

Resilience and alternative stable states after desert wildfires

SCOTT R. ABELLA ¹, DOMINIC M. GENTILCORE, AND LINDSAY P. CHIQUOINE

School of Life Sciences, University of Nevada Las Vegas, Las Vegas, Nevada 89154-4004 USA

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Abstract. Improving models of community change is a fundamental goal in ecology and has renewed importance during global change and increasing human disturbance of the biosphere. Using the Mojave Desert (southwestern United States) as a model system, invaded by nonnative plants and subject to wildfire disturbances, we examined models of resilience, alternative stable states, and convergent-divergent trajectories for 36 yr of plant community change after 31 wildfires in communities dominated by the native shrubs *Larrea tridentata* or *Coleogyne ramosissima*. Perennial species richness on average was fully resilient within 23 yr after disturbance in both community types. Perennial cover was fully resilient within 25 yr in the *Larrea* community, but recovery was projected to require 52 yr in the *Coleogyne* community. Species composition shifts were persistent, and in the *Coleogyne* community, the projected compositional recovery time of 550 yr and increasing resembled a deflected trajectory toward potential alternative states. Disturbed sites contained a perennial species composition of predominately short-statured forbs, subshrubs, and grasses, contrasting with the larger-statured shrub and tree structure of undisturbed sites. Auxiliary data sets characterizing species recruitment, annual plants including nonnative grasses, biocrust communities, and soils showed persistent differences between disturbed and undisturbed sites consistent with positive feedbacks potentially contributing to alternative stable states. Resprouting produced limited resilience for the large shrubs *L. tridentata* and *Yucca* spp. important to population persistence but did not forestall long-term reduced abundance of the species. The nonnative annual grass *Bromus rubens* increased on disturbed sites over time, suggesting persistently abundant nonnative plant fuels and reburn potential. Biocrust cover on disturbed sites was half and species richness a third of amounts on undisturbed sites. Soil nitrogen was 30% greater on disturbed sites and no significant trend was evident for it to decline on even the oldest burns. Disturbed desert plant communities simultaneously supported all three models of resilience, alternative stable states, and convergent-divergent trajectories among community measures (e.g., species richness, composition), timeframes since disturbance, and spatial resolutions. Accommodating expression within ecosystems of multiple models, including those opposing each other, may help broaden theoretical models of ecosystem change.

Key words: convergence; divergence; Mojave Desert; threshold; trajectory; vegetation change.

INTRODUCTION

The degree, rate, and nature of ecological community recovery from disturbance is an important but uncertain component in models of the status of global ecosystems (Murphy and Romanuk 2014, Kröel-Dulay et al. 2015). Community recovery can influence carbon storage, biodiversity and genetic pools, soil stability, and ecosystem services provided to humans (Truchy et al. 2015). While natural and some anthropogenic disturbances are central to the functioning of natural ecosystems, the potential for cumulative recovery debt is concerning in an increasingly human-dominated biosphere in various stages of anthropogenic disturbance (Venter et al. 2016).

In 348 studies globally, recovery debts, quantified as the difference in biodiversity and functions between undisturbed ecosystems and those recovering from anthropogenic disturbance, averaged deficits of 27–51% annually for species abundance and carbon cycling (Moreno-Mateos et al. 2017). Ecological recovery, or lack thereof, highlights opportunities in theoretical and applied ecology for improving models for post-disturbance community dynamics during global change, for novel disturbances with little historical precedent, and for more accurately simulating local and global fluctuations of biodiversity and ecosystem structure and function (Gigon 1983, Romme et al. 2016, D'Antonio et al. 2017).

The ecological literature has devoted extensive discussion to theoretical models of community change for understanding post-disturbance recovery (Westman 1978, Beisner et al. 2003, Ratajczak et al. 2018). Three of the major contemporary models of community change

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¹E-mail: scott.abella@unlv.edu

include resilience, alternative stable states, and convergent-divergent trajectories (Fig. 1). Several papers recently reviewed the complex history and diversity of ways ecologists define resilience (Standish et al. 2014, Hodgson et al. 2015, Donohue et al. 2016, Chambers et al. 2019). In this paper, we adopt one of the widely used definitions of resilience as the ability to return to pre-disturbance conditions or to converge with extant undisturbed conditions (Suding et al. 2004, Nimmo et al. 2015, Ingrisch and Bahn 2018). Basing resilience on convergence with current undisturbed conditions is advantageous for accommodating shifting baselines in ecosystems, such as through climatic variation (Ingrisch and Bahn 2018). While managing for resilient ecosystems is a dominant theme in contemporary ecology, unresolved issues in ecological resilience include how common it is in ecosystems, the timeframes in which it may be expressed, at what ranges of ecosystem structure or processes an ecosystem can be declared resilient, variability in resilience among components of ecosystems, and mechanisms fostering resilience such as resprouting in plant communities (Dudney et al. 2018). Adding to the complexity is that resilience could be contingent on disturbance type or timing, vary temporally in response to climate or other fluctuations, or be seemingly unpredictable until after recovery thresholds have already been exceeded.

When resilience is minimal, an alternative stable state model proposes that disturbance can deflect ecosystems to one or more states incapable of returning to pre-disturbance or undisturbed condition (Schröder et al. 2005). The alternative stable state model need not imply that fluctuations are absent within alternative states, but rather, that alternative states become relatively permanent features on the landscape. The theory of alternative stable states is that disturbance pushes ecosystems past thresholds where resilience is possible, and thereafter, self-reinforcing processes sustain the alternative state (Scheffer et al. 2001, Andersen et al. 2008). Examples include disturbances that remove plant cover to trigger soil erosion, in turn limiting plant reestablishment and perpetuating soil loss (Munson et al. 2011); grass-fire cycles in which nonnative grasses facilitate unnatural fires further stimulating the nonnative grasses and reducing native species (D'Antonio and Vitousek 1992); and ecological thermophilization where disturbances promote species of warmer and drier affinity that perpetuate warmer and drier microclimates (Stevens et al. 2015).

Resilience or alternative stable states can be associated with a third community change model: convergent-divergent ecological trajectories (Fig. 1). Convergence can occur with increasing similarity of disturbed sites with a baseline condition, or through increasing similarity among initially heterogeneous disturbed sites through time (Romme et al. 2016). If disturbed sites converge with each other but not with undisturbed sites, convergence could be associated with formation of one or more

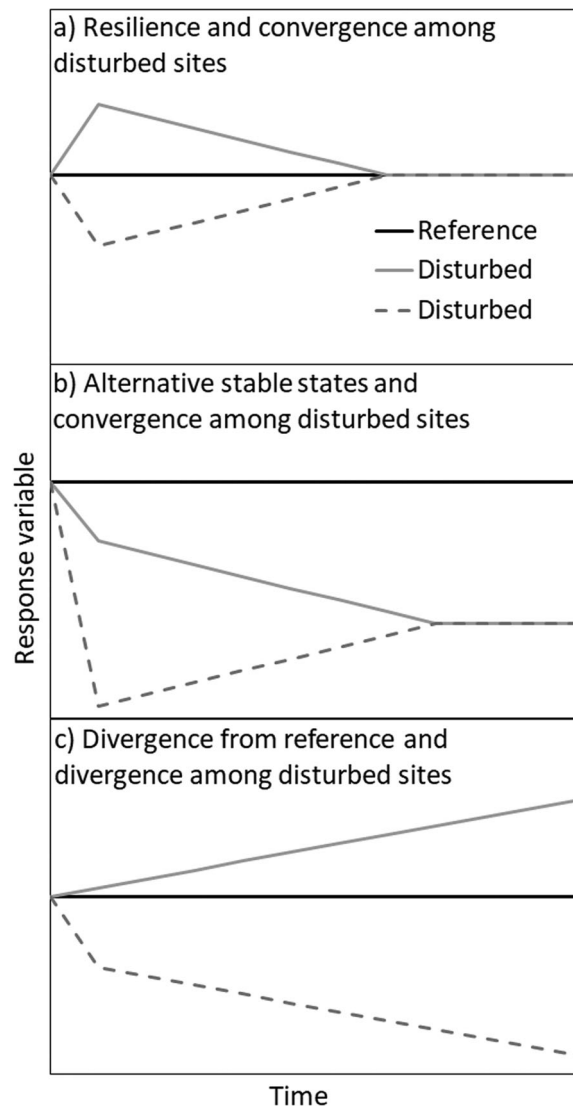


FIG. 1. Representations of theoretical models of resilience, alternative stable states, and convergent or divergent trajectories among disturbed sites. A reference state as a benchmark for assessing resilience is depicted with two disturbed sites. In panel a, resilience occurs through convergence of disturbed with undisturbed conditions and convergence additionally occurs among disturbed sites. Resilience could also be evident when divergence among disturbed sites occurs if each disturbed site were to converge with its own unique undisturbed reference site. In panel b, disturbed sites diverge from reference conditions to form an alternative stable state, and convergence among disturbed sites also occurs in this example. If instead divergence occurred among disturbed sites, multiple alternative stable states could potentially form. In panel c, disturbed sites diverge from the reference and from each other. This model represents lack of resilience and also potentially an absence of alternative stable states if disturbed sites continue diverging from each other. For simplicity of illustration, the models depict a single, constant, reference state. In our study design, each of 31 disturbed wildfire sites was paired with its own undisturbed site, accommodating fluctuations through time in undisturbed reference states.

alternative stable states. Decreasing similarity of disturbed with undisturbed sites or among disturbed sites is divergence. Divergence among disturbed sites could be associated with resilience if the disturbed sites transition toward their undisturbed counterparts. In contrast, divergence of disturbed from undisturbed sites over time could represent failure of resilience and potential for alternative stable states to form.

