass, which we based on back-transformed regression coefficients from mixed models. In figures, we used average partial residuals to isolate and express the effect of nonnative grass after we accounted for the effects of important covariates.

To examine effects of nonnative grass on species richness and total abundance of small mammals, we used the same regression approach that we used for population-level parameters ($n = 333$ plot samples). To characterize changes in composition of the small-mammal community along the gradient of nonnative grass invasion, we generated the first principal component derived from estimated abundances for the 9 most common species averaged across years for each season ($n = 162$ plot samples, 54 for each of 3 seasons). We then used linear regression to examine how changes in community composition of small mammals, as captured by the first principal component, varied with degree of invasion by including nonnative grass as the explanatory variable.

We used patchiness of vegetation as a measure of heterogeneity, quantified with the coefficient of variation of total live biomass of vegetation among all 25 quadrats on each plot. We used linear regression to examine how vegetation heterogeneity changed across the invasion gradient.

Effects of fire.— To evaluate effects of fire on small mammals, we compared values of response variables measured on each burned plot and associated unburned plot within the same group (i.e., plot pair). Contrasting plots within the same pair accounted for existing variation in values of response variables across the gradient of nonnative invasion that could confound fire effects and fire × nonnative grass interactions; further, this approach allowed us to assess effects of the 4 combinations of fire treatment simultaneously, despite fires being staggered in time. We assessed simple and immediate effects of fire by examining changes in small-mammal species and community parameters for only the first sampling period (4–8 weeks) following fire ($n = 36$ plot pairs).

For abundance and species richness of small mammals, we calculated the log ratio (Törnqvist et al. 1985) of estimates for each plot pair:

$$\begin{aligned}\text{log ratio} &= \frac{\ln(\text{burn}+1)}{\ln(\text{unburned}+1)}\\ &= \ln(\text{burn}+1) - \ln(\text{unburned}+1),\end{aligned}$$

which is a metric that accounts for any inherent variation in abundance across the gradient of nonnative grass. Although we analyzed log ratios to evaluate changes in abundance and present these results in tables, we report raw differences between burned and unburned plot pairs in the text to simplify interpretation of the magnitude of fire effects.

For presence of a species, differences between burned and unburned plots within a plot pair yielded 1 of 4 possible outcomes: present only on the unburned plot, present only on the burned plot, present on both plots, or absent on both plots. If 1 of the 4 outcome categories had <10% of the total number of observations, we excluded that category and analyzed only the remaining outcome categories for that species. Because we were primarily interested in understanding whether fire caused changes in presence of a species, we focused on 2 comparisons. First, we compared plot pairs where the species was present on the burned plot and not present on the unburned plot (fire created habitat and increased presence) to plot pairs where the species was absent on both plots (no change). Second, we compared plot pairs where the species was present on the unburned plot and not present on the burned plot (fire eliminated habitat and decreased presence) to plot pairs where the species was present on both plots (no change). We report proportions of plots in each outcome category to simplify interpretation of the magnitude of immediate fire effects.

Recovery, timing, and interaction of fire with nonnative grass.— We examined persistence of fire effects over time, influence of season and year of ignition on fire effects, and whether fire effects varied with degree of nonnative-grass invasion (i.e., fire × non-nonnative grass interaction) for all population and community-level responses. We developed models with 4 main effects: 1) time-since-fire; 2) fire season; 3) fire year; and 4) dominance of nonnative grass, and included all interactions among main effects. We quantified time-since-fire as the number of sampling periods after treatment, a continuous effect that ranged from 1 to 6, and restricted fire-related analyses to 2 years after treatment to maintain consistency in the amount of post-fire sampling for all fire treatments ($n = 216$ plot pairs). We used linear contrasts to evaluate variation in response variables between fire seasons and fire years, as well as the interaction between fire season and fire year. We quantified dominance of nonnative grass by averaging estimates of biomass of *E. lehmanniana* from the 2 fall sampling periods prior to fire treatment (i.e., fall 1999 and 2000 for plots burned in 2001, fall 2000 and 2001 for plots burned in 2002). For continuous response variables, we included the average of the log ratio for the 3 sampling periods (1 yr) preceding fire treatment as a covariate in each analysis to account for pre-existing differences among plots.

Because we modeled differences or ratios between burned and unburned plots as response variables, each effect in our model included an implicit interaction with fire; therefore, we described what each model term represented with regards to our principal set of questions (Table 2). Model terms that included a time-since-fire effect addressed questions about persistence of fire effects, terms that included fire season or fire year effects addressed questions about the effect of fire timing, and terms that included a nonnative grass effect addressed questions about the interactive effect of fire and dominance of *E. lehmanniana*. We evaluated the importance of simple or interactive effects to answer our questions of interest.

Restoration.— To assess compositional changes in the small-mammal community after fire, we used PCAs based on presence of 22 species and on abundance estimates for the 9 most common species. We ordinated data separately for each of the 6 sampling periods after fire ($n = 72$ for each ordination, 36 burned and the corresponding 36 unburned plots) to explore whether fires changed community composition of mammals in areas dominated by nonnative grass. Specifically, we examined whether community composition of areas shifted to become more similar to composition of unburned areas dominated by native grasses immediately after fire or over time.

RESULTS

We captured 11,226 individual small mammals representing 24 species during 198,720 trap nights (Table 1). *C. hispidus*, *P. flavus*, and *S. arizonae* were most abundant, comprising 37% of all individuals captured. Only 4% of individual small mammals were captured on >1 plot during a sampling period, indicating that populations of animals on adjacent plots were largely independent; species trapped on >1 plot at rates higher than 4% were not an obvious subset of the species we encountered during the study. Biomass of nonnative grass across the invasion gradient ranged from 0.0 g/m^2 to 466.3 g/m^2 per plot (average = 140.5 g/m^2, 95% CI = 120.8–160.3) and biomass of all live vegetation ranged from 96.5 g/m^2 to 522.3 g/m^2 (average = 281.0 g/m^2, 95% CI = 266.4–295.5). Vegetation heterogeneity was greatest at low to intermediate levels of nonnative grass and varied most where native plants were dominant (Fig. 1).

Response to Dominance of Nonnative Grass

Species richness of the small-mammal community averaged 8.4 species per plot (95% CI = 8.1–8.7) and did not vary linearly with dominance of nonnative grass ($t_{269} = 0.92$, $P = 0.356$), but varied quadratically ($t_{268} = -3.49$, $P < 0.001$, $n = 333$), with the highest richness at intermediate levels of nonnative grass dominance (Fig. 2), after accounting for important plot-level covariates (Appendix A). Total abundance of small mammals averaged 26.9 individuals per plot (95% CI = 25.0–28.9) and did not vary appreciably with dominance of nonnative grass ($t_{271} = 1.51$, $P = 0.131$, $n = 332$; Fig. 2; Appendix A). Species richness of plants explained only a small proportion of variation in species richness ($r^2 = 0.02$, $P = 0.01$, $n = 332$) and total abundance ($r^2 = 0.09$, $P < 0.001$, $n = 332$) of small mammals.

Composition of the small-mammal community varied across the gradient of nonnative grass. The first principal component

Table 2. Model terms and descriptions of what each term represents for univariate analyses examining effects of nonnative grass and fire on small mammals in semi-desert grasslands, southeastern Arizona, 2000–2004. Response variables represent differences between burned plots and unburned plots within a group (plot pairs).

Model term	Represents effects of fire based on:
Fire season	Spring versus summer ignition
Fire year	2001 versus 2002 ignition
Fire season × fire year	Season and year of ignition
Nonnative grass	Differences in nonnative grass dominance
Time-since-fire	Recovery after fire
Nonnative grass × fire season	Fire seasons across the gradient of nonnative grass
Nonnative grass × fire year	Fire years across the gradient of nonnative grass
Nonnative grass × fire season × fire year	Fire seasons and fire years across the gradient of nonnative grass
Time-since-fire × fire season	Recovery after fires set in 2 different seasons
Time-since-fire × fire year	Recovery after fires set in 2 different years
Time-since-fire × fire season × fire year	Recovery after fires set in 2 different seasons and 2 different years
Nonnative grass × time-since-fire	Recovery after fire across the gradient of nonnative grass
Nonnative grass × time-since-fire × fire season	Recovery after fires in 2 different seasons across the gradient of nonnative grass
Nonnative grass × time-since-fire × fire year	Recovery after fires in 2 different years across the gradient of nonnative grass
Nonnative grass × time-since-fire × fire season × fire year	Recovery after fires in 2 different seasons and years across the gradient of nonnative grass

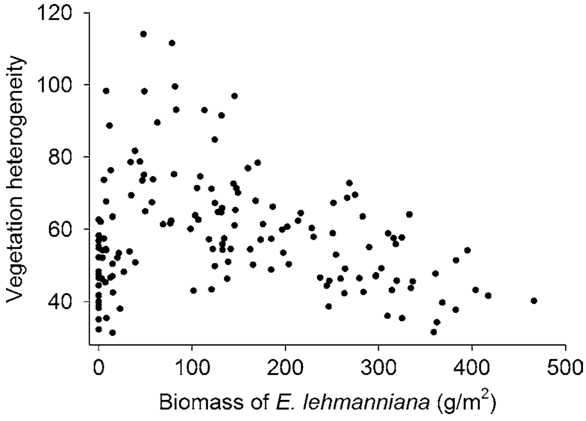

Figure 1. Change in vegetation heterogeneity, as measured by the coefficient of variation of live vegetation biomass, with increased dominance of nonnative grass, southeastern Arizona, 2000–2004.

(PC1) derived from abundances of the 9 most common species of small mammals explained 29% of variation in the original abundance data and was correlated negatively with dominance of nonnative grass ($r = -0.45$, $P < 0.001$, $n = 162$; Fig. 3). Abundances of *C. hispidus* ($r = 0.73$), *C. penicillatus* ($r = 0.51$), and *P. flavus* ($r = 0.79$) were correlated positively with PC1, and abundances of *R. fulvescens* ($r = -0.75$), *S. arizonae* ($r = -0.51$), and *S. ochrognathus* ($r = -0.53$) were correlated negatively with PC1 (all $P < 0.001$, $n = 162$; Fig. 3). Changes in abundance of *B. taylori* ($r = 0.22$), *D. merriami* ($r = 0.07$), and *O. leucogaster* ($r = -0.15$) across the gradient of nonnative grass explained less of the variation in community composition than other species. In general, the small-mammal community transitioned from one dominated by heteromyids (*Chaetodipus*, *Perognathus*) in areas dominated by native grasses to one dominated by murids (*Reithrodontomys*, *Sigmodon*) in areas dominated by nonnative grass.

Presence of 9 of 17 species changed across the gradient of nonnative grass (Table 3, Fig. 4). Presence of 1 heteromyid and 5 murids increased as dominance of nonnative grass increased (Table 3, Fig. 4). For each 100 g/m^2 increase in biomass of nonnative grass, presence of *D. merriami* increased by 30% (95% CI = −4 to 76), *R. fulvescens* by 50% (95% CI = 13–97), *Reithrodontomys megalotis* by 66% (95% CI = 29–113), *Reithrodontomys montanus* by 44% (95% CI = 13–85), *S. arizonae* by 110% (95% CI = 53–190), and *Sigmodon fulviventer* by 63% (95% CI = 17–127). Conversely, presence of 3 heteromyids decreased as dominance of nonnative grass increased (Table 3, Fig. 4). Presence of *C. hispidus* decreased by 32% (95% CI = 13–47), *C. penicillatus* by 24% (95% CI = 3–41), and *P. flavus* by 59% (95% CI = 43–70) for each 100 g/m^2 increase in biomass of nonnative grass, after accounting for important covariates. Presence of *B. taylori*, *Chaetodipus intermedius*, *Neotoma albigula*, *O. leucogaster*, *Onychomys torridus*, *Peromyscus leucopus*, *Peromyscus maniculatus*, and *S. ochrognathus* did not change appreciably with dominance of nonnative grass (Table 3, Fig. 4).

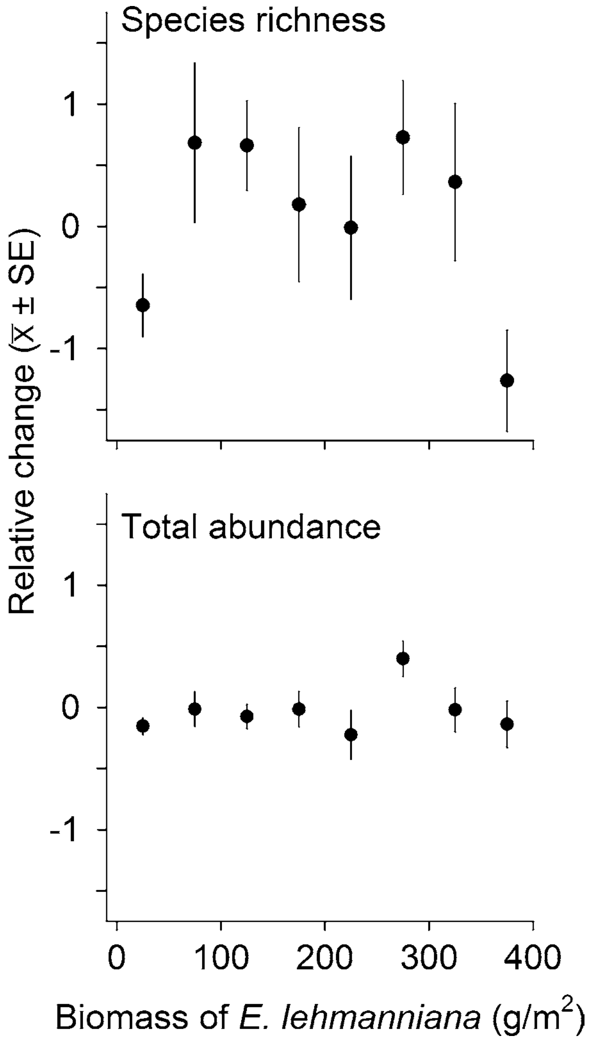

Figure 2. Relative changes in species richness and total abundance ($\bar{x}$ ± SE) of small mammals in response to increased dominance of nonnative grass, southeastern Arizona, 2000–2004. *Y*-axis represents partial residuals from models describing the estimated effect of nonnative grass after accounting for important covariates (Appendix A). We included only unburned plots in the analyses depicted in the figure.