Resilience and alternative stable state models in theory seem helpful for understanding ecological responses to disturbance, but uncertainties remain in their application to ecosystems. Three main uncertainties include (1) how resilience or susceptibility to enter alternative stable states could vary among components of ecosystems and implications of that variability for defining resilience of ecosystems, (2) the timeframes characterizing resilience or persistence of alternative stable states, and (3) how conformity with the models may vary with spatial scale. Theory often portrays resilience as a property of an entire ecosystem or major state variable, but ecologists have long conjectured potential difficulty in assigning a single value of resilience to an ecosystem (May 1975, Westman 1986, Donohue et al. 2016). Key components of an ecosystem, such as species diversity compared with composition or vascular plants compared with soil, could exhibit opposing trajectories, complicating identifying resilience as an ecosystem property. Moreover, theory has minimal guidance on the timeframe in which recovery must occur to be considered resilience (as opposed to a potential alternative stable state) or how long a state must persist to be considered an alternative stable state (Connell and Sousa 1983, Beisner et al. 2003). Additionally, identification of resilience or alternative stable states and underlying expression of convergent or divergent trajectories could vary with spatial resolution (Nimmo et al. 2015). For example, resilience may not be evident for a collection of sites at the landscape scale, but it could be evident within certain community types (Chambers et al. 2019).

We used the concepts of resilience, alternative stable states, and convergence–divergence to examine ecological trajectories in perennial plant communities after wildfires using a desert biome (Mojave Desert, USA) as a model system. This biome was invaded by nonnative annual plants (e.g., *Bromus rubens*) and susceptible to the novel fire regimes and grass–fire cycles proposed for many invaded drylands globally (Bowman et al. 2014, D’Antonio et al. 2017, Chambers et al. 2019). This is also a significant model system because despite drylands comprising a third of Earth’s land and supporting 20% of the human population (Safriel et al. 2005), they are poorly represented compared to temperate regions in the development and assessment of models of community change (Abella 2010). We addressed the following overarching question: how consistent were perennial plant community changes with the post-disturbance models of resilience, alternative stable states, and convergent–divergent ecological trajectories? We then examined three

specific questions: (1) Do different constituents (e.g., species richness, cover of dominant species) of a community vary in their consistency with resilience, alternative stable state, or convergence–divergence models of change? (2) In what timeframes might resilience or formation of alternative stable states be evident? (3) Does conformity with community change models vary with spatial scale inclusive of all study sites on a landscape or when partitioned into community types? To explore these questions for unplanned, landscape-scale disturbances, we combined three research designs including a time-since-fire chronosequence, burned/unburned comparisons to standardize a recovery benchmark for each site, and repeated temporal measures to directly assess change on 31 wildfires in two community types. We also collected auxiliary data sets characterizing ecosystem components potentially contributing to resilience or positive feedbacks maintaining alternative stable states.

METHODS

Study area

The study area was the eastern Mojave Desert in southern Nevada and northwestern Arizona, USA (Appendix S1: Fig. S1). Near the center of the study area, the Las Vegas, Nevada weather station (elevation 659 m) reported daily average minimum/maximum temperatures of 2°/14°C in January and 26°/40°C in July and 10.4 cm/yr of precipitation (1.4–25.1 cm/yr range) for 1949 through 2018 (Appendix S1: Fig. S2). Two main shrubland communities predominate across the Mojave Desert and the study area specifically: those dominated by the evergreen shrub *Larrea tridentata*, often with *Ambrosia dumosa* or other codominant woody or herbaceous perennials; and those dominated by the medium-sized shrub *Coleogyne ramosissima*, along with taller species such as *Yucca schidigera* or *Yucca brevifolia* (Brooks and Matchett 2006). *Larrea* communities inhabit hot and dry low elevations (~500–1,300 m), while *Coleogyne* communities inhabit cooler and moister elevations around 1,000–1,800 m. In years with sufficient precipitation, annual plants grow in fertile islands (areas of nutrient-enriched soil and ameliorated microclimate below the canopies of many perennial species) and in interspaces between perennials (Steers and Allen 2011).

Data collection

We studied 31 wildfires located within a 200-km east-west and 140-km south-north extent (Appendix S1: Fig. S1). To study these unplanned disturbances, we used a repeated-measures chronosequence design accommodating shifting baselines through time by pairing each burned area with its own unburned area for comparison (Table 1). The study sites constituted 31 of 32 originally established in 2007–2009 by Engel and Abella (2011), with one *Larrea* fire unable to be accessed

TABLE 1. Summary of variables measured to assess change in desert ecosystems after wildfires.

Variable	2007–2009	2016
Burn age gradient (yr)	1–29	9–36
Perennial plant species richness	×	×
Perennial plant cover	×	×
Perennial plant species composition	×	×
<i>Larrea</i> , <i>Yucca</i> resprouting and density	×	×
Density by species of all perennial plants		×
<i>Bromus rubens</i> cover	×	×
Cover by species of all annual plants		×
Soil properties	×	×
Biocrust cover and composition		×

Notes: The study design used permanent plots and was a repeated-measures chronosequence, measured in 2007–2009 and remeasured in 2016 with a corresponding increase in burn age, and with each burn ($n = 31$) paired with its own unburned area. The × symbol indicates a variable was measured that year.

in the present study and excluded. Fifteen of the fires were in *Larrea* and 16 were in *Coleogyne* communities. Each burn was paired with an adjoining unburned area of similar topography, soil parent material, and vegetation type (Fig. 2). Burns were ignited by both human and lightning sources and occurred between 1980 and 2007. Within that period, burns were irregularly distributed in time, a common temporal pattern of desert wildfires where fires often occur in a dry year with abundant dead annual fuel produced during one or more previous wet years (Rao et al. 2010). Although this necessarily resulted in temporal gaps in burn ages available to study, the repeated-measures part of the study design enabled directly assessing temporal change on each burned/unburned pair and expanded the time-since-fire gradient. Burn ages spanned 1–29 yr during initial sampling in 2007–2009 and 9–36 yr during the second sampling in 2016.

In 2007–2009, we randomly established 3–10 plots within each burned and unburned area, with the number of plots generally proportional to burn size. Each plot was 0.01 ha (10×10 m) and contained six 1×1 m quadrats (one at each plot corner and centered at the midpoints of the southern and northern plot lines). We categorized areal cover of each perennial species within each quadrat using cover classes (Peet et al. 1998). We then surveyed whole plots to categorize cover of perennial species not already in quadrats. We also categorized live + dead cover of the nonnative grass *Bromus rubens* as a measure of fuel. We sampled plots once initially during November–June in either 2007, 2008, or 2009 (hereafter 2007–2009), as multiple years were required to establish and sample plots. Using the same methods, we remeasured plots during February–June in 2016. That year in addition to perennial species and *B. rubens* cover, we recorded density of all woody plant and cactus species and categorized cover of each annual species in quadrats and plots using the same procedures as for

perennials. Nomenclature and classification of species by origin (native or nonnative to the United States), potential life span (perennial or annual, which included *Erodium cicutarium* normally growing as an annual in the Mojave Desert), and growth form (e.g., forb, shrub) followed the 2020 Natural Resources Conservation Service PLANTS database.

In addition to *B. rubens* cover, we collected three auxiliary data sets to characterize factors potentially associated with community change or stability: persistence and recruitment of four major perennial species, biological soil crusts (biocrusts), and soil properties. On each plot in 2007–2009 and 2016, we counted the number of individuals of *Larrea* and three *Yucca* spp. (*baccata*, *schidigera*, and *brevifolia*) according to life-cycle categories. These included unburned alive (no evidence of char on stems and live canopy present), burned stems but with live canopy, resprout (main stems dead but with basal sprouting), or dead (no evidence of green material). While it is possible that some burned wood escaped detection, burned wood in deserts can remain visible for decades owing to slow decomposition in the arid climate (Ebert and Ebert 2006). Charred wood was readily visible in 2016 on even the oldest burns. In 2016, we assessed biocrust communities on a subset of six 2005 fires. Parallel to and 20 m from each plot within burned and unburned areas, we established a 25-m transect containing six 25×25 cm quadrats positioned at 0, 5, 10, 15, 20, and 24.7 m along each transect. We categorized biocrust total cover as the percentage of 1-cm^2 cells covered within quadrats, proportionally allocated by biocrust species identified following the 2019 Consortium of North American Lichen and Bryophyte Herbaria. In 2007–2009 and 2016 in interspaces (≥ 1 m from a perennial plant) outside the southwestern and northeastern corners of each plot at all 31 sites, we collected four subsamples of soil (0–5 cm mineral soil depth, totaling 700 cm^3) combined into one plot sample. We focused sampling in interspaces because availability of below-shrub microsites and the species of shrub present varied among plots and previous research suggested that fire can homogenize fertile island and interspace soils by 7 yr post-fire (Fuentes-Ramirez et al. 2015). Samples were analyzed for texture (hydrometer method), pH (1:1 soil: water), total N and C concentration (dry combustion via C/N analyzer), and bulk density to convert N and C concentration to volumetric content.

Data analysis

We averaged data from plots within each burned and paired unburned area on a fire basis, such that each burned-unburned pair was an independent replicate pair. We calculated and analyzed a series of univariate response variables available for both study years (2007–2009 and 2016). These variables included perennial species richness (number of species/100 m^2), total perennial cover and cover by growth form, individual



FIG. 2. Examples of wildfire study sites in the Mojave Desert, USA. Left photos: a plot within the 2005 Loop Fire in 2008 (top) and 2018 (bottom), showing burned stems of *Yucca schidgera* and resprouts of *Larrea tridentata* increasing in height. Middle photos: a plot within the 2005 River Fire in a low-elevation *Larrea* community showing minimal change in *L. tridentata* cover and increase in *Sphaeralcea ambigua* (the beige-grayish forb during winter dormancy) between 2007 (top) and 2019 (bottom). Right photos: unburned-burned contrasts in 2007 after the 2005 Tramp Fire (top) and in 2009 after the 1988 Zipper Fire (bottom). Burned stems of *Yucca brevifolia*, with some resprouting, remain visible on the right side of the top photo. A persistent forb–small shrub community is in the burned foreground of the bottom photo, with unburned *Coleogyne ramosissima* (grayish shrubs) in the background. Photo credits: left and middle photos by S. R. Abella; right photos by E. C. Engel.

species cover (e.g., *L. tridentata* and *C. ramosissima*), live + dead cover of *B. rubens*, and Sørensen similarity of perennial species composition (relative cover as cover of species/ \sum cover of all species on a burned or unburned area) between years (2007–2009:2016) and burned:unburned pairs within years. For woody plant–cactus density and annual species data sets available for 2016, we calculated community measures (species richness, burned:unburned Sørensen similarity, and mean density or cover).

To analyze response variables, we used a complementary suite of univariate, bivariate, and multivariate analyses. We applied analysis of variance (ANOVA) to univariate variables available for both years using a partially hierarchical, mixed model including the fixed effects (and all interactions) of burn status (burned, unburned), burn age group (1980s, 1990s, 2000s), and community type (*Larrea*, *Coleogyne*), along with study year (2007–2009, 2016) as a repeated measure and site (31 burned-unburned pairs) as a random effect. Based on results for full models, minimum adequate models were then run for multiple comparisons of least-squares means using Tukey tests. We analyzed some variables on transformed scales (e.g., square-root- or arcsine-transformed) to improve normality of residuals. However, qualitative statistical conclusions changed little from analyses using the raw data, so we report results from untransformed data. Except for excluding the repeated

measure from models, we used the same procedures to analyze univariate variables available for 2016 only. Analyses were performed with PROC MIXED in SAS 9.4 (SAS Institute, Inc., Cary, North Carolina, USA).

We used regression to relate burn age to response variables on burned areas standardized to paired unburned areas and estimate how many years were required for burned and unburned conditions to fully converge. To accompany burned:unburned Sørensen similarity already standardized, we calculated ratios for perennial species richness and cover of burned relative to paired unburned values for each fire for 2007–2009 and 2016. If full resilience was not attained within the 36-yr post-fire period, we calculated theoretical future expectations of time to convergence with unburned areas, assuming continuation of linear trends. In some cases, theoretical projections of time to full resilience increased between 2007–2009 and 2016, or regression slopes were not significantly different from zero at $P < 0.05$. We proceeded with calculating recovery estimates in these cases to reflect the potential ecological importance of divergence between burned and unburned areas over time (i.e., potential lack of a resilience trajectory) and that small regression slopes could signify slow change over essentially indeterminately long time periods.

The multivariate response variables were species composition matrices (burned-unburned pairs \times species)

consisting of relative cover for perennials and annuals and relative density for the 2016 woody plant–cactus data set. We performed multivariate analyses in PC-ORD 7.07 using ordination (nonmetric multidimensional scaling, “thorough” default settings with Sørensen distance) and multi-response permutation procedures (MRPP; Mielke and Berry 2007). We performed analyses separately for perennials and annuals using all data or as subset analyses, such as for only burned sites comparing burn age categories. For comparisons involving paired data (burned:unburned comparisons or temporal comparisons within burned or unburned areas), we used blocked MRPP (BMRPP), with fire identity as the blocking variable. For MRPP, we used default group weighting and either Euclidean (for consistency with sets of analyses employing BMRPP) or Sørensen distance (for sets of analyses comparing burn ages testing for convergence or divergence). For BMRPP, we used Euclidean distance (the distance measure required by BMRPP) and median alignment within blocks to standardize burned:unburned comparisons. To identify species producing multivariate differences identified in MRPP and BMRPP and associated with particular groups each study year, we used indicator species analysis (Dufrêne and Legendre 1997) or blocked indicator species analysis in PC-ORD with the same blocking structure as for BMRPP. Significance of indicator values for each species was tested via permutation (4,999 randomizations) at $P < 0.05$. To avoid inflating Type 2 errors, P values for indicator species analysis are traditionally not corrected for multiple tests because each species is of interest independently. At $P = 0.05$, 5.9 of the 118 perennial species in the *Larrea* and 6.2 of the 125 perennial species in the *Coleogyne* community could be significant indicators by chance.

To analyze the auxiliary data sets, we calculated means and confidence intervals for density by life-cycle category and species for *Larrea* and *Yucca* spp. We used a paired t test to compare burned and unburned means for biocrust cover and species richness (number of species/0.375 m² consisting of the six quadrats per transect). To assess soil properties, we used the same mixed-model analysis of variance as for univariate vegetation variables measured in both study years.

RESULTS

Perennial vegetation

Species richness (number of species/100 m²) was resilient, fully recovering on burned areas to levels of unburned areas within 23 yr in both the *Larrea* and *Coleogyne* communities (Fig. 3). Supporting the bivariate results, richness varied through a burn status \times age interaction and study year main effect in ANOVA (Appendix S1: Table S1). Young burns (age 1–11 yr) had lower richness than their unburned counterparts, whereas old burns (age 21–36 yr) had greater richness

than unburned areas (Appendix S1: Fig. S3). Among burns, richness increased with burn age, increasing by 66% from young to old burns. Richness differed by year, increasing from 8.3 ± 0.5 (mean \pm SE) in 2007–2009 to 11.6 ± 0.6 species/100 m² in 2016. Richness averaged 11.5 ± 0.5 in the *Coleogyne* and 8.3 ± 0.6 species/100 m² in the *Larrea* community.

Perennial cover was lower but more resilient in the *Larrea* than in the *Coleogyne* community. This variation manifested through three two-way interactions, including via burn status \times age, burn status \times community type, and community type \times year (Appendix S1: Table S1). For example, in the burn status \times community type interaction, cover was lower in burned ($8\% \pm 1\%$) than unburned ($24\% \pm 2\%$) *Larrea* and each was lower than the respective cover in burned ($19\% \pm 2\%$) and unburned ($36\% \pm 2\%$) *Coleogyne*. Based on regressions with burn age for 2016, cover in the *Larrea* community was fully resilient by 25 yr after fire, which was within the study period (Fig. 3). In comparison, full resilience of cover was projected to require 52 yr in the *Coleogyne* community.

Variable patterns in cover among plant growth forms were evident ranging from no significant differences among study factors (cacti) to differences across main effects (forbs varying with burn status and year) or various two- and three-way interactions (graminoids, shrubs, and trees; Appendix S1: Table S1). Forb cover was elevated on burned compared to unburned areas within 1–2 yr after fire. Except for low cover on some burns, the elevated forb cover generally persisted across study years and the 36-yr burn age gradient (Appendix S1: Fig. S4). Graminoids generally exhibited elevated cover on burned compared to unburned areas, especially in *Coleogyne* communities and in 2016. Shrub cover was positively related to the number of years since fire on burned areas in 2007–2009 ($y = 0.54x + 0.29$, SE of slope = 0.05; $r^2 = 0.80$, $P < 0.001$) and 2016 ($y = 0.75x - 2.91$, SE of slope = 0.12; $r^2 = 0.57$, $P < 0.001$). Shrub cover on burned areas doubled from $6\% \pm 1\%$ in 2007–2009 to $12\% \pm 2\%$ in 2016. Because of this increase by 2016, the oldest burns had shrub cover nearly equivalent to unburned areas, although the species contributing the cover were not necessarily the same. Trees (primarily *Yucca brevifolia*) had low and variable cover with no discernable pattern with burn age.

Perennial species distributions supported a three-way classification of response to disturbance: increasers (e.g., the forb *Sphaeralcea ambigua*); versatile, showing increases or decreases in approximately equal proportions among burns (e.g., the grass *Pleuraphis rigida*); and decreasers (e.g., the small tree *Y. brevifolia*; Appendix S1: Fig. S5). In 2016, for example, the fire-promoted *S. ambigua* had higher cover on burned compared to unburned areas for 27 of 31 (87%) sites, *Gutierrezia sarothrae* for 72% of sites when the species was present, and *Encelia virginensis* for 78% of sites. The versatile *Ambrosia dumosa* had greater cover on burned

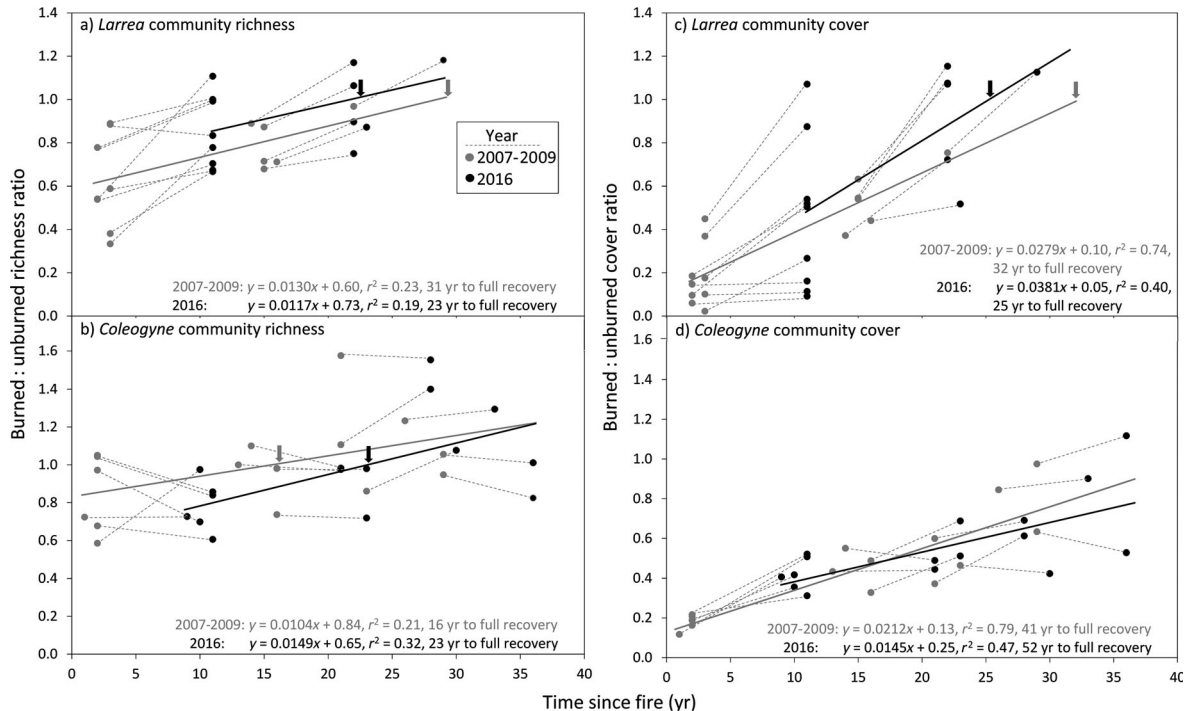


FIG. 3. Variation in perennial plant species richness (species/100 m²) and cover in burned relative to unburned areas with time since fire in two community types for 31 wildfires in the Mojave Desert, USA. Points represent individual fires sampled during two study years, shown connected by dotted lines. Arrows note attainment of full resilience (burned : unburned = 1.0) when resilience was achieved during the study period. Regression lines and estimated years to full resilience are shown separately for 2007–2009 and 2016 study years. Standard errors (SE) and *P* values for slopes of lines are as follows and are formatted as 2007–2009 SE (*P*), 2016 SE (*P*): (a) 0.007 (0.070), 0.007 (0.109); (b) 0.005 (0.073), 0.006 (0.023); (c) 0.004 (<0.001), 0.013 (0.012); (d) 0.003 (<0.001), 0.004 (0.003).

areas on 41% of sites (compared with 59% of unburned sites) the species inhabited, and *P. rigida* had higher cover on equal numbers (eight sites for each) of burned and unburned areas. Exemplifying decreasees, *Yucca schidigera* had lower cover on burned compared to unburned areas on 91% of the 22 sites the species inhabited.