Abundance of 6 of the 9 most abundant small-mammal species varied across the invasion gradient (Table 4, Fig. 5). For each 100 g/m^2 increase in biomass of nonnative grass, abundance of *D. merriami* increased by 13% (95% CI = −2 to 29), *R. fulvescens* by 13% (95% CI = 3–24), and *S. arizonae* by 32% (95% CI = 17–49), after accounting for important covariates (Table 4, Fig. 5). Conversely, abundance of *C. penicillatus* decreased by 12% (95% CI = −2 to 24), *O. leucogaster* by 10% (95% CI = 3–17), and *P. flavus* by 18% (95% CI = 4–31) (Table 4, Fig. 5). Abundance of *B. taylori*, *C. hispidus*, and *S. ochrognathus* did not change appreciably across the invasion gradient (Table 4, Fig. 5).

Immediate Response to Fire

Prescribed fires consumed nearly all vegetation, burning an average of 92% of the vegetation on each plot (95% CI = 88.6–95.8). At ignition, air temperature averaged 23.2°C (range = 10.0–33.3°C) and relative humidity averaged 25.6% (range = 4–88%; Table 5). Burn completeness varied among seasons and years of fire, especially for spring 2001 when soil moisture was higher and fires were less complete and more variable than fires in other seasons and years (Table 5). In general, fires in 2002 (97% complete, range = 94.0–99.3) averaged 9% more complete than

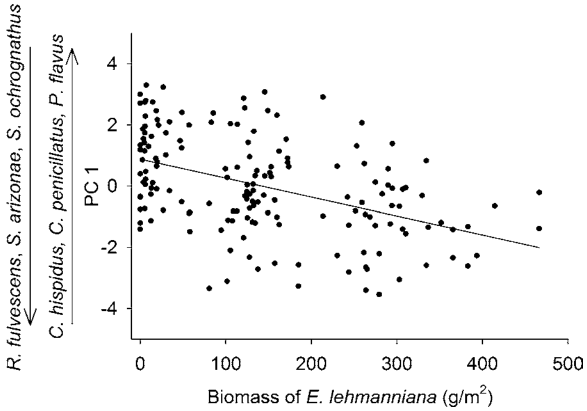

Figure 3. Change in community composition of small mammals in response to increased dominance of nonnative grass, southeastern Arizona, 2000–2004. *Y*-axis is the first principal component (PC1) from an ordination of abundance estimates for 9 common species of small mammals averaged over time for each season of sampling ($n = 162$ plot samples, 54 in each of 3 seasons); this measure was correlated with changes in abundance of the 6 species listed ($|r| \geq 0.50$, $P < 0.001$). We included only unburned plots in the analyses depicted in the figure.

fires in 2001 (88%, range = 81.4–94.1), probably because of lower fuels on plots burned in 2001 (Table 5). Fires during summer (95%, range = 91.9–100) averaged 6% more complete than fires during spring (89%, range = 82.8–96.1). Across all years and seasons combined, vegetation biomass averaged 66% lower 3–6 months after fire compared to pre-fire levels (range = 6–96% decrease; Table 5).

In the 4–8 weeks after fire, species richness of small mammals decreased by an average of 3.3 species per plot (95% CI = 2.2–4.5, 38% decrease) and total abundance of small mammals decreased by an average of 15.6 individuals per plot (95% CI = 10.0–21.2, 61% decrease) compared to unburned plots

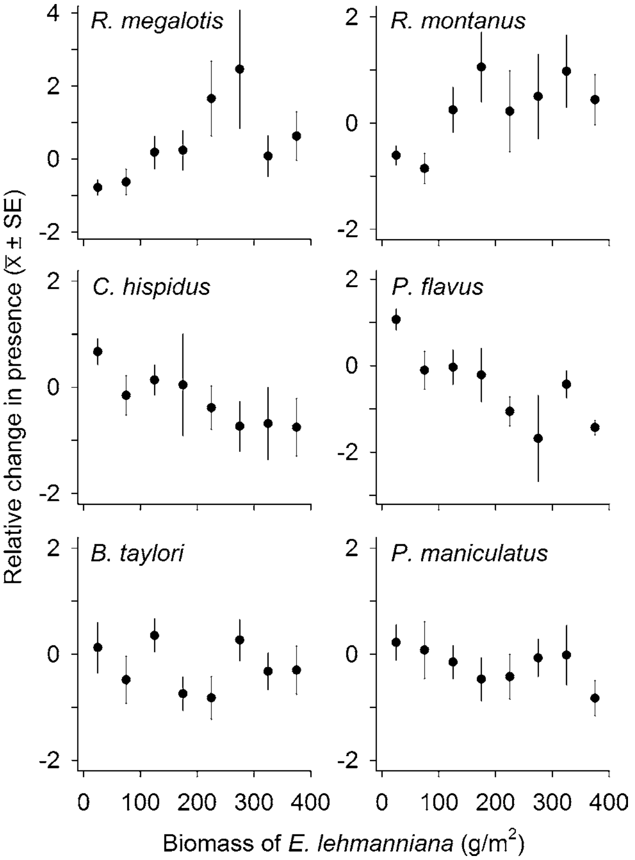

Figure 4. Relative changes in presence ($\bar{x} \pm$ SE) of small mammals in response to increased dominance of nonnative grass, southeastern Arizona, 2000–2004. *Y*-axis represents partial residuals from models describing the estimated effect of nonnative grass after accounting for important covariates (Appendix B). We included only unburned plots in the analyses depicted in the figure.

Table 3. Effects of changes in dominance of nonnative grass on presence of small mammals, southeastern Arizona, 2000–2004. Presence is defined as the proportion of $n = 333$ plot samples where each species was present. Covariates listed are those that were included in the generalized linear-mixed model we used for inference from all covariates considered: biomass of litter, woody species, and herbaceous species, density of all shrubs, density of shrubs >30-cm tall, cover of cobble, and season and year of sampling. The sign preceding vegetation and soil covariates represents the direction of the individual regression coefficient in the final model. We report back-transformed estimates and standard errors, which represent the multiplicative percentage change in presence for each 100 g/m^2 increase in biomass of nonnative grass. Estimates, test statistics, and *P*-values for covariates are provided in Appendix B.

Response	Covariates	Estimate	SE	*t*	*P*
Increased					
Dipodomys merriami	Season	30.02	1.17	1.70	0.090
Reithrodontomys fulvescens	+Herbaceous, +cobble, season, year	49.54	1.15	2.85	0.005
Reithrodontomys megalotis	+Cobble, season, year	65.78	1.14	3.99	<0.001
Reithrodontomys montanus	+Woody, season	44.25	1.13	2.93	0.004
Sigmodon arizonae	+Litter, +all shrubs, −woody, season, year	110.48	1.18	4.60	<0.001
Sigmodon fulviventer		62.87	1.18	2.88	0.004
Decreased					
Chaetodipus hispidus	−Cobble, season	−32.23	1.13	−3.11	0.002
Chaetodipus penicillatus	−All shrubs, season, year	−24.04	1.13	−2.21	0.028
Perognathus flavus	+Herbaceous, −all shrubs, −cobble, season, year	−58.93	1.18	−5.43	<0.001
Did not change					
Baiomys taylori	+Herbaceous, +litter, −cobble, year	−18.54	1.17	−1.32	0.189
Chaetodipus intermedius	−Litter, −cobble, season, year	−21.73	1.22	−1.23	0.219
Neotoma albigula	+All shrubs, +cobble, −shrubs >30 cm, season	29.78	1.22	1.32	0.188
Onychomys leucogaster	+Herbaceous, −litter, −cobble, season, year	−19.10	1.15	−1.53	0.128
Onychomys torridus	Season	−2.66	1.12	−0.24	0.813
Peromyscus leucopus	Season, year	−1.09	1.14	−0.08	0.934
Peromyscus maniculatus	+Cobble, season	−17.22	1.12	−1.62	0.107
Sigmodon ochrognathus	+All shrubs, +cobble, −woody, season	12.37	1.13	0.93	0.351

Table 4. Effects of changes in dominance of nonnative grass on abundance of small mammals, southeastern Arizona, 2000–2004. We examined changes in estimated abundance for all plot samples (*n*) where we captured ≥1 individual of the species during the 5-day sampling period. Covariates listed are those that were included in the generalized linear-mixed model we used for inference from all covariates considered: biomass of litter, woody species, and herbaceous species, density of all shrubs, density of shrubs >30-cm tall, cover of cobble, and season and year of sampling. The sign preceding vegetation and soil covariates represents the direction of the individual regression coefficient in the final model. We back-transformed estimates and standard errors, which represent the multiplicative percentage change in abundance for each 100 g/m^2 increase in biomass of nonnative grass. We provide estimates, test statistics, and *P*-values for covariates in Appendix C.

Response	*n*	Covariates	Estimate	SE	*t*	*P*
Increased						
Dipodomys merriami	105	+Herbaceous, −litter, season, year	12.63	1.07	1.72	0.090
Reithrodontomys fulvescens	177	+All shrubs, season, year	13.38	1.05	2.79	0.006
Sigmodon arizonae	204	+All shrubs, year	31.92	1.06	4.53	<0.001
Decreased						
Chaetodipus penicillatus	130	Season, year	−11.57	1.08	−1.66	0.101
Onychomys leucogaster	187	−Cobble, season	−10.06	1.04	−2.79	0.006
Perognathus flavus	175	+Herbaceous, −cobble, year	−18.54	1.09	−2.51	0.013
Did not change						
Baiomys taylori	175	+Herbaceous, −all shrubs, −cobble, season, year	−5.64	1.08	−0.79	0.430
Chaetodipus hispidus	191	−Litter, −all shrubs, −cobble, season, year	−6.57	1.05	−1.45	0.150
Sigmodon ochrognathus	98	+All shrubs, year	4.70	1.10	0.49	0.629

(Table 6). For most species, fire had little immediate effect on species presence (Table 7). For ≥7 species (*C. hispidus*, *D. merriami*, *N. albigula*, *O. leucogaster*, *O. torridus*, *P. flavus*, and *P. maniculatus*), presence on plots did not change immediately after fire relative to unburned plots (Table 7). Conversely, presence of *B. taylori*, *R. fulvescens*, and *S. arizonae* decreased immediately after fire relative to unburned plots, although data for these species were insufficient for formal analysis (Table 7).

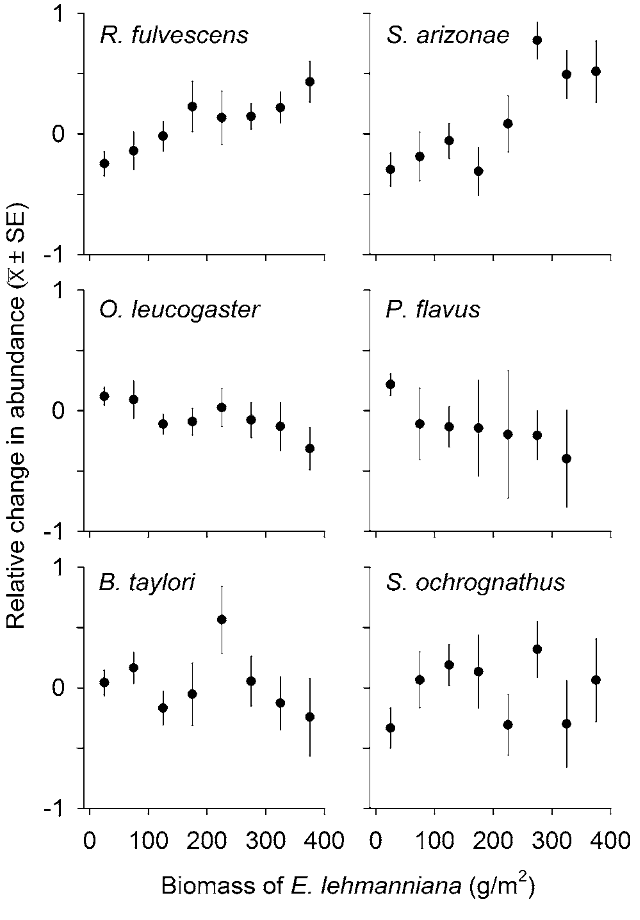

Figure 5. Relative changes in abundance ($\bar{x}$ ± SE) of small mammals in response to increased dominance of nonnative grass, southeastern Arizona, 2000–2004. *Y*-axis represents partial residuals from models describing the estimated effect of nonnative grass after accounting for important covariates (Appendix C). We included only unburned plots in the analyses depicted in the figure.

In contrast to presence, abundance of 6 of the 9 most abundant species changed immediately after fire, decreasing for 5 species and increasing for 1 species relative to unburned plots (Table 6). *B. taylori* decreased by an average of 3.9 individuals per plot (95% CI = 2.3–5.6, 98% decrease), *C. penicillatus* by 1.2 individuals (95% CI = −0.1 to 2.5, 70% decrease), *R. fulvescens* by 3.6 individuals (95% CI = 2.2–5.0, 94% decrease), *S. arizonae* by 7.8 individuals (95% CI = 3.5–12.1, 97% decrease), and *S. ochrognathus* by 1.4 individuals (95% CI = 0.5–2.2, 100% decrease). In contrast, abundance of *D. merriami* increased by an average of 0.7 individuals per plot (95% CI = 0.2–1.3, 145% increase). Abundance of *C. hispidus*, *O. leucogaster*, and *P. flavus* did not change immediately after fire.