The community dominants varied in their resilience, with *Larrea tridentata* more resilient than *Coleogyne ramosissima*, although both had high variability in recovery among burns (Fig. 4). Some burns exhibited appreciable recovery of the species while other burns had no recovery.

Species composition displayed minimal resilience, instead trending toward divergence of burned from unburned communities through time. The estimated time to full recovery of species composition (Sørensen similarity) in burned *Larrea* sites was 51 yr for the 2007–2009 data, but this subsequently increased as burned sites diverged from unburned sites (Fig. 4). The relationship between burn age and burned:unburned similarity was minimal in *Coleogyne* sites and the projected time to recovery of species composition lengthened to 550 yr in 2016.

Multivariate analyses revealed that species composition varied with community type and burn status, with differences persisting across study years. An ordination using relative cover of perennial composition accounted for 58% of the variance in the first two axes and was correlated with an Axis 1 gradient of *Larrea* or *Coleogyne* species assemblages (Fig. 5a). Although the dominant species *L. tridentata* and *C. ramosissima* had low cover in burned areas, *L. tridentata* in particular remained important in burned species composition because other species supplied minimal cover. Axis 2 was correlated with burn-associated *S. ambigua* and *G. sarothrae* and unburned-associated *Ephedra nevadensis*. All permutation tests were significant comparing species composition between burn statuses and community types (Fig. 5a inset). These results were supported by blocked indicator species analyses identifying suites of species distinguishing community type–burn status combinations in 2016 (Fig. 6). Some species, such as *S. ambigua* and *Dasyochloa pulchella*, were significantly associated with burned areas in both the *Larrea* and *Coleogyne* communities. Other species were associated with burned areas in only one community type, such as *Baileya multiradiata* and *G. sarothrae* in the *Coleogyne* community.

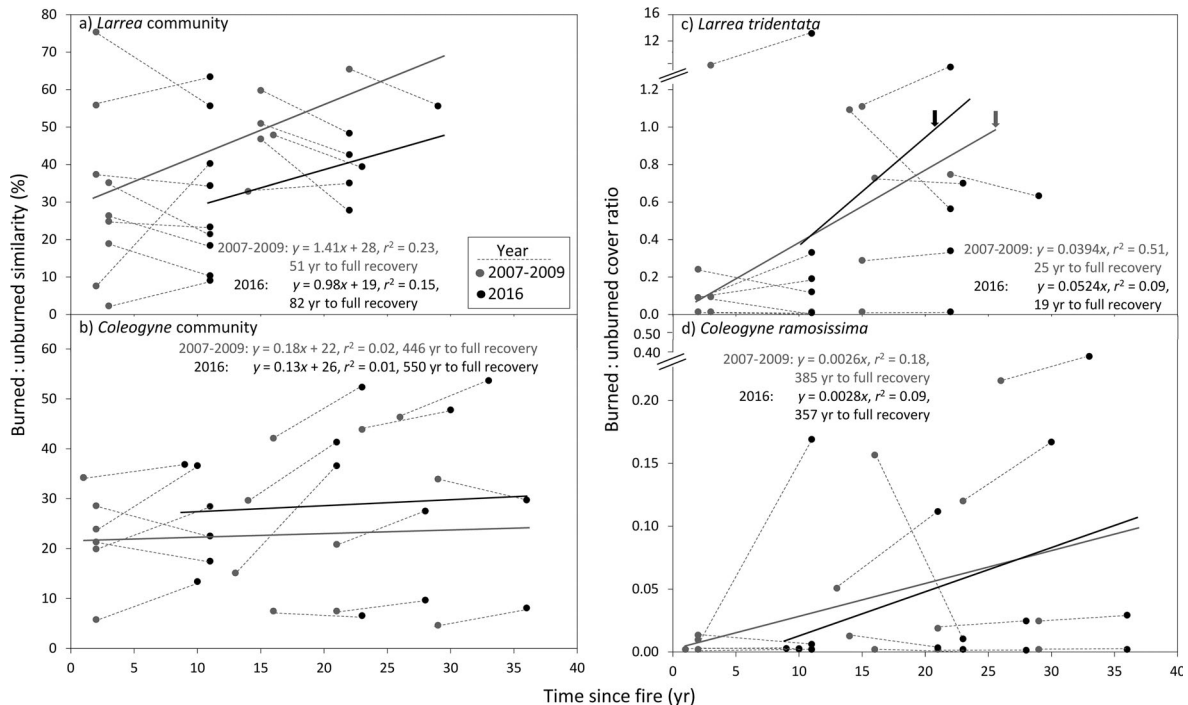


FIG. 4. Similarity of perennial species composition between burned and unburned areas in two community types and cover of their dominant shrub species for 31 wildfires in the Mojave Desert, USA. Points represent individual fires sampled during two study years, shown connected by dotted lines. Similarity is expressed as the Sørensen index. Arrows note attainment of full resilience (burned:unburned similarity = 100% for composition and 1.0 for cover) when resilience was achieved during the study period. Regression lines and estimated years to full resilience are shown separately for 2007–2009 and 2016 study years. In panel c, the burn shown on the top left of the graph with an unusually high cover ratio was not included in the regressions so that recovery estimates were more conservative. Standard errors (SE) and P values for slopes of lines are as follows and are formatted as 2007–2009 SE (P), 2016 SE (P): (a) 0.72 (0.071), 0.66 (0.160); (b) 0.35 (0.619), 0.42 (0.752); (c) 0.0060 (<0.001), 0.0129 (0.001); (d) 0.0015 (<0.001), 0.0006 (<0.001).

While burn status was a significant main effect, burn age was minimally related to species composition. Shown for 2007–2009, ordinations for all sites (59% of variance represented in the first two axes), for the *Larrea* (50% of variance for Axis 1 in a one-dimensional solution), and for the *Coleogyne* community (75% of variance in the first two axes) depicted some separation of species composition between burned and unburned areas but minimal separation among burn ages (Appendix S1: Fig. S6). In permutation tests, burned and unburned species composition differed within young (age 1–3 and 9–11 yr for 2007–2009 and 2016), but not medium-aged (13–16 and 21–23 yr) burns in both study years (Appendix S1: Fig. S6 inset). *Larrea* burned composition did not differ among burn ages in either study year. In *Coleogyne* communities both years, burned and unburned composition differed within all burn age classes. However, burned-area species composition (using the Euclidean distance measure) did not differ among burn ages.

Evidence for convergent or divergent trajectories among burned sites varied with spatial scale (Fig. 7). Including all fires, similarity of species composition among burned sites was low within age groups and

varied little on average across age groups in either 2007–2009 (20–24% similarity) or 2016 (19–25%). However, specifically for the burned *Coleogyne* community, there was slight opposing evidence for divergence and convergence. Similarity among burned sites decreased slightly between 2007–2009 and 2016 within two of three burn age classes, indicating divergence among sites within the age groups. This divergence paradoxically resulted in convergence at a broader scale among all burned *Coleogyne* sites. The disappearance in 2016 of the permutation-based compositional difference (using the Sørensen distance measure) that had been present in 2007–2009 between age classes suggested convergence among age classes, albeit precisely because composition became more heterogeneous at the finer scale within burn age classes. The increased variability within burn age classes resulted in an overall heterogeneous species assemblage no longer even weakly structured by burn age.

Density data for 80 species of woody plants and cacti in 2016 suggested that, compared to unburned areas, burned areas contained fewer total plants, cacti, and large-statured shrubs, but proportionally more small subshrubs (Fig. 8; Appendix S1: Table S1). Total mean density for all woody plants and cacti varied with the