Persistence of Fire Effects

Fifteen to 18 months after fire, vegetation biomass averaged 59% lower than pre-fire levels (range = 92% decrease to 32% increase; Table 5). Although some vegetation had recovered, degree of recovery varied among plots and biomass generally had not yet returned to pre-fire levels (Table 5). Decreases in species richness and total abundance of the small-mammal community were greatest immediately after fire (Fig. 6). Effects were ephemeral, however, as measures from burned areas typically approached those from unburned areas within 2 years after fire (Table 8, effects that include time-since-fire; Fig. 6). Although the magnitude of fire effects changed over time, effects of fire on presence of 9 species remained evident 2 years after fire: *C. hispidus*, *C. penicillatus*, *D. merriami*, *O. leucogaster*, *O. torridus*, *P. leucopus*, *P. maniculatus*, *R. montanus*, and *S. arizonae* (Table 9, effects that include time-since-fire; Fig. 7). For some species, effects of fire on presence were complex. For example, presence of *C. hispidus* and *O. torridus* both decreased and increased after fire, suggesting that additional factors mitigated whether fire increased or decreased the amount of habitat for these species (Fig. 8).

Changes in abundance after fire diminished with time as vegetation recovered (Fig. 9). For some species, especially *C. hispidus*, *C. penicillatus*, and *O. leucogaster*, fire effects decreased to nearly

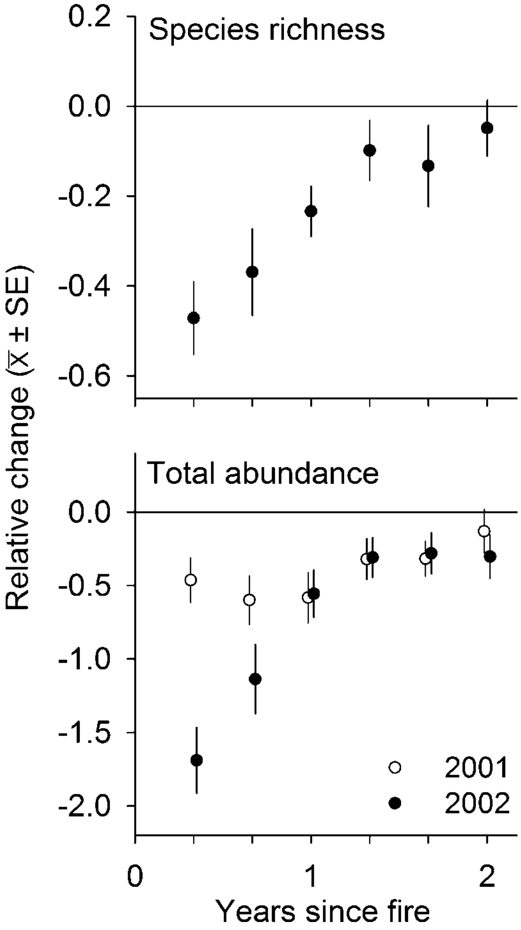

Figure 6. Persistence of fire effects for species richness and total abundance ($\bar{x}$ ± SE) by fire year plotted as the log ratio of burned plots relative to unburned plots over time, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

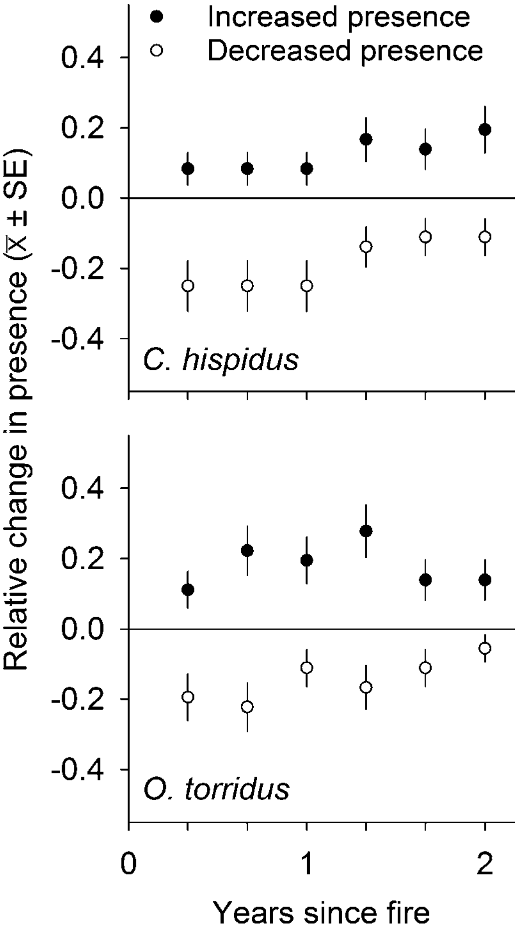

Figure 8. Persistence of fire effects on species presence ($\bar{x}$ ± SE) plotted as the proportion of plots where presence of *Chaetodipus hispidus* and *Onychomys torridus* changed on burned plots relative to unburned plots over time, southeastern Arizona, 2000–2004. Symbols above the reference line at zero indicate the proportion of plots where presence increased after fire and symbols below the reference line indicate the proportion of plots where presence decreased after fire.

zero within 2 years after fire. For other species, however, abundance had not yet returned to levels on unburned plots even after 2 years, including *B. taylori*, *D. merriami*, *R. fulvescens*, and *S. arizonae* (Table 10, effects that include time-since-fire; Figs. 9 and 10).

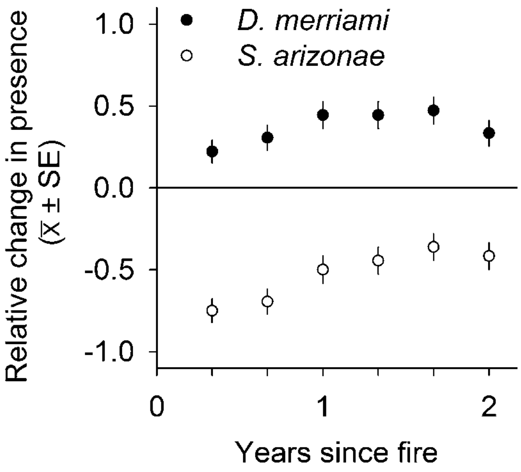

Figure 7. Persistence of fire effects on species presence ($\bar{x}$ ± SE) plotted as the proportion of plots where presence of *Dipdomys merriami* and *Sigmodon arizonae* changed on burned plots relative to unburned plots, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

Timing of Prescribed Fire

Fires ignited during spring and summer affected species richness of the small-mammal community similarly, although total abundance of the community decreased slightly more following summer fires (average difference between burn and control = 10.6 fewer individuals, 95% CI = 7.8–13.1) than following spring fires (average = 9.1 fewer individuals, 95% CI = 6.4–11.8; Table 8, fire season effects). The decrease in total abundance after fire and over time also varied between years and was slightly larger for fires set in 2002 than 2001, at least for the first 3–9 months after fire (Table 8, time-since-fire × fire year interaction; Fig. 6).

Effects of fire on presence of small-mammal species varied more between years of fire treatment than between fire seasons (Table 9, effects that include fire year or fire season). In general, changes in presence of small mammals were greater after fires set in 2002 than after fires set in 2001. For example, presence of *D. merriami* increased on 46% of plots after fires in 2002

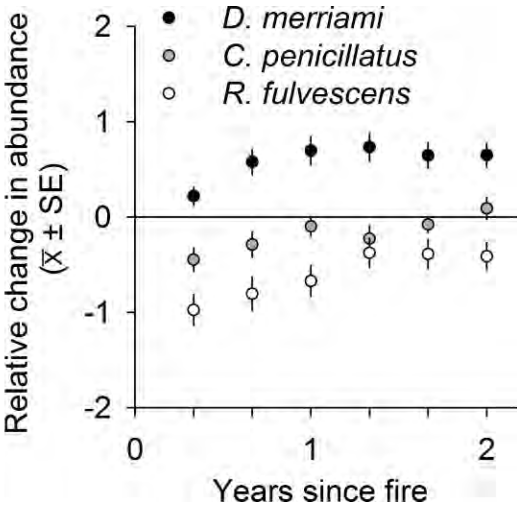

Figure 9. Persistence of fire effects on abundance (x̄ ± SE) of 3 small-mammal species plotted as the log ratio of burned plots relative to unburned plots over time, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

compared to 28% after fires in 2001 and *D. ordii* increased on 18% of plots after fires in 2002 compared to 8% after fires in 2001; in contrast, presence of *O. leucogaster* decreased on 20% of plots after fires in 2002 compared to 11% after fires in 2001 and *S. arizonae* decreased on 63% of plots after fires in 2002 compared to 43% after fires in 2001. When effects differed between fires ignited in spring and summer, changes in presence of small mammals were only slightly greater after summer fires than after spring fires. For example, *O. torridus* increased on 18% of plots after spring fires and 19% after summer fires.

Effects of fire on abundance of small mammals also differed more often between years of fire treatment than between seasons (Table 10, effects that include fire year or fire season). As with changes in species presence and total abundance, more complete fires in 2002 (Table 5) caused larger decreases in abundance after fire for several species (*B. taylori*, *C. hispidus*, *O. leucogaster*, *S. arizonae*, Table 10, Fig. 10) compared to 2001 fires. Where fire effects differed between seasons (Table 10, effects that include fire season), changes in abundance tended to be slightly greater after summer fires than after spring fires (*C. hispidus*, *S. arizonae*, Fig. 10).

Influence of Nonnative Grass Invasion on Fire Effects

Decreases in species richness of the small-mammal community after fire were fairly uniform across the gradient of dominance by nonnative grass (Table 8, nonnative grass effect; Fig. 11). In contrast, decreases in total abundance following fire were greater in areas dominated by nonnative grass than in areas dominated by native grasses (Table 8, nonnative grass × time-since-fire interaction; Fig. 11), especially immediately after fire.

Degree of dominance by nonnative grass changed the effects of fire on presence of 12 of 14 species of small mammals (Table 9, effects that include nonnative grass), with the interaction manifesting in several ways (Figs. 12–14). For some species, degree of

Table 5. Means, standard errors, and ranges for total standing biomass, weather and soil moisture (0–5 cm below surface) at ignition, burn completeness, and change in vegetation biomass 3–6 months and 15–18 months after fire for spring and summer fires in 2001 and 2002, southeastern Arizona; $n = 9$ plots per fire treatment.

	2001						2002					
	Spring			Summer			Spring			Summer		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Total biomass (g/m^2)	358.5	33.6	226 to 553	312.7	36.5	62 to 437	438.4	32.0	255 to 518	500.5	35.9	265 to 658
Relative humidity (%)	43.3	9.2	15 to 88	13.0	2.4	6 to 25	10.0	1.5	4 to 18	40.0	2.2	33 to 55
Air temperature (°C)	13.2	1.8	10 to 22	31.6	0.7	28 to 33	17.3	2.0	10 to 27	27.4	0.6	24 to 29
Soil moisture (%)	2.0	0.4	0.5 to 4.2	0.7	0.3	0.2 to 2.6	0.5	0.1	0.2 to 0.8	1.4	0.2	0.4 to 2.1
Burn completeness (%)	80.8	4.8	53 to 99	94.7	1.9	84 to 100	98.1	0.8	93 to 100	95.2	2.3	79 to 100
Change in biomass 3 months after fire (%)	−36.6	5.6	−52 to −6	−70.2	1.4	−76 to −64	−78.5	3.0	−93 to −68	−77.7	4.4	−96 to −60
Change in biomass 15–18 months after fire (%)	−25.7	9.0	−56 to 32	−62.7	4.7	−75 to −37	−75.9	3.1	−90 to −65	−71.3	4.3	−92 to −58

Table 6. Relative changes in species richness and abundance of small mammals immediately (4–8 weeks) after fires ignited in 2001 or 2002 in southeastern Arizona, computed as the log ratio of burned to unburned plots with standard errors, *t*-statistics, and *P*-values, $n = 36$ plot pairs. Raw differences (burned—control, means and 95% CIs) are provided in the text.

Response	Estimate	SE	*t*	*P*
Species richness	−0.47	0.08	−5.77	<0.001
Total abundance	−1.05	0.17	−6.24	<0.001
Species abundance				
Baiomys taylori	−1.04	0.17	−5.99	<0.001
Chaetodipus hispidus	−0.13	0.12	−1.06	0.298
Chaetodipus penicillatus	−0.43	0.12	−3.54	0.001
Dipodomys merriami	0.23	0.09	2.41	0.021
Onychomys leucogaster	−0.11	0.14	−0.84	0.405
Perognathus flavus	0.22	0.15	1.47	0.151
Reithrodontomys fulvescens	−0.98	0.16	−6.04	<0.001
Sigmodon arizonae	−1.32	0.18	−7.34	<0.001
Sigmodon ochrognathus	−0.35	0.11	−3.20	0.003

Table 7. Proportion of 4 possible outcome categories for changes in presence of small-mammal species on burned and unburned plot pairs immediately (4–8 weeks) following fires ignited in 2001 or 2002 in southeastern Arizona: present only on unburned plot (fire decreased presence), present on both plots (no change), present only on burned plot (fire increased presence), or absent on both plots (no change). We report t-statistics and P-values where data were sufficient for a test, $n = 36$ plot pairs. Where there was evidence of a difference between categories, the category denoted with an asterisk (*) was more likely to occur.

	Did fire decrease presence?				Did fire increase presence?			
Species	**Present on unburned only**	**Present on both**	t	P	**Present on burned only**	**Absent on both**	t	P
Baiomys taylori	0.53	0.03			0.00	0.44		
Chaetodipus hispidus	0.25	0.50^{*}	−1.70	0.100	0.08	0.17		
Chaetodipus intermedius	0.08	0.06			0.06	0.81		
Chaetodipus penicillatus	0.31	0.14	1.46	0.153	0.03	0.53		
Dipodomys merriami	0.06	0.17			0.22	0.56^{*}	−2.19	0.036
Dipodomys ordii	0.00	0.00			0.06	0.94		
Neotoma albigula	0.22	0.00			0.14	0.64^{*}	−3.09	0.004
Onychomys leucogaster	0.11	0.47^{*}	−2.60	0.014	0.14	0.28	−1.27	0.215
Onychomys torridus	0.19	0.11	0.89	0.378	0.11	0.58^{*}	−3.04	0.005
Perognathus flavus	0.14	0.42^{*}	−2.13	0.041	0.31	0.14	1.46	0.153
Peromyscus boylii	0.00	0.00			0.00	1.00		
Peromyscus eremicus	0.06	0.03			0.00	0.92		
Peromyscus leucopus	0.08	0.00			0.22	0.69		
Peromyscus maniculatus	0.06	0.19			0.22	0.53^{*}	−2.05	0.048
Reithrodontomys fulvescens	0.58	0.06			0.00	0.36		
Reithrodontomys megalotis	0.11	0.06			0.03	0.81		
Reithrodontomys montanus	0.22	0.03			0.03	0.72		
Sigmodon arizonae	0.75	0.03			0.00	0.22		
Sigmodon fulviventer	0.06	0.00			0.00	0.94		
Sigmodon ochrognathus	0.25	0.00			0.00	0.75		
Spermophilus spilosoma	0.03	0.06			0.08	0.83		

dominance by nonnative grass changed the magnitude, but not the overall direction, of the fire effect (Figs. 12 and 13). For example, fire was more likely to increase presence of species such as *Dipodomys ordii* in areas dominated by native grasses (Fig. 12) and more likely to increase presence of species such as *D. merriami*, *P. flavus*, and *P. maniculatus* in areas dominated by nonnative grass (Fig. 13). In contrast, fire was more likely to decrease presence of species such as *R. fulvescens*, *R. montanus*, and *S. arizonae* in areas dominated by nonnative grass than in areas dominated by native grasses (Figs. 12 and 13). For some species of small mammals, including *C. hispidus*, *O. leucogaster*, and *O. torridus*, the direction of fire effects on presence was less consistent, with presence both increasing and decreasing across the gradient of nonnative grass (Fig. 14). Persistence of fire effects on presence also varied over the invasion gradient, with presence of some species, including *C. hispidus* and *C. penicillatus*, often recovering to levels on unburned areas more quickly in areas supporting a strong native-grass component than areas dominated by nonnative grass (Figs. 14 and 15).

Dominance of nonnative grass also changed the effects of fire on abundance of 7 of 9 species. As with presence, these changes manifested in different ways (Table 10, effects that include

Table 8. Factors affecting relative changes in species richness and total abundance of small mammals computed as the log ratio of burned plots to unburned plots, with test statistics and P-values, $n = 216$ plot pairs, southeastern Arizona, 2000–2004. There were 172 denominator degrees of freedom for F-tests that include time-since-fire and 27 for all other tests. We describe the meaning of each factor in Table 2.

	Species richness		Total abundance	
Factor	F	P	F	P
Pre-treatment	2.32	0.139	1.20	0.283
Fire season	0.17	0.688	2.88	0.101
Fire year	0.90	0.350	10.30	0.003
Fire season × fire year	0.28	0.598	0.12	0.733
Nonnative grass	0.09	0.768	7.73	0.010
Time since fire	4.87	0.029	4.30	0.040
Nonnative grass × fire season	0.13	0.717	0.39	0.538
Nonnative grass × fire year	0.15	0.702	1.21	0.280
Nonnative grass × fire season × fire year	0.00	0.976	0.92	0.346
Time-since-fire × fire season	0.65	0.422	1.81	0.181
Time-since-fire × fire year	1.15	0.285	6.50	0.012
Time-since-fire × fire season × fire year	0.53	0.468	0.12	0.731
Nonnative grass × time-since-fire	1.28	0.260	3.43	0.066
Nonnative grass × time-since-fire × fire season	0.00	0.984	0.26	0.611
Nonnative grass × time-since-fire × fire year	0.39	0.533	0.90	0.344
Nonnative grass × time-since-fire × fire season × fire year	0.04	0.846	0.28	0.600

Table 9. Factors affecting changes in presence of small mammals between burned and unburned plot pairs, with sample size, *F*-statistics (listed above), and *P*-values (listed below), southeastern Arizona, 2000–2004. With 1 exception, terms that included interactions between fire season and fire year were not significant (all $P \geq 0.110$) and we do not report them here; the exception was the nonnative grass × time-since-fire × fire season × fire year for *Peromyscus leucopus* ($F_{1,174} = 5.49$, $P = 0.020$). We describe the meaning of each factor in Table 2.

Species	*n*	Fire season	Fire year	Nonnative grass	Time-since-fire	Nonnative grass × fire season	Nonnative grass × fire year	Time-since-fire × fire season	Time-since-fire × fire year	Nonnative grass × time-since-fire	Nonnative grass × time-since-fire × fire season	Nonnative grass × time-since-fire × fire year
Chaetodipus hispidus	216	0.70	2.04	2.70	3.57	1.34	0.14	1.01	1.34	4.33	1.88	0.92
		0.556	0.111	0.047	0.015	0.264	0.933	0.389	0.263	0.006	0.134	0.432
Chaetodipus penicillatus	201	0.10	1.66	5.11	7.44	0.81	0.72	0.29	1.32	3.43	0.23	0.13
		0.905	0.193	0.007	<0.001	0.445	0.487	0.748	0.271	0.035	0.882	0.882
Dipodomys merriami	208	0.73	0.49	1.00	1.06	0.11	0.08	0.25	0.18	1.24	0.49	2.57
		0.486	0.614	0.369	0.348	0.899	0.928	0.775	0.835	0.292	0.611	0.079
Dipodomys ordii	201	0.96	2.46	0.34	2.70	1.39	2.78	1.17	2.04	1.36	2.34	1.69
		0.330	0.119	0.558	0.102	0.240	0.097	0.280	0.155	0.246	0.128	0.196
Neotoma albigula	203	0.61	0.75	0.94	0.00	0.68	0.78	0.04	0.14	0.10	0.07	0.08
		0.543	0.486	0.393	0.998	0.507	0.459	0.959	0.874	0.908	0.937	0.927
Onychomys leucogaster	216	1.49	2.37	0.05	2.12	0.87	1.29	1.33	2.38	2.13	0.95	2.43
		0.218	0.073	0.987	0.099	0.455	0.280	0.267	0.071	0.098	0.419	0.067
Onychomys torridus	216	3.41	3.20	1.46	3.10	0.86	2.16	3.27	2.87	4.69	0.20	0.94
		0.019	0.025	0.227	0.028	0.461	0.095	0.023	0.038	0.004	0.894	0.425
Perognathus flavus	201	0.21	1.09	2.97	0.19	0.97	1.07	0.08	1.09	0.43	0.74	1.17
		0.808	0.338	0.054	0.824	0.379	0.346	0.927	0.340	0.650	0.479	0.313
Peromyscus leucopus	190	1.00	2.98	1.53	1.03	1.93	0.06	2.34	3.16	0.00	4.57	0.43
		0.320	0.086	0.217	0.312	0.167	0.801	0.128	0.077	0.972	0.034	0.514
Peromyscus maniculatus	203	0.67	2.38	2.99	2.75	0.84	3.18	0.84	1.88	2.29	1.04	2.47
		0.515	0.096	0.053	0.067	0.435	0.044	0.432	0.156	0.105	0.357	0.088
Reithrodontomys fulvescens	202	0.09	0.80	4.21	0.30	0.28	0.98	0.13	1.50	1.14	0.50	1.39
		0.910	0.449	0.017	0.743	0.757	0.377	0.876	0.226	0.322	0.610	0.252
Reithrodontomys megalotis	209	1.68	1.65	0.71	0.16	1.56	1.40	1.69	0.81	0.44	1.25	0.68
		0.190	0.196	0.494	0.853	0.213	0.249	0.188	0.445	0.643	0.289	0.507
Reithrodontomys montanus	216	1.11	0.42	2.40	0.29	1.20	1.66	1.06	1.08	3.11	0.74	2.10
		0.345	0.736	0.069	0.832	0.313	0.177	0.368	0.361	0.028	0.527	0.102
Sigmodon arizonae	213	0.17	3.11	7.50	2.19	0.25	2.41	0.17	1.84	3.21	0.52	1.97
		0.841	0.047	<0.001	0.115	0.776	0.093	0.840	0.161	0.043	0.595	0.143

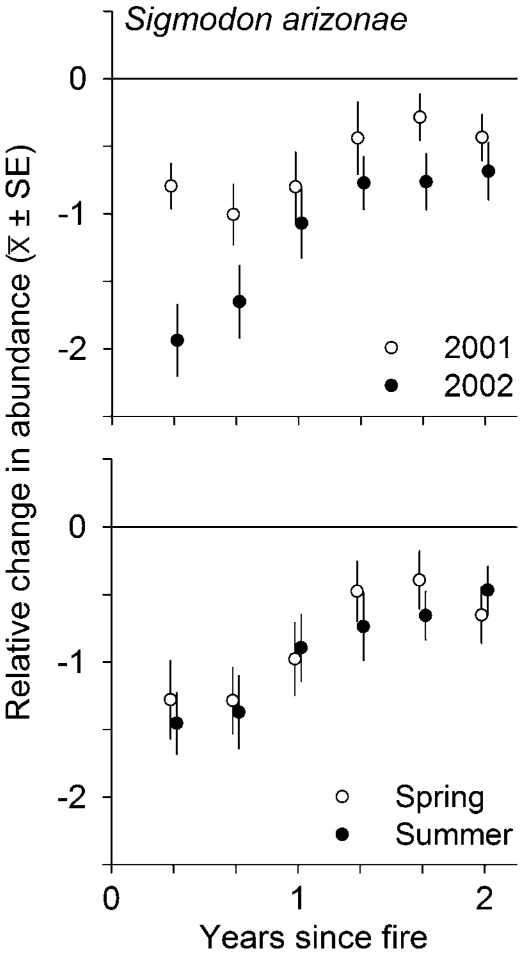

Figure 10. Effects of fire year and fire season on abundance ($\bar{x}$ ± SE) of *Sigmodon arizonae* over time plotted as the log ratio of burned plots relative to unburned plots, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

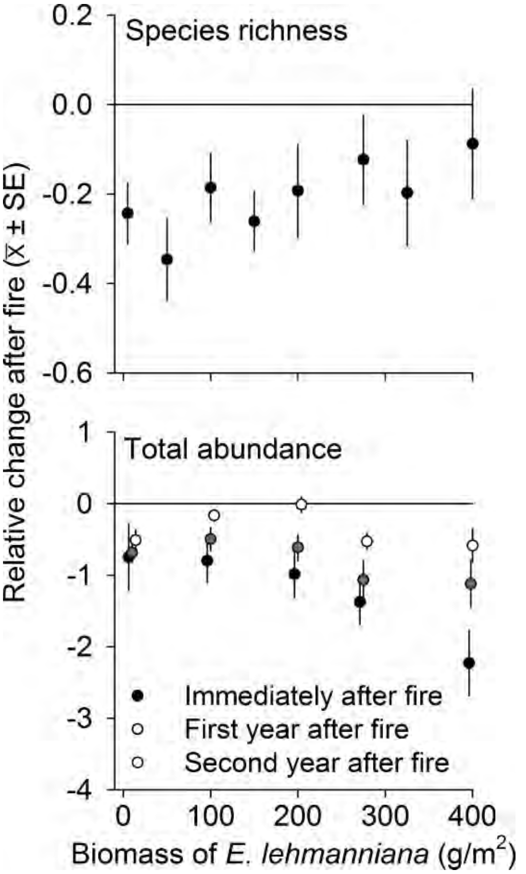

Figure 11. Effects of fire on species richness and total abundance ($\bar{x}$ ± SE) of small mammals in response to dominance of nonnative grass plotted as the log ratio for burned plots relative to unburned plots, southeastern Arizona, 2000–2004. Changes in total abundance are separated by time-since-fire. The reference line at zero represents no effect of fire.

nonnative grass; Fig. 16). For some species, including *R. fulvescens* and *S. arizonae*, decreases in abundance after fire were larger in areas dominated by nonnative grass, whereas for other species, including *B. taylori*, *C. hispidus*, *C. penicillatus*, *O. leucogaster*, and *P. flavus*, decreases in abundance after fire were larger in areas dominated by native grasses (Fig. 16). In addition to altering the magnitude of changes in abundance after fire, dominance of nonnative grass also changed the direction of fire effects for 3 species (*C. hispidus*, *O. leucogaster*, *P. flavus*, Fig. 16). For these species, fire generally decreased their abundance in areas dominated by native grasses and increased their abundance in areas dominated by nonnative grass.

Fire as a Potential Tool for Restoration in Areas Invaded by Nonnative Grass

Composition of the small-mammal community changed in response to fire, with greater changes in composition between burned and unburned plots in areas dominated by nonnative grass than in areas dominated by native grasses (Figs. 17 and 18). Immediately after fire, species composition of small mammals on burned plots, regardless of dominance of nonnative grass, was more similar to each other than to unburned plots (Figs. 17 and 18). In subsequent sampling periods, composition of small mammals on burned plots, regardless of dominance of nonnative grass, was more similar to composition on unburned plots dominated by native grasses than to unburned plots dominated by nonnative grass, suggesting that fire functioned to restore structure of the small-mammal community (Figs. 17 and 18). Even 2 years after fire, some compositional differences in the small-mammal community persisted between burned and unburned plots dominated by nonnative grass (Figs. 17 and 18, Tables 11 and 12). Changes in species composition in response to fire were explained principally by changes in presence and abundance of numerically dominant species, especially by decreases in *Reithrodontomys* and *Sigmodon* spp. and increases in *Chaetodipus*, *Dipodomys*, and *Perognathus* spp. (Tables 11 and 12).