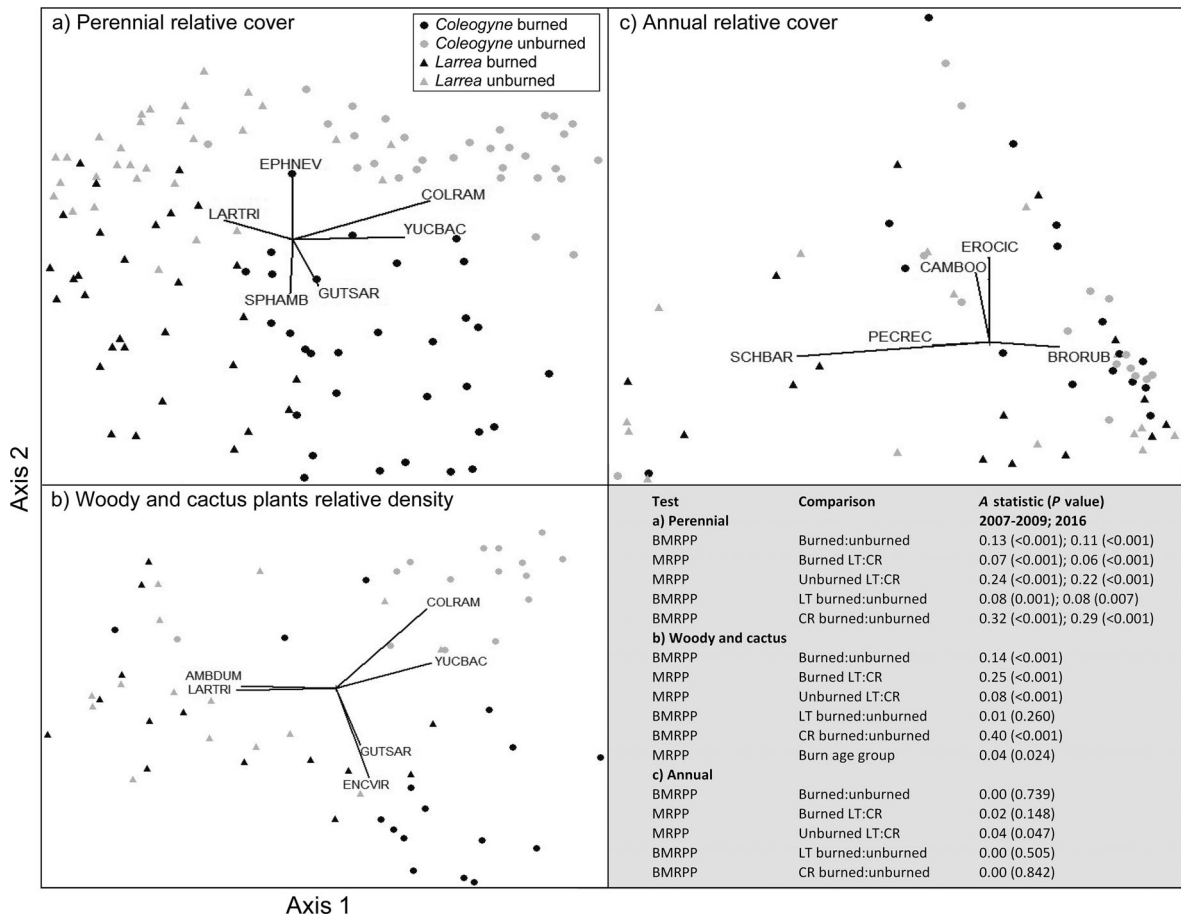


FIG. 5. Nonmetric multidimensional scaling ordinations of species composition and statistical comparisons of composition associated with each ordination for burned and unburned areas in two community types in the Mojave Desert, USA. The ordination in panel a displays 31 wildfires and their paired unburned areas, for 2007–2009 and 2016 study years. The ordinations in panels b and c show data for 2016. In the ordinations, vectors display species correlated ($r \geq 0.45$) with species compositional gradients (AMBDUM, *Ambrosia dumosa*; BRORUB, *Bromus rubens*; CAMBOO, *Camissonia boothii*; COLRAM, *Coleogyne ramosissima*; ENCVIR, *Encelia virginensis*; EPHNEV, *Ephedra nevadensis*; ERODIC, *Erodium cicutarium*; GUTSAR, *Gutierrezia sarothrae*; LARTRI, *Larrea tridentata*; PECREC, *Pectocarya recurvata*; SPHAMB, *Sphaeralcea ambigua*; YUCBAC, *Yucca baccata*). Statistical comparisons in the inset are via multi-response permutation procedures (MRPP) and blocked MRPP (BMRPP) for paired burned–unburned comparisons all using Euclidean distance (CR, *Coleogyne* community; LT, *Larrea* community).

main effects of burn status (29% lower density in burned than unburned areas) and community type (44% lower in the *Larrea* than in the *Coleogyne* community; Fig. 8 inset). An ordination of cactus and woody plant relative density that represented 63% of the variance (first two axes) in species composition, accompanied by permutation tests, supported these results (Fig. 5b). There was clustering of unburned *Coleogyne* sites dominated by shrubs, correlation of the subshrub *G. sarothrae* with burned sites, and less distinction between burned and unburned species composition in the *Larrea* community. Permutation tests revealed that, within burned areas, woody plant and cactus species composition on old burns differed from young and medium-aged burns. Indicator species analysis revealed that this difference arose from old burns containing a mixture of subshrubs

(e.g., *G. sarothrae*) and low density of shrubs (e.g., *C. ramosissima*, *Prunus fasciculata*, *Yucca baccata*).

Resprouting

Although cover and density of the major shrubs *L. tridentata* and *Yucca* spp. were minimal on burned compared to unburned areas, resprouting was a resilience mechanism for persistence of some individuals. *Larrea* resprouts constituted 32% of all live individuals of the species in 2007–2009 and 18% in 2016, after seedlings had increased in density (Appendix S1: Fig. S7). For *Yucca baccata* and *Y. schidigera*, 67–97% of live individuals on burned areas in either study year were resprouts (Appendix S1: Fig. S8). While these resprouts grew slowly to remain <1 m tall in 2016, they comprised

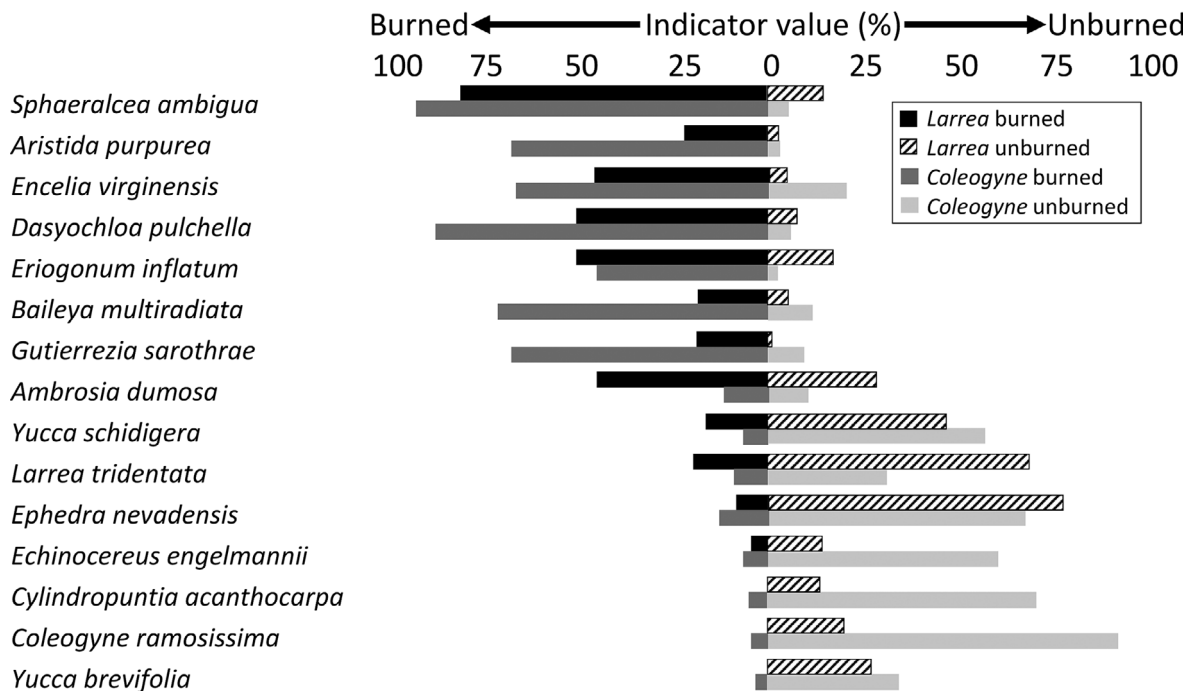


FIG. 6. Blocked indicator species analysis identifying species significantly associated ($P < 0.05$) in 2016 with burned and unburned areas and community types in the Mojave Desert, USA. Indicator values integrate relative frequency among sites and relative cover and range from 0 (no association) to 100 (maximum association with a particular group).

most of the remaining individuals of the species along with minimal seedling recruitment and some individuals apparently escaping burning. Resprouting was less frequent for *Y. brevifolia*, but aided population persistence as the few resprouters constituted nearly all the species' live individuals on burned areas.

Annual plants

Variation in the annual plant community was primarily driven by the cosmopolitan nonnative *Bromus rubens*, which dominated cover on unburned areas and increased through time on burned areas indicative of persistently high nonnative grass cover. This was shown through a burn status \times year interaction, where *B. rubens* increased from 2007–2009 to 2016 in burned but not unburned areas, where it already had high cover (Fig. 9). For 2016 with data available for all 95 annual species recorded on sites, *B. rubens* comprised one-half of the total annual plant cover (native + nonnative) on both burned and unburned areas (Fig. 10). Four nonnative species, including *B. rubens* along with *Bromus tectorum*, *Schismus* spp., and *Erodium cicutarium*, constituted 99.6% of total nonnative cover in both burned and unburned areas. Total mean nonnative annual cover was higher in burned compared to unburned areas, while native annual cover was comparatively low and nearly identical between burned and unburned areas. The top

four native annuals comprised 40% of total native annual cover in both burned and unburned areas and included *Lepidium lasiocarpum*, *Pectocarya recurvata*, *Plantago ovata*, and *Eriogonum deflexum*. Annual community composition displayed minimal separation between burned and unburned areas in an ordination (79% of variance expressed in the first two axes) and burn status was not significant in permutation tests (Fig. 5c).

Biocrusts

Biocrust on burned areas had one-half of the species and one-third the cover of biocrust on unburned areas (Fig. 11). Species composition also differed (BMRPP A statistic = 0.10, $P = 0.019$). The squamulose lichen *Placidium lacunculatum* comprised greater relative cover on burned (39%) than unburned areas (23%). In contrast, the moss *Syntrichia caninervis* had 14% relative cover on burned compared to 26% on unburned areas.

Soils

The main variation in soil properties included greater concentration and volumetric content of N in burned compared to unburned areas and of C in *Coleogyne* compared to *Larrea* communities (Fig. 12; Appendix S1: Table S1). Soil texture differed by <2%

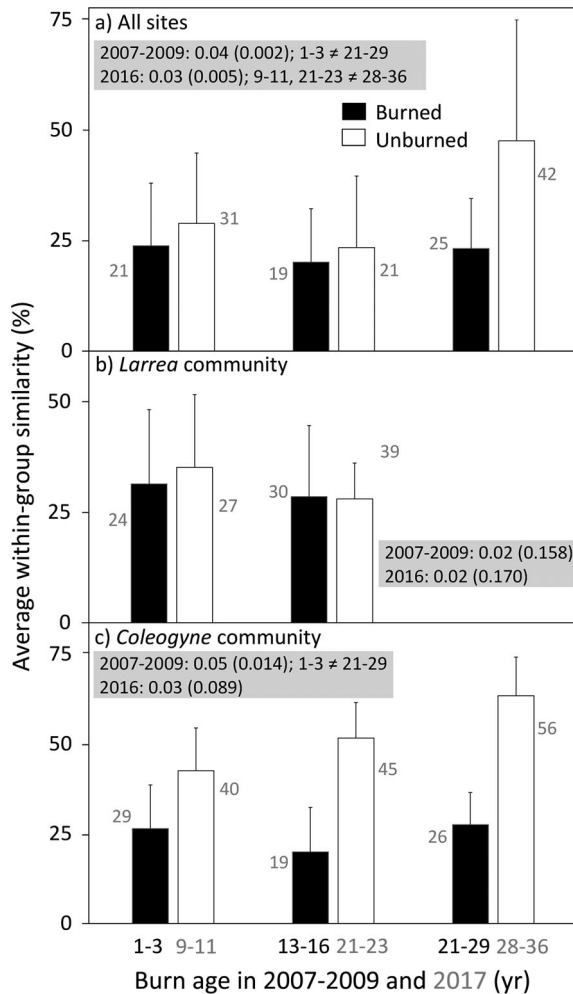


FIG. 7. Similarity of perennial species composition within age groups of burned and unburned areas for (a) all 31 wildfire sites and (b, c) within community types in the Mojave Desert, USA. The bars show average within-group similarity (average among burns and their paired unburned areas within age class groups) for the first study year (2007–2009). Numbers in gray font next to bars represent means for the second study year (2016). Error bars are one standard error of means. Gray boxes display permutational comparisons of species composition for burned areas across burn age groups separately for both study years. The A statistic is provided (P value in parentheses) followed by which age groups differ at $P < 0.05$. These analyses use Sørensen distance.

between burned and unburned areas and pH was also nearly identical (7.63 ± 0.05 for burned compared to 7.66 ± 0.05 for unburned areas).

DISCUSSION

The data suggest variable consistency of plant community dynamics with models of resilience, alternative stable states, and convergent-divergent trajectories. There was at least partial support for each of the

three models, and often evidence for multiple models was simultaneously expressed during community dynamics. Support for models varied among components of communities (e.g., species richness, species composition), between study years (2007–2009 or 2016) and timeframes of burn age gradients, whether the scale of analysis included all study sites combined or was within community type, and if the benchmark for comparison for some models was to undisturbed conditions or to earlier disturbed conditions. Additionally, auxiliary data sets (e.g., nonnative grasses, soil properties) showed long-term differences between burned and unburned areas consistent with positive feedbacks often associated with persistently altered communities or alternative stable states (D’Antonio et al. 2017).

Support for models across ecosystem components, timeframes, spatial scales, and benchmarks

Ecosystem components.—Two ideas are that resilience is a property specific to components of ecosystems or that resilience is a property of an entire community or ecosystem (Lavorel 1999, Hodgson et al. 2015). Our study supports the idea that resilience varies on a continuum among components of ecosystems, with some components resilient and others potentially not. To what extent this variability may influence whole-ecosystem resilience is unclear and may hinge on the types of interactions among ecosystem components (e.g., compensatory interactions strengthening ecosystem resilience) or the relative contributions of components to ecosystem outputs (e.g., structure, biotic composition, or functions; Donohue et al. 2016). While ecological knowledge for that level of integration within ecological networks is still developing for most ecosystems with more than a few species and for multi-century timeframes accommodating long-lived individuals of species, some areas of ongoing research are accumulating on the complexity expected for integrating ecosystem components in resilience frameworks. For example, research on foundation species, the insurance hypothesis relating biodiversity to ecosystem functions, and effects of removing species or constituents (e.g., seed banks, soil nitrogen) from ecosystems have begun unraveling how ecosystem components and their interactions affect whole-ecosystem properties (Díaz et al. 2003, Hernandez and Sandquist 2011, Ellison 2019). Our data suggest that efforts to develop whole-ecosystem indices of resilience may need to account for opposing resilience trends among ecosystem components and how the opposing influences affect ecosystem outputs.

Timeframe.—Consensus is lacking in the literature for how fast an ecosystem must recover to be considered resilient or for how long resilience must be absent for an alternative stable state to have formed. Connell and

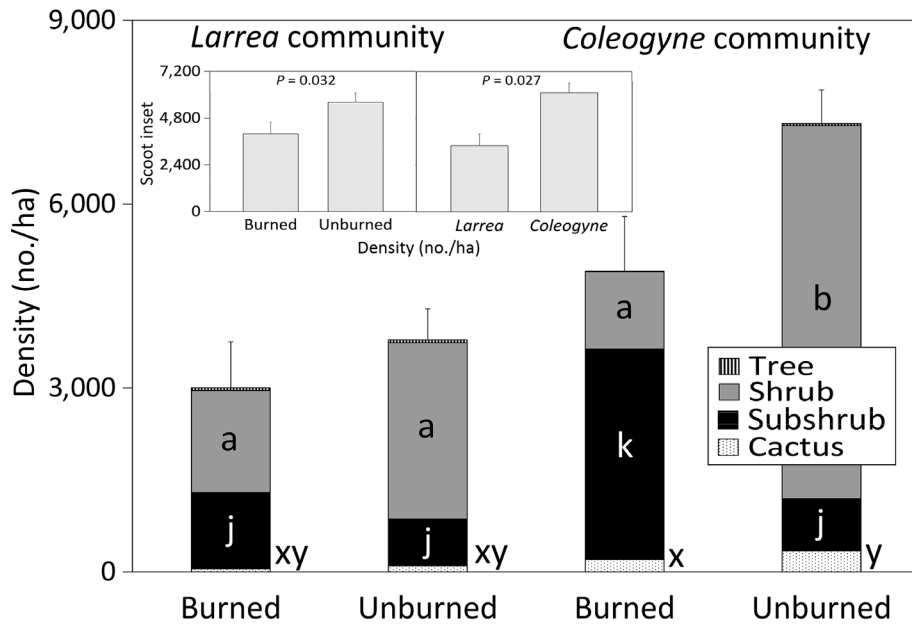


FIG. 8. Density of woody and cactus plants in burned and unburned areas of two community types in the Mojave Desert, USA. Sets of letters compare means within a growth form across burn status × community categories (means without shared letters differ at $P < 0.05$). Trees did not differ among categories and hence have no letters. Error bars are one standard error of means for total mean density. The inset graphs display main effects of burn status and community type on total mean woody and cactus plant density (number/ha), which did not have statistical interactions.

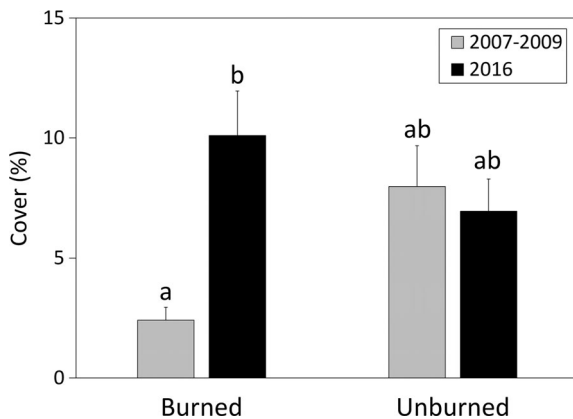


FIG. 9. Cover of the nonnative annual *Bromus rubens* in burned and unburned areas in two study years in the Mojave Desert, USA. Means without shared letters differ at $P < 0.05$. Error bars are one standard error of means.

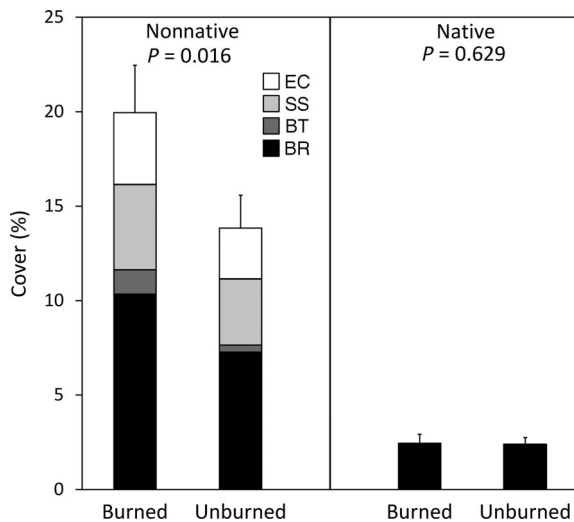


FIG. 10. Cover of annual plants in 2016 in burned and unburned areas of the Mojave Desert, USA. Separately for nonnative and native annuals, P values compare means between burned and unburned areas. Error bars are one standard error of means. Abbreviations for nonnative species: BR, *Bromus rubens*; BT, *Brassica tournefortii*; EC, *Erodium cicutarium*; SS, *Schismus* spp. Native annuals are not broken down by species because of low cover for individual species.

Sousa (1983) discussed how criteria for defining stability, such as one complete turnover of individuals of an ecosystem’s longest-lived species, are challenging to apply in perennial plant communities where individuals can live for millennia. Our data for recovery of perennial plant composition illustrate the uncertainties and multiple potential interpretations of resilience, alternative stable states, and convergent-divergent trajectories. For example, one interpretation of species compositional change in the *Coleogyne* community could be that,

despite the forecasted long recovery time (more than five centuries) and slowing recovery rate between study years, composition is in fact resilient based on assuming an albeit slow recovery trend continues.