DISCUSSION

Response to Dominance of Nonnative Grass

Structural characteristics of vegetation are among the environmental features most important for determining which areas function as habitat for terrestrial vertebrates (Price and Waser 1984, Morrison et al. 2006). Consequently, the degree to which invasions by nonnative plants affect habitat for a species will

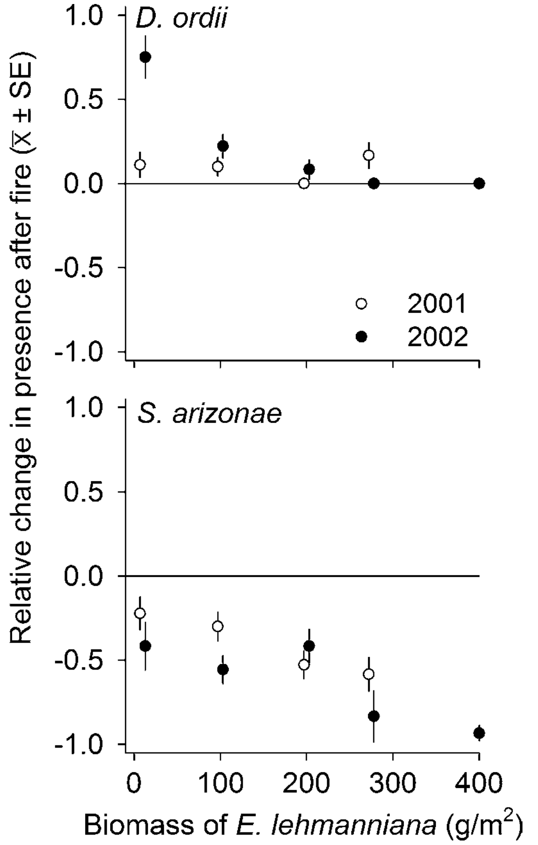

Figure 12. Effects of nonnative grass dominance and fire year on the proportion of plots where presence ($\bar{x}$ ± SE) of *Dipodomys ordii* and *Sigmodon arizonae* changed on burned plots relative to unburned plots, southeastern Arizona, 2000–2004. Filled symbols above the reference line at zero indicate the proportion of plots where presence increased after fire and open symbols below the reference line indicate the proportion of plots where presence decreased after fire.

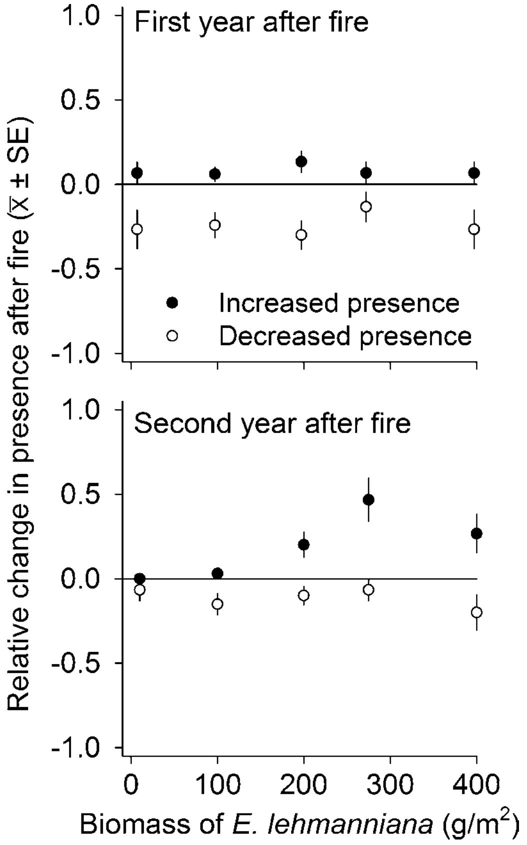

Figure 14. Effects of fire versus dominance of nonnative grass plotted as the proportion of plots where presence ($\bar{x}$ ± SE) of *Chaetodipus hispidus* changed on burned plots relative to unburned plots in the first and second years after fires ignited in 2001 or 2002, southeastern Arizona. Filled symbols above the reference line at zero indicate where presence increased after fire and open symbols below the reference line indicate where presence decreased after fire.

depend largely on the structural contrasts between nonnative and native plants and the degree to which nonnative plants dominate the plant community. For some vertebrates, nonnative plants function as structural equivalents to the native plants they replace (Paradzick and Woodward 2003, Jones and Bock 2005, Sogge et al. 2008). For example, southwestern willow flycatchers (*Empidonax traillii extimus*) nest in nonnative saltcedar (*Tamarix* spp.) and native willows (*Salix* spp.), as both provide the dense vegetation structure they select as breeding habitat (Paradzick and Woodward 2003, Sogge et al. 2008). For many other species, however, nonnative plants alter vegetation structure to such a degree that invaded areas no longer function as habitat. In our study, *E. lehmanniana* provided habitat that was similar or superior to native grasses for several small-mammal species, especially those that inhabit areas with dense cover and high vertical complexity, such as *Neotoma*, *Reithrodontomys*, and *Sigmodon* (Hoffmeister 1986, Brown and Heske 1990, Clark et al. 1998). As dominance of *E. lehmanniana* increased, presence or abundance of these species also increased. In contrast, as dominance of *E. lehmanniana* increased, presence or abundance of species that inhabit areas with sparse vegetation decreased, such as *Chaetodipus*, *Onychomys*, and *Perognathus* (Hoffmeister 1986, Paulson 1988, Clark et al. 1998), indicating that habitat quantity and quality decreased for these species. Therefore, effects of the plant invasion were conditional on habitat preferences of each small-mammal species, proving favorable for some species and unfavorable for others (e.g., Figs. 3–5; Bock et al. 1986, Wilson and Belcher 1989, Lambrinos 2000, Scheiman et al. 2003, Wilson and Wheeler 2005).

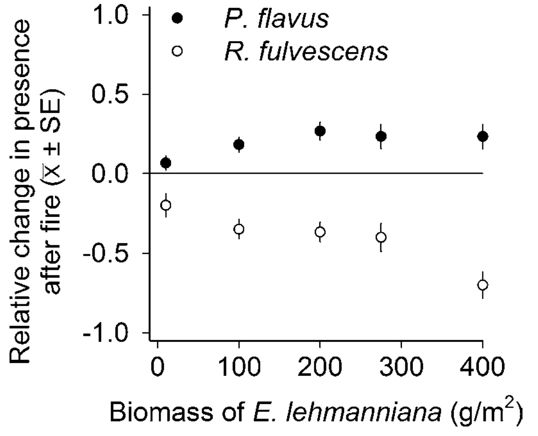

Figure 13. Effects of fire versus dominance of nonnative grass plotted as the proportion of plots where presence ($\bar{x}$ ± SE) of *Perognathus flavus* and *Reithrodontomys fulvescens* changed on burned plots relative to unburned plots, southeastern Arizona, 2000–2004. Filled symbols above the reference line at zero indicate the proportion of plots where presence increased after fire and open symbols below the reference line indicate the proportion of plots where presence decreased after fire.

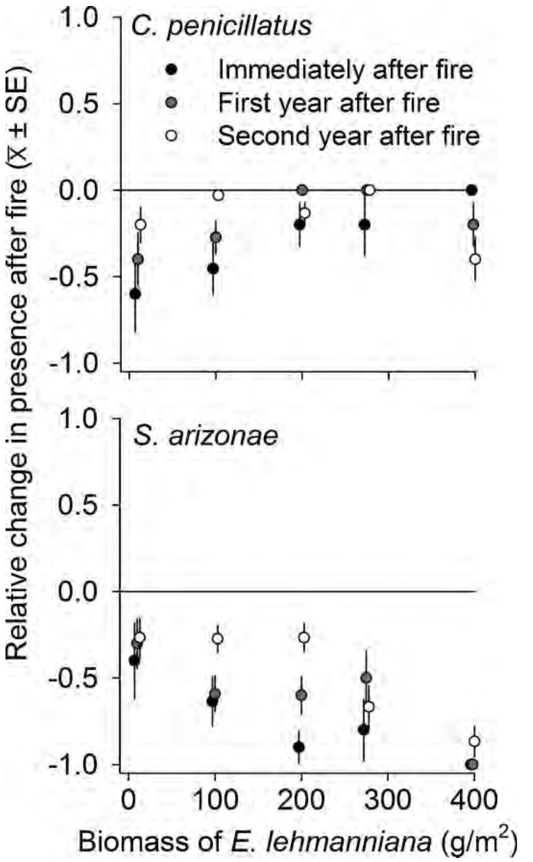

Figure 15. Presence (x̄ ± SE) of *Chaetodipus penicillatus* and *Sigmodon arizonae* after fire versus dominance of nonnative grass plotted as the proportion of plots where presence changed on burned plots relative to unburned plots, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

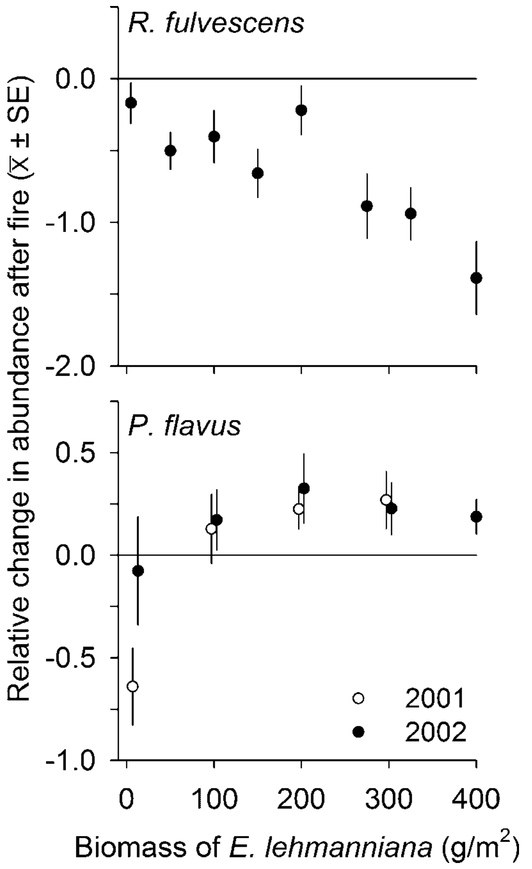

Figure 16. Effects of fire versus dominance of nonnative grass plotted as the log ratio of abundance (x̄ ± SE) of *Reithrodontomys fulvescens* pooled across years and *Perognathus flavus* by year on burned plots relative to unburned plots, southeastern Arizona, 2000–2004. The reference line at zero represents no effect of fire.

As dominance of nonnative grass increased along the invasion gradient, vegetation composition and structure became increasingly homogeneous, which also may explain some of the changes we observed in presence and abundance of small mammals (Fuhlendorf et al. 2006, Riojas-Lopez 2006). Although vegetation structure in some areas dominated by native grasses also was relatively homogeneous, areas dominated by native grasses spanned a much wider range of heterogeneity (Fig. 1). This pattern suggests that areas dominated by native grasses provided a wider range of vegetation structures and correspondingly greater potential to support higher levels of animal diversity, including species with unique habitat requirements (Huston 1979, Collins 1992, Fuhlendorf et al. 2006, Riojas-Lopez 2006).

Plant invasions not only change vegetation structure but also change composition of the plant community, which can affect both the abundance and breadth of food resources available to animals. Because areas dominated by nonnative grass had lower biomass of native grasses and herbaceous species (Geiger 2006), these areas likely produced fewer native seeds and a narrower range of seed types than areas dominated by native plants. Further, areas dominated by *E. lehmanniana* had higher litter biomass, potentially making seeds more difficult for rodents to harvest (Reed et al. 2006). These differences could explain the decreases we observed in presence and abundance of granivorous heteromyids, such as *Chaetodipus* and *Perognathus*, in areas dominated by nonnative grass. Similarly, many groups of insects are less abundant in areas dominated by *E. lehmanniana* (Bock et al. 1986, Litt and Steidl 2010*b*), which could explain the decreases we observed in abundance of insectivores, such as *Onychomys* (Fig. 5). As dominance of nonnative grass increased, richness of insect families, richness of insect morphospecies, and overall abundance of insects decreased in these semi-desert grasslands (Litt and Steidl 2010*b*). Specifically, with every 100 g/m^2 increase in biomass of *E. lehmanniana*, the average number of insect families decreased by 5%, average number of morphospecies decreased by 6%, and overall abundance decreased by 14%. For omnivores that consume both plants and insects, such as *Sigmodon* and *Reithrodontomys* (Cameron and Spencer 1981, Spencer and Cameron 1982, Stancampiano and Caire 1995), changes in vegetation composition may have had lesser effects than on species with narrower diet breadths. Changes in vegetation composition also may have contributed to reductions in reproductive activity we observed in females of 5 species (*C. penicillatus*, *P. flavus*, *P. maniculatus*, *R. montanus*, and *S. arizonae*; A. R. Litt and R. J. Steidl, University of Arizona, unpublished work), as the amount and variety of food resources available to small mammals are important determinants of reproductive rates (Jameson 1953, Beatley 1969, Boutin 1990, Wingfield and Kenagy 1991, Randolph and Cameron 2001).

Species-specific responses to variation in dominance of nonnative grass resulted in a shift in community composition of small

Table 10. Factors affecting relative differences (log ratios) in abundance of small mammals between burned and unburned plot pairs based on mixed models, $n = 216$, F-statistics (listed above) and P-values (listed below), southeastern Arizona, 2000–2004. There were 172 denominator degrees of freedom for tests that include time-since-fire and 27 for all other tests. With 1 exception, terms that included interactions between fire season and fire year were not significant (all $P \geq 0.120$) and we do not report them here; the exception was the time-since-fire × fire season × fire year for *Onychomys leucogaster* ($F_{1,172} = 3.29$, $P = 0.072$). We describe the meaning of each factor in Table 2.