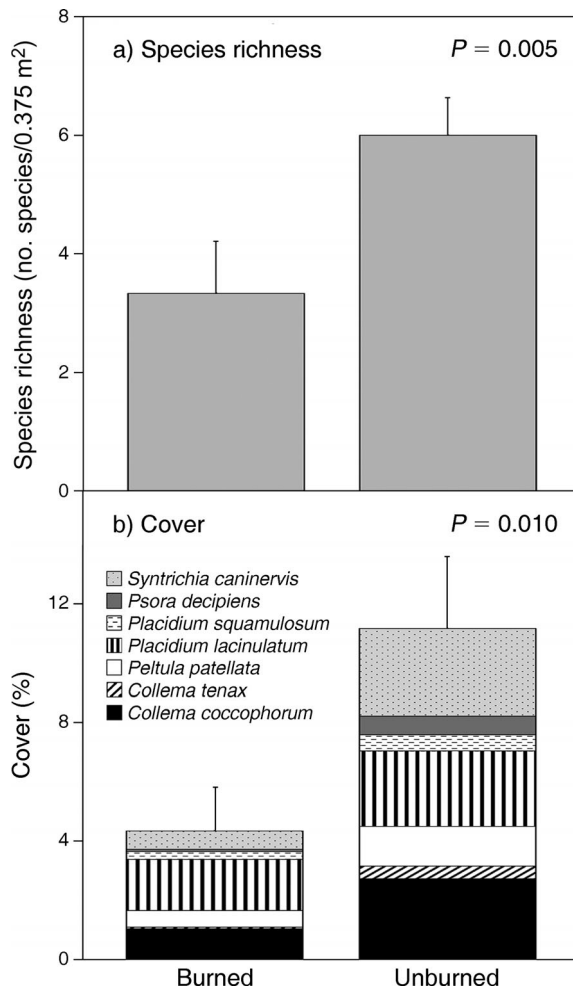


FIG. 11. Biocrust characteristics in 2016 in burned and unburned areas of the Mojave Desert, USA. Error bars are one standard error of means. P values compare means between burned and unburned areas (paired t tests).

Another interpretation could be that community composition is instead in an alternative stable state and trending to continue as such, based on the weak relationship between time since fire and burned:unburned similarity, declining rate of recovery, and positive feedbacks suggested by the data sets. For example, the increase in *Bromus rubens* fuel suggests reburn potential already observed on some desert landscapes (Brooks 2012, Chambers et al. 2019). Given transition to fire-prone annual grassland, reburning seems likely in the study area within the next five centuries, before full resilience of perennial species composition would be attained. A second fire on a previously burned site can be particularly devastating to mature desert shrublands by nearly eliminating on-site regeneration potential (Brooks 2012). Major climatic shifts or further biological invasions are also possible that could alter recovery within the projected 550-yr recovery period. Such events occurred in the previous five centuries encompassing the

Little Ice Age and pervasive invasion of the desert biome by nonnative plants (Webb et al. 1987, Vamstad and Rotenberry 2010). Another consideration for identifying potential formation of alternative stable states is that many of the early colonizing forbs and small shrubs on burned areas have individual life spans of decades to a century, shorter than the mature shrubland dominants *Larrea tridentata* and *Coleogyne ramosissima* (Bowers et al. 1995). As a result, multiple turnovers of individuals of the early colonizing species could occur within a ~500-yr timeframe, meeting a stringent criterion of turnover of individuals within species assemblages for identifying a persistent alternative stable state (Connell and Sousa 1983).

Spatial scale.—Support for models varied from a broad scale including all study sites on the landscape to finer scales when the landscape was partitioned into community types. For example, the same community measure of species composition at different spatial scales could simultaneously support models that actually oppose each other. When data were viewed as the average (among sites) of site-level dynamics in the *Coleogyne* community, slightly increasing heterogeneity among burned sites in two of three age classes between 2007–2009 and 2016 suggested divergence among burned sites (average similarities in Fig. 7c). Simultaneously, however, data indicated convergence among burned sites through time if sites were viewed as a whole collection (disappearance between 2007–2009 and 2016 of the significant compositional difference among burn age classes in the Fig. 7c inset) rather than averaging among sites. This difference across scales occurred because previously internally similar age groups weakened to result in a single heterogeneous state (thereby convergence, by going from multiple distinct groups to one). Thus, divergence among burned sites produced statistical convergence of composition for the collection of burned sites via dissolution of earlier differences among burn age groups. This complexity across spatial scales highlights an uncertainty in alternative stable theory regarding whether a collection of heterogeneous sites is defined as a single alternative stable state or is viewed as multiple stable states.

Exemplifying differential resilience between community types, perennial cover was fully resilient within the study period in the *Larrea* but not in the *Coleogyne* community. This difference could stem in part from autecological traits of the major species of the mature shrubland communities. Based on species traits, large burns likely pose formidable challenges to recruitment for *L. tridentata*, *C. ramosissima*, and *Yucca* spp. (Shryock et al. 2014). *Larrea tridentata* forms only transient soil seed banks and has episodic and low recruitment (Bowers 2002). However, *L. tridentata*'s ability to at least occasionally resprout and grow comparatively fast (Molinari et al. 2019) could account for more resilience in the *Larrea* than in the *Coleogyne* community.

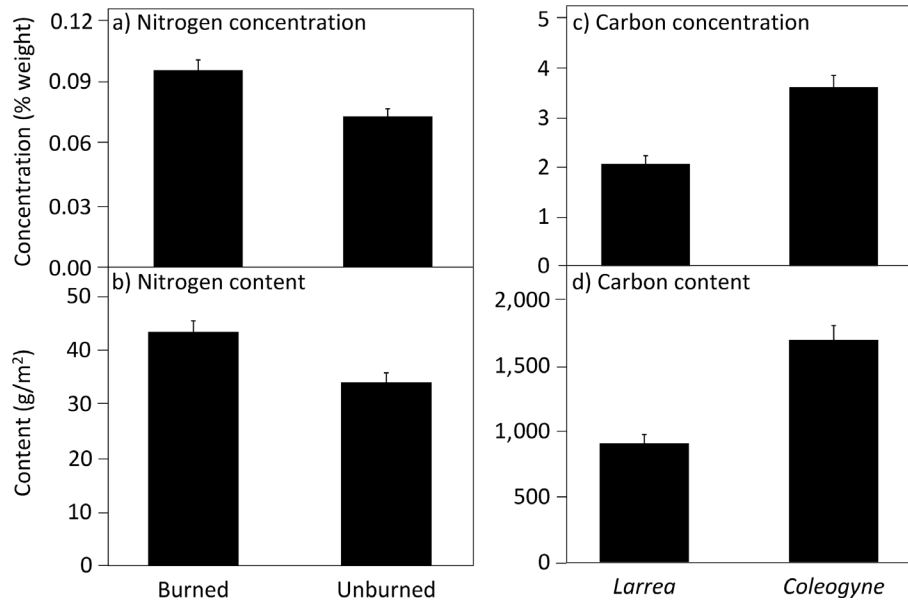


FIG. 12. Variation in 0–5 cm soil nitrogen and carbon with burn status or community type in the Mojave Desert, USA. Means within a panel differ at $P < 0.05$. Error bars are one standard error of means.

Coleogyne ramosissima lacks resprouting capability, forms minimal persistent soil seed banks, is a temporally irregular mast-seeder dependent on abundant seed-producing adults, exhibits minimal seed dispersal, grows slowly (often only 0.5–1 cm in height/yr), and may rely on a “seedling bank” readily destroyed by fire (Pendleton et al. 2015). Furthermore, the species’ main seed disperser, the kangaroo rat *Dipodomys microps*, avoids open habitats (i.e., burned areas) and areas with high cover of nonnative annual grasses (Pendleton et al. 2015).

Likely with similar challenges to recruitment, *Yucca brevifolia* forms a persistent but relatively short-lived soil seed bank (~4 yr; Reynolds et al. 2012) that is readily killed by temperatures sustained below shrubs during wildfire (Keeley and Meyers 1985, Brooks 2002). Although the species can resprout at low frequencies, resprouts may require over 30 yr to produce seed (Esque et al. 2015), indicating that plants on even the oldest burns (36 yr) we studied may not yet be capable of reproduction. Furthermore, seeds typically disperse only short distances (<25 m) from adults via small mammals, and seedling establishment is contingent on availability of nurse plants (Waitman et al. 2012), which are sparse on burns. Less is known about the recruitment of *Y. baccata* and *schidigera*, but one study found that the proportion of flowering *Y. baccata* on 8-yr-old burns was only half that of unburned areas (Lybbert and St. Clair 2017). Collectively, previous research suggests that sparse seed availability, limited seed dispersal, and lack of suitable regeneration microsites (nurse plants) hinder these species’ recruitment. These limitations could form feedbacks deterring resilience and promoting alternative states with low densities of these species, consistent with our data.

Benchmarks.—The baseline for comparison is an uncertainty in resilience and alternative stable state theory, and our study highlights challenges in choosing references and accommodating fluctuations through time in disturbed and reference sites. The essentially ubiquitous invasion of the Mojave Desert (including our study area) by nonnative annual plants resulted in unburned reference areas serving as benchmarks for assessing resilience that potentially themselves represented alternative stable states. These states could be characterized as unburned mature shrublands dominated by nonnative annuals that negatively affect emergence of native annuals, recruitment and physiology of native perennials, and several species of native fauna (Brooks 2000, Rodríguez-Buriticá and Miriti 2009, Horn et al. 2012). Had data been available on pre-fire condition, using pre-fire condition as a benchmark for assessing resilience would not have avoided this issue because nonnative annuals were already abundant long before the oldest fires we studied (Beatley 1966). Species removal experiments to understand ecosystem characteristics when nonnative species are absent could enhance understanding how potential degradation of reference sites influences assessments of resilience (Díaz et al. 2003).