Species	Pre-treatment	Fire season	Fire year	Nonnative grass	Time-since-fire	Nonnative grass × fire season	Nonnative grass × fire year	Time-since-fire × fire season	Time-since-fire × fire year	Nonnative grass × time-since-fire	Nonnative grass × time-since-fire × fire season	Nonnative grass × time-since-fire × fire year
Baiomys taylori	0.71	0.02	4.59	0.34	0.14	0.05	9.82	0.00	0.51	4.33	0.06	4.53
	0.406	0.901	0.041	0.567	0.705	0.819	0.004	0.970	0.475	0.039	0.801	0.035
Chaetodipus hispidus	2.28	2.42	6.33	0.93	0.43	1.09	4.38	4.33	3.63	8.79	2.79	6.64
	0.143	0.131	0.018	0.342	0.512	0.306	0.046	0.039	0.059	0.004	0.097	0.011
Chaetodipus penicillatus	5.81	0.07	0.05	4.36	11.37	0.00	0.01	0.01	0.41	3.26	0.15	0.06
	0.023	0.801	0.827	0.046	0.001	0.977	0.932	0.917	0.524	0.073	0.699	0.811
Dipodomys merriami	17.61	0.17	0.62	1.43	4.85	0.07	0.33	0.25	0.43	0.77	0.09	0.65
	<0.001	0.687	0.439	0.242	0.029	0.796	0.569	0.616	0.515	0.382	0.767	0.422
Onychomys leucogaster	33.44	0.34	6.54	3.13	0.74	0.09	0.11	0.29	8.52	0.07	0.01	2.09
	<0.001	0.566	0.017	0.088	0.392	0.772	0.742	0.592	0.004	0.786	0.921	0.150
Perognathus flavus	0.68	1.09	0.63	1.56	2.64	0.31	3.09	1.28	0.15	0.02	0.33	0.53
	0.416	0.306	0.434	0.223	0.106	0.584	0.090	0.259	0.701	0.897	0.566	0.468
Reithrodontomys fulvescens	2.82	0.51	1.15	4.52	3.83	1.28	2.38	0.40	1.37	0.82	0.02	0.12
	0.105	0.479	0.293	0.043	0.052	0.268	0.134	0.527	0.244	0.365	0.881	0.734
Sigmodon arizonae	6.15	4.56	15.44	43.37	4.61	0.46	1.42	4.14	13.81	5.85	0.31	1.68
	0.020	0.042	<0.001	<0.001	0.033	0.502	0.244	0.044	<0.001	0.017	0.576	0.196
Sigmodon ochrognathus	0.75	0.02	0.49	0.38	1.96	0.03	0.00	0.06	0.40	1.51	0.06	0.21
	0.394	0.879	0.489	0.544	0.163	0.869	0.962	0.809	0.526	0.221	0.810	0.651

mammals across the invasion gradient (Fig. 19). In general, as dominance of nonnative grass increased, granivorous heteromyids and insectivorous murids decreased in presence and abundance (e.g., *Chaetodipus*, *Onychomys*, *Perognathus*), and herbivorous and omnivorous murids increased (e.g., *Reithrodontomys*, *Sigmodon*). Dominance of granivorous species on sites with low cover and herbivorous species on sites with high cover are compositional patterns consistent with small-mammal communities in grassland systems throughout North America; granivorous species are especially prominent in semi-desert grasslands (Grant and Birney 1979). The shift in functional composition of the small-mammal community away from granivores in areas dominated by nonnative grass could further affect vegetation composition and soil properties because granivorous small mammals play pivotal roles in seed dispersal, seed predation, and soil disturbance (Brown et al. 1979, Brown and Heske 1990).

In some grassland plant communities invaded by dense nonnative grasses, stands of vegetation formed by invading grasses are thought to facilitate spread of these nonnative plants by providing refuges for mammalian consumers (Caccia et al. 2006, Orrock et al. 2008). If consumers prefer the dense cover provided by nonnative grasses but forage preferentially on native plants, consumers may confer an apparent competitive advantage to the nonnative plant (Orrock et al. 2008). We observed the strongest positive responses to increased dominance of nonnative grass from species within the genera *Reithrodontomys* and *Sigmodon* (Tables 3 and 4), which are comprised principally of omnivores and herbivores (Spencer and Cameron 1982, Hoffmeister 1986, Stancampiano and Caire 1995). If these species consume plants and seeds of native plant species preferentially—which seems likely given that seeds of most native plants are much larger and have greater caloric content than the small seeds of *E. lehmanniana* (Reichman 1975)—these species may be influencing dynamics of the invasion by *E. lehmanniana*.

Immediate Response to Fire

Because small mammals are linked closely to vegetation structure, any process that alters that structure is likely to affect the distribution and demography of small-mammal populations and composition of the community. Responses of small mammals to fire, therefore, will generally reflect the magnitude of changes in vegetation structure caused by fire and will vary with fire severity, which is a function of fuel load and characteristics of the dominant plant species on a site (McPherson 1995). Relative to fires in forested ecosystems, fires in grasslands commonly consume nearly all aboveground biomass because plants are highly flammable and the plant community structurally simple, with less vertical structure and fewer fuel layers than forests. These characteristics of grasslands make studying the effects of fire on animals somewhat simpler and more efficient than in many other plant communities, as effects tend to be much more consistent among fires (Steidl and Litt 2009).

Short-term changes in abundance of small mammals due to fire that we observed were explained well by the relative importance of vegetation density for each species, which generally reflected their responses to changes in vegetation structure caused by

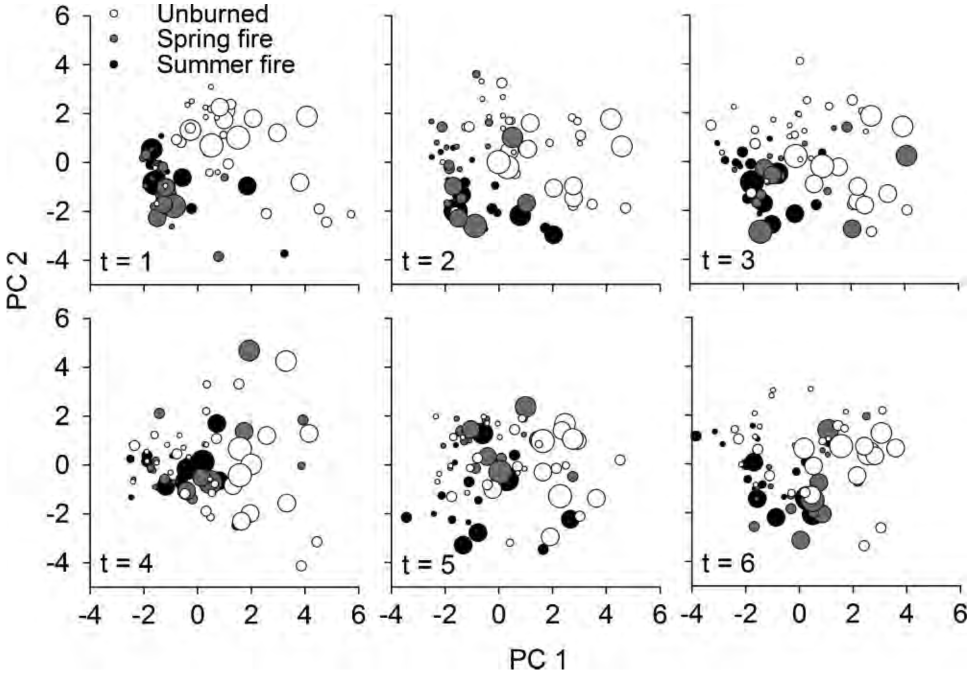

Figure 17. Changes in composition of the small-mammal community based on presence of species on plots and illustrating effects of nonnative-grass dominance, fire treatment, and time-since-fire (t) in species-space where 1 year after fire corresponds to sampling period $t = 3$ and 2 years after fire corresponds to $t = 6$, southeastern Arizona, 2000–2004. Burned plots are represented with filled symbols and unburned plots with open symbols. The size of the symbol indicates the degree of dominance by nonnative grass, with small symbols representing plots dominated by native grasses and large symbols representing plots dominated by nonnative grass. Axes are based on the first 2 principal components (PC1 and PC2, $n = 72$ plots, 36 burned plots and the respective unburned plots sampled at the same time) of presence of 22 species; see Table 11 for a list of species that contributed most to changes in composition.

invasion of dense nonnative grass. Species that prefer areas of dense vegetation, such as *Reithrodontomys* and *Sigmodon*, were most abundant in areas dominated by nonnative grass and decreased greatly in abundance immediately after fire. In contrast, species that inhabit more open areas, including heteromyids such as *Chaetodipus* and *Perognathus*, were more abundant in areas dominated by native grasses and decreased less in abundance immediately after fire, patterns also observed in previous studies (Bock and Bock 1978, Simons 1991, Fitzgerald et al. 2002).

By drastically altering vegetation structure in grassland plant communities, fire effectively resets vegetation succession that in turn drives changes in composition of the small-mammal community. Changes in vegetation and other habitat characteristics resulting from fire can generate a predictable succession of animal species as vegetation recovers, with each species reaching their highest abundance when their ideal habitat conditions develop (Fox 1982, 1990; Monamy and Fox 2000; Fox et al. 2003; Letnic et al. 2004).

Table 11. Species contributions to composition of the small-mammal community based on presence of 22 species, southeastern Arizona, 2000–2004 (Fig. 17). Contributions are based on correlation of species presence with the first 2 principal components; we generated a separate principal components analysis for each of the six sampling periods after fire ($n = 72$ plots). We list species only if $|r| \geq 0.50$. Time = 3 corresponds to sampling done 1 year after fire and time = 6 corresponds to sampling done 2 years after fire. For all sampling periods, the first principal component explained 14–16% of variation in community composition and the second explained 10–12%.

	Principal component 1						**Principal component 2**					
Species	**Time = 1**	**2**	**3**	**4**	**5**	**6**	**Time = 1**	**2**	**3**	**4**	**5**	**6**
Baiomys taylori							0.72		0.55	0.58		0.58
Chaetodipus hispidus				−0.58				0.63	0.54			
Chaetodipus penicillatus						−0.51		0.62		−0.51		
Dipodomys merriami								−0.57				
Dipodomys ordii						−0.52						
Neotoma albigula	0.51			0.50	0.58				−0.54			
Perognathus flavus				−0.55							0.65	
Peromyscus leucopus							−0.59				−0.54	
Peromyscus maniculatus							−0.53	−0.51			−0.63	−0.59
Reithrodontomys fulvescens	0.63	0.71	0.73	0.62	0.66	0.56						
Reithrodontomys megalotis	0.69	0.67	0.62	0.61							−0.60	
Reithrodontomys montanus		0.55								0.56		
Sigmodon arizonae	0.69	0.68	0.78	0.63	0.60	0.56						
Sigmodon fulviventer		0.50							0.55	0.63		
Sigmodon ochrognathus	0.72	0.75	0.68	0.58	0.71	0.64						

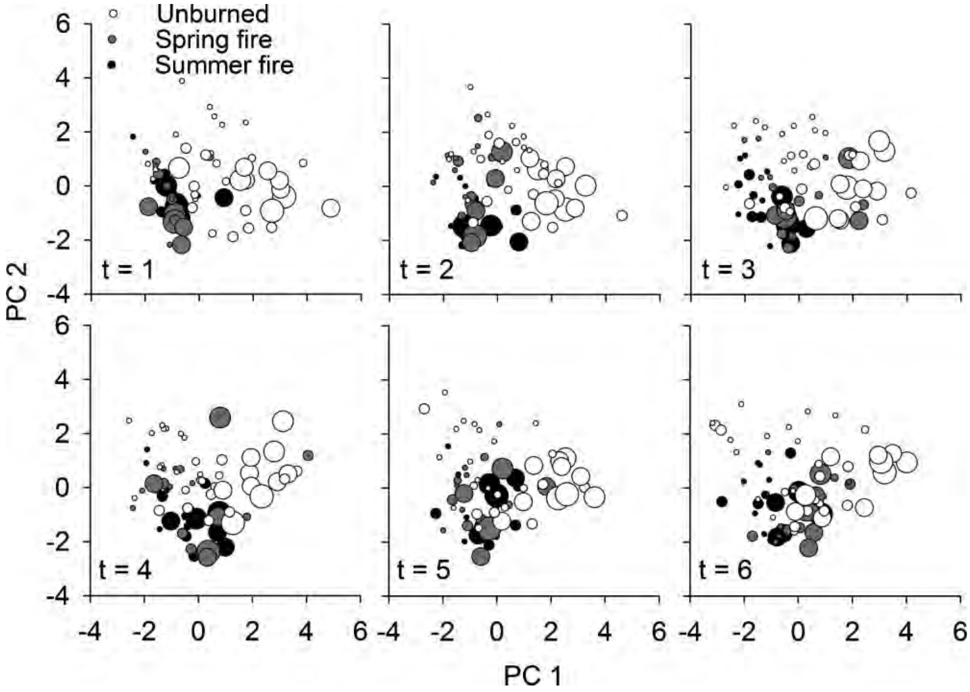

Figure 18. Changes in composition of the small-mammal community based on abundances of common species on plots and illustrating effects of nonnative-grass dominance, fire treatment, and time-since-fire (*t*) based in species-space where 1 year after fire corresponds to sampling period $t = 3$ and 2 years after fire corresponds to $t = 6$, southeastern Arizona, 2000–2004. Burned plots are represented with filled symbols and unburned plots with open symbols. The size of the symbol indicates the degree of dominance by nonnative grass, with small symbols representing plots dominated by native grasses and large symbols representing plots dominated by nonnative grass. Axes are based on the first 2 principal components (PC1 and PC2, $n = 72$ plots, 36 burned plots and the respective unburned plots sampled at the same time) of estimated abundance of 9 species; see Table 12 for a list of species that contributed most to changes in composition.

Persistence of Fire Effects

In grassland ecosystems, including the semi-desert grasslands we studied, fire effects on animals and plants are ephemeral, with characteristics of small-mammal populations often recovering to pre-fire levels within a few years despite large changes immediately after fire (Figs. 6–10; Bock and Bock 1978, 1992; Valone et al. 2002). Rapid recovery of small-mammal populations in grassland ecosystems reflects rapid recovery of vegetation, which is governed principally by precipitation (Humphrey 1949, Cable 1967, Monamy and Fox 2000, Baez et al. 2006). Despite lower than normal precipitation during the entire post-fire period we sampled, and lower vegetation biomass on burned areas relative to unburned areas even 1–2 years after fire (Table 5; Geiger 2006), vegetation structure in burned areas recovered sufficiently within 2 years to provide habitat for many small-mammal species whose populations had decreased markedly after fire.

Timing of Prescribed Fire

We found that responses of small mammals to fire varied more between fires set in different years than between fires set in different seasons. Annual variation in responses of small mammals to fire likely reflected variation in fire severity, driven by differences in fuel loads, soil moisture, and weather conditions at the time of ignition. Years with less complete burns resulted in more heterogeneous vegetation conditions that allowed many species to find the structural features necessary to persist on burned areas after fire. Years with more complete burns reduced cover more completely and more uniformly, creating vegetation

Table 12. Species contributions to composition of the small-mammal community based on abundances of the 9 most common species, southeastern Arizona, 2000–2004 (Fig. 18). Contributions are based on correlation of log-transformed estimates of abundance with the first 2 principal components; we generated a separate principal components analysis for each of six sampling periods after fire ($n = 72$ plots). We list species only if $|r| \geq 0.50$. Time = 3 corresponds to sampling done 1 year after fire and time = 6 corresponds to sampling done 2 years after fire. For all sampling periods, the first principal component explained 24–28% of the variation in community composition and the second explained 17–21%.

	Principal component 1						**Principal component 2**					
Species	**Time = 1**	**2**	**3**	**4**	**5**	**6**	**Time = 1**	**2**	**3**	**4**	**5**	**6**
Baiomys taylori	0.55						0.64		0.71	0.63	0.73	0.72
Chaetodipus hispidus			−0.57	−0.67		−0.52		0.71				
Chaetodipus penicillatus						−0.57		0.59				
Dipodomys merriami							−0.55	−0.51		−0.66	−0.51	−0.64
Onychomys leucogaster									0.61			
Perognathus flavus	−0.54		−0.56	−0.62	−0.55	−0.58	0.63	0.54			0.60	0.53
Reithrodontomys fulvescens	0.88	0.82	0.74	0.72	0.72	0.65						
Sigmodon arizonae	0.87	0.77	0.74	0.64	0.65	0.63						
Sigmodon ochrognathus	0.54	0.58	0.60	0.60	0.69	0.55						

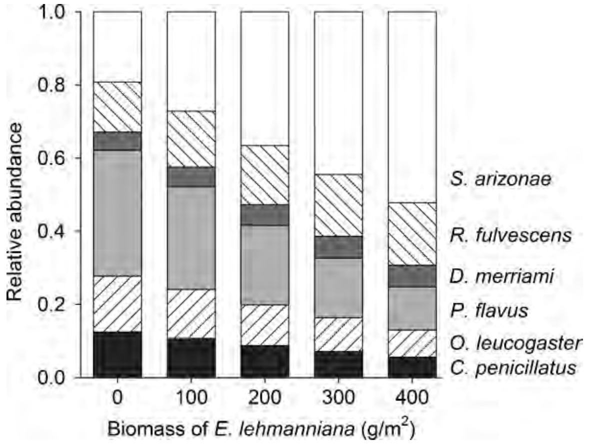

Figure 19. Changes in composition of dominant species in the small-mammal community in response to increased dominance of nonnative grass, southeastern Arizona, 2000–2004.

conditions that were more favorable for species that typically inhabit more open areas and less favorable for species that inhabit areas with dense cover (Brown and Heske 1990, Clark et al. 1998).

In general, we found effects of fire season on small mammals to be small, with little evidence to indicate differences between fires set in spring and summer. Where there were seasonal differences, however, effects of fire were somewhat greater after summer fires than after spring fires, a pattern consistent with other studies that found larger, more persistent changes in plants and small mammals after hotter summer fires (Glendening and Paulsen 1955, Tschirley and Martin 1961, Pase 1971, Bock and Bock 1978, Martin 1983, Brockway et al. 2002). Overall, however, effects of fires set in spring—the timing preferred by managers for safety concerns—were similar to effects of fires set in summer—the timing of most natural wildfires. This finding is important to managers developing prescriptions to restore fire to areas where it has been suppressed historically.

Influence of Nonnative Grass Invasion on Fire Effects

Reintroduction of fire has been proposed as a strategy to reduce dominance of nonnative plants and restore the structure and function of semi-desert grasslands and other fire-governed ecosystems (Geiger and McPherson 2005). In many areas where nonnative grasses have become dominant, however, reestablishing fire has instead caused an increase in dominance of these species (Cable 1965, Martin 1983, Anable et al. 1992, Mack and D'Antonio 1998, D'Antonio 2000). Therefore, whether fire can serve to reduce dominance of nonnative plants will depend in part on how these invading plants respond to fire. In our study system and similar systems, dominance of *E. lehmanniana* did not change markedly in response to fire (Bock and Bock 1992, McGlone and Huenneke 2004, Geiger 2006), probably because this species, like local native grasses, evolved in a fire-governed ecosystem.

In addition to fire not shifting plant composition toward a native-dominated community, fire also functioned differently in areas dominated by nonnative grass relative to areas dominated by native grasses. Specifically, higher vegetation biomass and differences in plant-species composition in areas invaded by nonnative plants changed the way that fire affected the community and populations of small mammals. We found that the magnitude, persistence, and direction of fire effects on many small mammals varied with dominance of *E. lehmanniana*. The specific magnitude and degree of persistence of fire effects on a species depended largely on the level of vegetation density preferred by that species. For mammals that inhabit areas of dense vegetation, we and others found that the reduction of vegetation cover following fire reduced habitat quality dramatically (Bock and Bock 1978, Lyon et al. 2000). In contrast, for mammals that inhabit areas of sparse vegetation, the reduction of vegetation cover following fire improved habitat quality (Figs. 7 and 9). For these species, the lack of vegetation on a site is likely a more important determinant of habitat than whether the dominant vegetation is native or nonnative.

The effect of fire on habitat—either positive or negative—changed across the invasion gradient for *C. hispidus*, *O. leucogaster*, *O. torridus*, and *P. flavus*, suggesting that for these species fire functioned differently in areas invaded by nonnative grass than in areas dominated by native grasses. Differences in composition of the small-mammal community between burned and unburned areas were greatest and most persistent in areas dominated by nonnative grass, mainly because of decreases in presence and abundance of *Reithrodontomys* and *Sigmodon*, species that inhabit areas of dense vegetation, and increases in presence and abundance of *Chaetodipus*, *Dipodomys*, and *Perognathus*, species that inhabit areas of sparse vegetation.

Fire as a Potential Tool for Restoration in Areas Invaded by Nonnative Grass

After fire, the small-mammal community in areas dominated by nonnative grass transitioned to more closely resemble composition of the community in areas dominated by native grasses (Figs. 17 and 18). Prescribed fires, therefore, seemingly offered some potential to restore function of grasslands invaded by nonnative grass for small mammals. Although these restorative effects persisted for only the first few years after fire, this was likely an artifact of studying small mammals in grassland plant communities that recover quickly after fire. Consequently, in ecosystems where the natural fire-return interval is short, such as 10 years in the semi-desert grasslands we studied (McPherson 1995), restoring frequent fires might function to maintain the small mammal community and other biotic elements in a condition that is more consistent with grasslands dominated by native grasses, despite some degree of invasion by nonnative grasses.

Fires in grasslands increase vegetation heterogeneity across the landscape, increasing habitat heterogeneity and maintaining high animal diversity (Fuhlendorf et al. 2006, Steidl and Litt 2009). In areas dominated by *E. lehmanniana* and other similarly dense nonnative grasses, fuels are more continuous and fuel loads greater, resulting in fires that burn hotter and more uniformly than fire in grasslands dominated by native grasses (Rossiter et al. 2003). Therefore, fires in grasslands dominated by nonnative grasses are less likely to develop and maintain the highly heterogeneous conditions necessary to support the highest diversity of animals.

Like several other problematic nonnative grasses such as buffelgrass (*Pennisetum ciliare*, Franklin et al. 2006) and cheatgrass (*Bromus tectorum*, Chambers et al. 2007), *E. lehmanniana* is predicted to increase in dominance and distribution throughout the western United States and Mexico (Schussman et al. 2006).

The frequency, intensity, and extent of fires in areas invaded by these species will also increase, affecting plant and animal communities in novel ways (Dale et al. 2001, Hellmann et al. 2008). These changes are likely to be consequential given the wide array of habitat conditions required to support the high diversity of organisms that inhabit semi-desert grasslands. If, as we suspect, the existing gradient of dominance by nonnative grass that we studied reflects an intermediate point in an ongoing invasion, we anticipate continued changes in the vegetation community, fire regime, and communities of small mammals and other animals in these areas.

MANAGEMENT IMPLICATIONS

Climate change and other aspects of global change will likely serve to further increase rates of establishment and spread of nonnative species (Hellmann et al. 2008). These invasions will change the structure and function of native ecosystems, affecting native plants and animals that inhabit these ecosystems in complex ways (Paine et al. 1998). Despite the potential complexity of these changes, natural resource managers must evaluate whether it is necessary to modify existing management strategies in areas invaded by nonnative species (Paine et al. 1998, Emery and Gross 2005, Hellmann et al. 2008). For example, managers will need to consider how reestablishing fire in ecosystems dominated by nonnative plants might affect wildlife and plants differently given that fires will be more intense, more uniform, and more frequent than fires in ecosystems dominated by native plants.

Managers typically prefer to set prescribed fires in spring, when moisture levels in vegetation and soil are higher, so that fire intensity will be lower and fires easier to contain. With regards to small mammals, seasonal variation in fire effects was slight, therefore fires can be set in spring rather than summer with little change in their effectiveness for providing habitat for small mammals.

Although reintroducing fire did not reduce dominance of *E. lehmanniana* (Geiger 2006), fires increased structural heterogeneity of the plant community at the landscape scale and created a wider range of vegetation conditions for small mammals and other animals, which likely increased the probability that a diversity of species can persist in these invaded grasslands. Restoring fire also will promote other important ecosystem functions, such as nutrient cycling, primary productivity, and seed germination (e.g., Hobbs and Huenneke 1992, Bond and van Wilgen 1996). Therefore, despite the apparent ineffectiveness of restoration fires to reduce dominance of nonnative plants and the novel effects we observed on some small mammals, we recommend that managers seek to mimic the natural fire regime as closely as possible with periodic prescribed fires. This strategy will help to provide the mosaic of structural vegetation elements across the landscape necessary to maintain the diversity of this small-mammal community and other organisms that inhabit areas invaded by nonnative plants (Fuhlendorf et al. 2006).

SUMMARY

1. Invasions by nonnative plants have changed the structure of nearly all grassland ecosystems, which has important consequences for animals that inhabit these ecosystems.
2. Grassland plant communities invaded by nonnative grasses typically have lower vegetation heterogeneity and much higher biomass than the native plant community, which can increase the frequency, intensity, and severity of fires.
3. In semi-desert grasslands of southern Arizona, effects of nonnative-grass invasion varied with habitat preferences of resident small-mammal species. Effects were positive for species that preferred areas of dense vegetation with high biomass and negative for species that preferred areas of sparse vegetation and bare ground.
4. As dominance of nonnative grass increased, presence and abundance of granivorous heteromyids and insectivores decreased, and presence and abundance of omnivorous and herbivorous murids increased.
5. Immediately after fire, species richness of small mammals decreased by an average of 3 species (38%) and abundance of all species combined decreased by an average of 16 individuals (61%) on burned relative to unburned plots. Abundance of 5 species decreased and 1 species increased on burned relative to unburned plots in the weeks immediately after fire.
6. Immediately after fires in areas dominated by nonnative grass, composition of the small-mammal community shifted towards composition of areas dominated by native grasses. This pattern suggests that restoration fires have some positive, short-term benefit for small mammals in grasslands invaded by nonnative plants.
7. Effects of fire diminished through time, although effects on vegetation and on presence and abundance of some small mammal populations remained evident for ≥ 2 years after fire.
8. For most small mammals, effects of fire varied with the degree of nonnative-grass dominance, indicating that the fire functioned differently in areas dominated by nonnative grass relative to areas dominated by native grasses.
9. Fires set in spring had similar effects on small mammals to fires set in summer, the timing of most natural wildfires.
10. Although fires may not restore dominance of native vegetation in grasslands invaded by nonnative plants, they may function to maintain the complex vegetation mosaic necessary to provide habitat for the diverse assemblage of native animals that inhabit fire-governed ecosystems.

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APPENDIX A

Estimates[a], standard errors, sample sizes, dominator degrees of freedom[b], test statistics, and *P*-values for vegetation and temporal variables used in models to describe changes in community-level responses of small mammals over a gradient of dominance by nonnative grass, southeastern Arizona, 2000–2004.

Response	*n*	Explanatory	Estimate	SE	df	*F*	*P*
Species richness	333	*E. lehmanniana*^{2}	−0.0001	0.0000	268	12.2	<0.001
		E. lehmanniana	0.0165	0.0046	268	13.0	<0.001
		Litter	−0.0062	0.0025	268	6.0	0.015
		Herbaceous	0.0168	0.0053	268	10.0	0.002
		Year[c]			95	3.5	0.011
		2000	0.1728	0.6820			
		2001	−0.7751	0.5897			
		2002	−0.5347	0.6284			
		2003	−1.7674	0.6323			
		Season[c]			108	3.6	0.032
		Spring	−0.4253	0.3650			
		Summer	−1.0575	0.4007			
Total abundance[d]	332	*E. lehmanniana*	0.0007	0.0005	271	2.3	0.131
		Herbaceous	0.0078	0.0013	271	34.0	<0.001
		Shrubs (all)	1.3797	0.7207	52	3.7	0.061
		Cobble (ln)	−0.0735	0.0310	52	5.6	0.022
		Year			95	24.1	<0.001
		2000	1.1011	0.1732			
		2001	0.2413	0.1546			
		2002	0.3886	0.1587			
		2003	−0.3034	0.1413			

[a] For this and subsequent appendices, for log-transformed or binary response variables, the inverse natural log of the estimate is equal to the multiplicative change in the response with each 1-unit change in the explanatory variable.

[b] Numerator degrees of freedom were 4 for tests involving sampling year, 2 for sampling season, and 1 for all other explanatory variables.

[c] Reference level is 2004 for sampling year and winter for season.

[d] We log-transformed abundance values.

APPENDIX B

Estimates, standard errors, dominator degrees of freedom, test statistics, and *P*-values for vegetation and temporal variables used in models to describe changes in presence of small mammals over a gradient of dominance by nonnative grass (Table 3), $n = 333$ plot samples for all species, southeastern Arizona, 2000–2004.

Species	Explanatory	Estimate	SE	df	*F*	*P*
Baiomys taylori	*E. lehmanniana*	−0.0021	0.0016	271	1.7	0.189
	Herbaceous	0.0147	0.0056	271	6.9	0.009
	Litter	0.0063	0.0030	271	4.5	0.035
	Cobble (ln)	−0.2221	0.1071	53	4.3	0.043
	Year			95	6.5	<0.001
	2000	0.7711	0.5978			
	2001	−0.3464	0.5414			
	2002	0.8754	0.5800			
	2003	−1.3339	0.5754			
Chaetodipus hispidus	*E. lehmanniana*	−0.0039	0.0012	275	9.7	0.002
	Cobble (ln)	−0.2634	0.0829	53	10.1	0.003
	Season			108	44.6	<0.001
	Spring	2.5505	0.3426			
	Summer	3.6408	0.3964			
Chaetodipus intermedius	*E. lehmanniana*	−0.0025	0.0020	270	1.5	0.219
	Litter	−0.0087	0.0038	270	5.1	0.025
	Cobble (ln)	−0.4141	0.1274	53	10.6	0.002
	Year			95	5.7	<0.001
	2000	−2.3557	0.7192			
	2001	−2.5966	0.6491			
	2002	−5.2017	1.3516			
	2003	−2.0368	0.7009			
	Season			108	7.9	<0.001
	Spring	1.8502	0.6764			
	Summer	2.9046	0.7463			
Chaetodipus penicillatus	*E. lehmanniana*	−0.0028	0.0012	271	4.9	0.028
	Shrubs (all)	−4.1670	1.9097	53	4.8	0.034
	Year			95	3.3	0.015
	2000	−0.6393	0.5573			
	2001	−1.4440	0.4912			
	2002	−1.4028	0.5084			
	2003	−1.2069	0.5089			
	Season			108	12.0	<0.001
	Spring	1.0908	0.2994			
	Summer	1.5500	0.3181			
Dipodomys merriami	*E. lehmanniana*	0.0026	0.0015	275	2.9	0.090
	Season			108	3.1	0.049
	Spring	−0.2486	0.1415			
	Summer	−0.3631	0.1505			
Neotoma albigula	*E. lehmanniana*	0.0026	0.0020	275	1.7	0.188
	Shrubs (all)	13.2544	3.1089	51	18.2	<0.001
	Shrubs (>30 cm)	−12.8403	6.9355	51	3.4	0.070
	Cobble (ln)	1.4706	0.3301	51	19.9	<0.001
	Season			108	2.4	0.099
	Spring	0.1652	0.2510			
	Summer	0.5134	0.2457			
Onychomys leucogaster	*E. lehmanniana*	−0.0021	0.0014	269	2.3	0.128
	Herbaceous	0.0095	0.0050	269	3.6	0.058
	Litter	−0.0047	0.0025	269	3.4	0.067
	Cobble (ln)	−0.1988	0.0933	53	4.5	0.038
	Year			95	2.5	0.048
	2000	−1.2290	0.5844			
	2001	−1.1423	0.5145			
	2002	−0.4701	0.5402			
	2003	−0.0099	0.5168			
	Season			108	11.5	<0.001
	Spring	−0.6865	0.3055			
	Summer	−1.6113	0.3408			
Onychomys torridus	*E. lehmanniana*	−0.0003	0.0012	275	0.1	0.813
	Season			108	8.2	<0.001
	Spring	−1.0142	0.2808			
	Summer	−0.9580	0.2968			
Perognathus flavus	*E. lehmanniana*	−0.0089	0.0016	270	29.5	<0.001
	Herbaceous	0.0101	0.0061	270	2.8	0.097
	Shrubs (all)	−3.2781	1.8952	52	3.0	0.090
	Cobble (ln)	−0.3595	0.0917	52	15.4	<0.001

(*continued*)

APPENDIX B. (*continued*)

Species	Explanatory	Estimate	SE	df	*F*	*P*
	Year			95	3.2	0.016
	2000	1.3896	0.6877			
	2001	−0.0337	0.5541			
	2002	−0.3586	0.6115			
	2003	−0.7982	0.6146			
	Season			108	9.4	<0.001
	Spring	1.2350	0.3426			
	Summer	1.5487	0.3799			
Peromyscus leucopus	*E. lehmanniana*	−0.0001	0.0013	271	0.0	0.934
	Year			95	3.6	0.009
	2000	−2.8760	1.0885			
	2001	−1.4506	0.4841			
	2002	−0.8908	0.4571			
	2003	−1.4694	0.5875			
	Season			108	3.3	0.041
	Spring	−0.2156	0.3675			
	Summer	−2.0034	0.7813			
Peromyscus maniculatus	*E. lehmanniana*	−0.0019	0.0012	275	2.6	0.107
	Cobble (ln)	0.2821	0.0766	53	13.6	<0.001
	Season			108	12.7	<0.001
	Spring	−1.1151	0.3131			
	Summer	−1.9160	0.4192			
Reithrodontomys fulvescens	*E. lehmanniana*	0.0040	0.0014	270	8.2	0.005
	Herbaceous	0.0130	0.0047	270	7.7	0.006
	Cobble (ln)	0.2823	0.0842	53	11.2	0.002
	Year			95	4.3	0.003
	2000	−0.4977	0.5782			
	2001	−0.2222	0.4789			
	2002	1.3799	0.5613			
	2003	−0.2249	0.5009			
	Season			108	4.4	0.014
	Spring	−0.5290	0.2850			
	Summer	−0.9220	0.3105			
Reithrodontomys megalotis	*E. lehmanniana*	0.0051	0.0013	271	15.9	<0.001
	Cobble (ln)	0.1877	0.0813	53	5.3	0.025
	Year			95	3.9	0.006
	2000	−0.0040	0.6467			
	2001	0.0599	0.4873			
	2002	0.7080	0.4952			
	2003	−1.4651	0.6259			
	Season			108	25.3	<0.001
	Spring	−2.0711	0.3623			
	Summer	−3.2065	0.4986			
Reithrodontomys montanus	*E. lehmanniana*	0.0037	0.0013	274	8.6	0.004
	Woody	0.0175	0.0059	274	8.9	0.003
	Season			108	12.2	<0.001
	Spring	−0.6153	0.2834			
	Summer	−1.9847	0.4031			
Sigmodon arizonae	*E. lehmanniana*	0.0074	0.0016	269	21.1	<0.001
	Woody	−0.0162	0.0077	269	4.4	0.036
	Litter	0.0057	0.0026	269	4.6	0.032
	Shrubs (all)	4.4462	2.2486	53	3.9	0.053
	Year			95	6.3	<0.001
	2000	0.7597	0.6313			
	2001	1.6054	0.5586			
	2002	2.3987	0.6094			
	2003	0.0819	0.5556			
	Season			108	6.4	0.002
	Spring	−0.3946	0.3034			
	Summer	0.7248	0.3507			
Sigmodon fulviventer	*E. lehmanniana*	0.0049	0.0017	277	8.3	0.004
Sigmodon ochrognathus	*E. lehmanniana*	0.0012	0.0012	274	0.9	0.351
	Woody	−0.0245	0.0083	274	8.6	0.004
	Shrubs (all)	8.3118	1.7931	52	21.5	<0.001
	Cobble (ln)	0.5157	0.1118	52	21.3	<0.001
	Season			108	2.6	0.079
	Spring	−0.6287	0.3082			
	Summer	−0.6218	0.3256			

APPENDIX C

Estimates, standard errors, sample sizes, dominator degrees of freedom, test statistics, and *P*-values for vegetation and temporal variables used in models to explain changes in abundance[a] of the 9 most common small mammals over a gradient of dominance by nonnative grass, southeastern Arizona, 2000–2004 (Table 4).

Species	*n*	Explanatory	Estimate	SE	df	*F*	*P*
Baiomys taylori	175	*E. lehmanniana*	−0.0006	0.0007	119	0.6	0.430
		Herbaceous	0.0032	0.0019	119	2.9	0.089
		Shrubs (all)	−2.4565	1.0080	45	5.9	0.019
		Cobble (ln)	−0.1350	0.0467	45	8.3	0.006
		Year			48	8.3	<0.001
		2000	0.9602	0.2431			
		2001	0.1810	0.2085			
		2002	0.5498	0.2038			
		2003	0.0325	0.2332			
		Season			60	19.3	<0.001
		Spring	−0.7531	0.1312			
		Summer	−0.2193	0.1502			
Chaetodipus hispidus	191	*E. lehmanniana*	−0.0007	0.0005	132	2.1	0.150
		Litter	−0.0016	0.0009	132	3.3	0.073
		Shrubs (all)	−1.7856	0.6542	48	7.5	0.009
		Cobble (ln)	−0.0877	0.0335	48	6.9	0.012
		Year			55	13.0	<0.001
		2000	0.3845	0.2329			
		2001	0.2475	0.2236			
		2002	−0.6081	0.2304			
		2003	−0.3954	0.2318			
		Season			59	11.7	<0.001
		Spring	0.6620	0.1557			
		Summer	0.7643	0.1578			
Chaetodipus penicillatus	130	*E. lehmanniana*	−0.0012	0.0007	85	2.8	0.101
		Year			42	3.8	0.010
		2000	0.5251	0.2438			
		2001	−0.1041	0.2237			
		2002	0.0945	0.2381			
		2003	−0.0809	0.2057			
		Season			38	4.6	0.017
		Spring	0.1074	0.1397			
		Summer	0.3735	0.1498			
Dipodomys merriami	105	*E. lehmanniana*	0.0012	0.0007	70	3.0	0.090
		Herbaceous	0.0056	0.0028	70	4.1	0.046
		Litter	−0.0037	0.0013	70	7.9	0.006
		Year			28	5.4	0.003
		2000	0.9812	0.2234			
		2001	0.3726	0.1955			
		2002	0.2990	0.2248			
		2003	0.2970	0.2031			
		Season			36	7.2	0.002
		Spring	−0.2546	0.1314			
		Summer	−0.5848	0.1540			
Onychomys leucogaster	187	*E. lehmanniana*	−0.0011	0.0004	133	7.8	0.006
		Cobble (ln)	−0.0627	0.0207	49	9.2	0.004
		Season			50	5.7	0.006
		Spring	−0.1537	0.0903			
		Summer	−0.3770	0.1127			
Perognathus flavus	175	*E. lehmanniana*	−0.0021	0.0008	123	6.3	0.013
		Herbaceous	0.0035	0.0018	123	3.9	0.052
		Cobble (ln)	−0.0686	0.0389	44	3.1	0.084
		Year			46	12.5	<0.001
		2000	0.7176	0.2751			
		2001	−0.1941	0.2627			
		2002	−0.6798	0.2828			
		2003	−0.7137	0.2828			
Reithrodontomys fulvescens	177	*E. lehmanniana*	0.0013	0.0005	119	7.8	0.006
		Shrubs (all)	2.2289	0.6702	49	11.1	0.002
		Year			54	7.1	<0.001
		2000	−0.0392	0.2450			
		2001	0.2686	0.1954			
		2002	0.7088	0.1836			
		2003	0.4305	0.1977			
		Season			62	7.2	0.002
		Spring	−0.2184	0.0945			

(*continued*)

APPENDIX C. (*continued*)

Species	*n*	Explanatory	Estimate	SE	df	*F*	*P*
		Summer	−0.4193	0.1121			
Sigmodon arizonae	204	*E. lehmanniana*	0.0028	0.0006	150	20.5	<0.001
		Shrubs (all)	4.5991	0.9196	47	25.0	<0.001
		Year			65	4.4	0.003
		2000	0.8880	0.3346			
		2001	0.8183	0.2929			
		2002	0.7431	0.2942			
		2003	0.0192	0.3208			
Sigmodon ochrognathus	98	*E. lehmanniana*	0.0005	0.0009	58	0.2	0.629
		Shrubs (all)	3.5127	1.1699	33	9.0	0.005
		Year			29	3.4	0.022
		2000	0.2041	0.4003			
		2001	−0.1504	0.3391			
		2002	0.1703	0.3480			
		2003	−0.7121	0.3383			

[a] We log-transformed all abundance values.

A Sherman trap placed in semi-desert grasslands dominated by a nonnative grass, *Eragrostis lehmanniana.* Photo by Andrea Litt and Robert Steidl.

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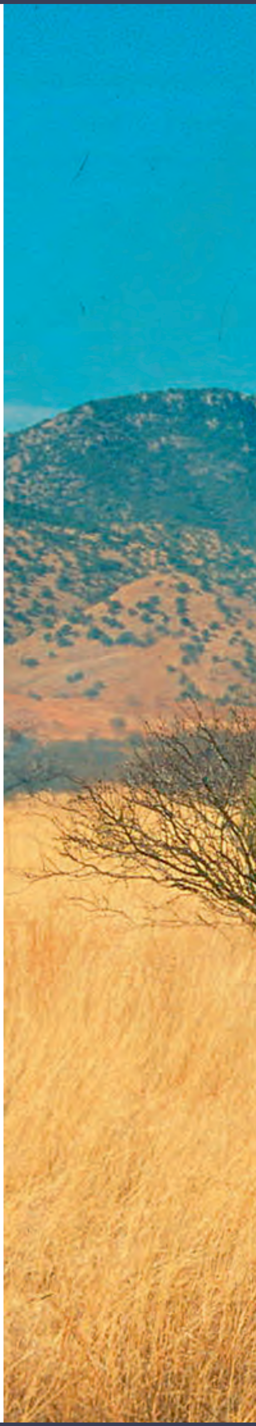

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