Potential factors in community change

Climate.—Dry climatic conditions or other climatic variability could temper ecological resilience or perpetuate alternative stable states (Winkler et al. 2019). In the study area after 2005, the year with the most precipitation in the 67-yr record, 8 of the next 11 yr were dry (Appendix S1: Fig. S2). Despite the dry climate, perennial cover and species richness increased between 2007–

2009 and 2016 on burned and unburned areas. While it could be hypothesized that increasing atmospheric CO₂ concentration would enhance plant water-use efficiency and productivity to compensate for dry conditions, a Mojave Desert experiment found that 10 yr of CO₂ enrichment minimally affected perennial cover and richness (Newingham et al. 2014). Although it is uncertain if community dynamics would have been different had a different set of climatic contingencies occurred in years following burns, the set of climatic conditions that did occur was sufficiently favorable for overall increases in plant cover and richness. It is possible that the reduced frequency in the recent climate (since the 1970s) of freezing temperatures, to which many desert species are sensitive, was associated with increases in perennial plants (Guida et al. 2014).

Alternatively, it is possible that climate had minimal influence in comparison to reduced grazing pressure. Livestock grazing and to some extent feral burros (*Equus asinus*) have been reduced around the study area since the 1990s (Abella et al. 2019). With minimal evolutionary history of intensive large-herbivore grazing, native plant cover and diversity could be expected to increase after grazing ceases. Indeed, a 12-yr enclosure experiment in the central Mojave Desert found that perennial cover increased by 50% without grazing (Brooks 1995). This increase is similar to what we found in the decade between study years, suggesting that reduced grazing alone was potentially capable of stimulating the observed plant increases. It is noteworthy, however, that because cover and richness increased on burned as well as unburned areas, the increase did not necessarily enhance recovery on burned relative to unburned areas.

Soil and biocrusts.—Post-fire soil and biocrusts displayed consistency with feedbacks that could maintain alternative stable states. For example, soil nitrogen content was greater on burned compared to unburned areas, likely owing to fire converting aboveground plant material into soil organic matter (Allen et al. 2011, Abella and Engel 2013). High soil nitrogen on burned areas was unrelated to burn age and persisted between 2007–2009 and 2016, apparently representing a nutrient-enriched state stable for at least decades. Although it may seem that elevated soil nutrient concentration in the short term would encourage native plant recovery, this may not be the case because of differential nutrient use by native and nonnative species and altered spatial distributions of nutrients. Nitrogen-addition experiments indicate that nonnative annuals respond more vigorously to increased N availability than do native desert plants (Brooks 2003, DeFalco et al. 2003, Abella et al. 2012). Previous Mojave Desert studies have further reported dissolution of spatial patterns of soil nutrients within a decade after fires, via homogenization of nutrient-rich fertile islands with nutrient-poor interspaces (Soulard et al. 2013, Fuentes-Ramirez et al. 2015). Given the

centrality of fertile islands and nurse plants to the recruitment of many species in mature desert communities, degradation of fertile islands would be anticipated to be a feedback encouraging alternative stable states (Allen et al. 2011). In a 22-yr study, for example, 28% of *Y. brevifolia* seedlings survived below nurse plants in fertile islands, compared to zero survival for seedlings in interspaces (Esque et al. 2015). Burned areas likely select for species less dependent on nurse plants for recruitment, which may account for burned areas containing relatively small-statured perennial species capable of recruiting in open areas.

Biocrusts were a major part of soil cover on unburned areas but were sharply reduced on 12-yr-old burns. While we did not sample biocrusts across the entire burn age gradient, our results of depauperate biocrusts on the 12-yr-old burns supported a previous study in the north-eastern Mojave Desert. There, biocrust cover was 10× lower on a 12-yr-old burn than on unburned areas and remained low 37 yr after fire (Callison et al. 1985). Relationships between biocrusts and facilitation or deterrence of vascular plant establishment, including of nonnative plants, have been variable among undisturbed dryland sites (Hernandez and Sandquist 2011). When biocrusts have been disturbed, however, nonnative plants including *B. rubens* have often increased disproportionately to natives (Hernandez and Sandquist 2011). These observations suggest that reduced biocrust on burned areas could have partly promoted the disproportionate increase in nonnative annuals on burns, and coupled with degraded biocrust functions, contributed to sustained differences in burned and unburned species composition.

Persistence of early colonizing species.—In general and compared with dominants of mature shrublands, perennial colonizers of burned areas were species consisting of small-statured individuals (e.g., *Gutierrezia sarothrae*) with relatively short life spans (decades to a century) and wind-dispersed seeds able to form persistent soil seed banks (Jurand and Abella 2013, Shryock et al. 2014). High fecundity and persistent seed banks suggest that while life spans of individuals of these species might be short (Bowers et al. 1995), the species possess other mechanisms for long-term persistence after their initial establishment. Indeed, studies on debris flows and other disturbances suggest that initially colonizing suites of Mojave Desert species can persist for centuries (Webb et al. 1987). This could represent a fundamental difference in community change between deserts and moister biomes. In moister biomes such as forests or perennial grasslands where canopy closure is a filter, colonizing species lacking competitive or shade-tolerance traits often quickly become excluded (Halpern and Lutz 2013). This process may be absent in deserts where canopy closure is not an ecological feature, potentially enabling species possessing traits for early colonization to persist for longer after

disturbance including forming persistent alternative stable states.

Nonnative annuals and grass-fire cycles.—Nonnative species dominated the annual plant community in both burned and unburned areas and could influence native species recovery via both fire and non-fire processes. While testing for a grass-fire cycle was beyond the scope of our study, the major increase in nonnative annual grasses would meet thresholds for wildfire spread identified in previous research (Rao et al. 2010). This suggests reburning potential consistent with the idea of a system shift to an alternative disturbance regime (Brooks 2012). Additionally, persistent dominance by nonnative annuals could alter recovery of native communities through non-fire processes. For example, a Mojave Desert experiment revealed that removing nonnative annuals increased native annual biomass and species richness during wet but not dry years (Brooks 2000). Nonnative annuals have better exploited available moisture than have native annuals in Mojave Desert experiments (DeFalco et al. 2001). This raises the possibility that perpetual nonnative plant dominance hinders abilities of native plants to utilize rainfall events. This idea is supported by the fact that nonnative annuals often comprise over 90% of the total seeds any given year to dominate the persistent soil seed bank and their seeds have minimal dormancy (Esque et al. 2010, Jurand and Abella 2013). Additionally, interactions between nonnative annuals and native shrubs are asymmetrical, where the nonnatives utilize facilitative benefits (e.g., shading) of a shrub while harming its growth (Rodríguez-Buriticá and Miriti 2009). This can manifest as nonnative annuals displacing native species from favorable regeneration microsites, including below nurse plants (Rodríguez-Buriticá and Miriti 2009). These observations suggest that persistent dominance of nonnative annuals could contribute to alternative stable states even if sites do not reburn through a grass-fire cycle (Clarke et al. 2005, Olsson et al. 2012, D'Antonio et al. 2017).

Implications for recovery debts

Potential habitat utilization by wildlife species illustrates an anticipated complexity in identifying how post-fire resilience or alternative stable states in plant communities may influence ecosystem functions. Previous research indicates that desert tortoises (*Gopherus agassizii*) have utilized small burned areas, if forage plants occur on burns, but tortoises must retreat to unburned areas containing large shrubs with protective shade, features sparse on burns (Drake et al. 2015). This suggests that while perennial plant cover in our study showed partial resilience, not all forms of cover might be equal for ecological functions. Much of the perennial cover on burned areas consisted of forbs and small shrubs, which do not provide the shaded, protective functions that cover provides when composed of large shrubs. This

example suggests that implications of resiliency of cover are likely to be mediated by dynamics in species composition, which displayed minimal resilience.

In another example, previous research indicated that the *Yucca* species in our study support specialized invertebrate pollinators (Lybbert and St. Clair 2017). Although limited resprouting fostered minimal resilience of *Yucca* density in our study, stems sufficiently large to flower were largely absent from burns, and thus, *Yucca* flowers were unavailable to pollinators for decades. This highlights that some resilience may not translate to functional resilience and that recovery debts can accrue while limited resilience is occurring. Multi-decade absences of *Yucca* floral resources from extensive burned areas and potential influences on specialized pollinators could trigger alternative stable states in pollinator networks (Lybbert and St. Clair 2017).

CONCLUSION

Perennial vegetation change during a 36-yr period after desert wildfires supported resilience, alternative stable state, and convergent-divergent trajectories as generalized conceptual models of ecological change, while highlighting remaining uncertainties in model theory and application. Although variability was high among burns, three main measures of perennial plant communities generally could be ranked from most to least resilient: species richness was fully resilient within three decades, cover was intermediate, and species composition was least resilient and potentially trending toward alternative stable states. Auxiliary data sets characterizing ecosystem components, such as annual plants, soils, and biocrusts, indicated lack of resilience or alternative stable states during the study.

An unresolved question in model theory is whether resilience is a property of components of ecosystems or entire ecosystems, and what that may mean for defining resilience and implications for ecosystem functions. For example, if an ecosystem is only as resilient as its slowest recovering critical component, then resilience would probably be absent from our study's burned desert ecosystems, which instead would persist as alternative stable states projected for at least the next 500 yr. The slow- to non-recovering species composition, characterized by replacement of a relatively large-statured, shrub-tree composition on unburned areas with a smaller-statured, forb-subshrub composition on burned areas, is a critical ecosystem component influencing ecosystem functions. For example, even if total plant cover is the same, numerous small plants do not necessarily provide the same protective functions as fewer, larger plants do for desert tortoises and other wildlife (Drake et al. 2015). Many such ecological functions are likely inseparable from species composition (Donohue et al. 2016). Complicating matters, the most resilient measure—species richness—could enter an alternative stable state of elevated richness on burned areas if burned sites were to

continue diverging from unburned sites (Abella and Fornwalt 2015). While sites diverse in native species might seem positive, whether this diversity would meet desired functions or even hinder recovery of mature shrubland species is unclear.

Another question in model theory is identifying at what point or in which timeframes thresholds have been passed that foster or limit resilience, particularly for ecosystems with long-lived individuals such as desert shrublands. Our recovery projection of 500+ yr for species composition clearly has a great deal of uncertainty given the seemingly high probability that major climatic shifts, other disturbances such as reburning, or other major ecological changes (e.g., biological invasions, unusual recruitment events of perennials) would occur in the next five centuries as they did during the previous five centuries. From a perspective of applying resilience ecology to land management, it is possible that erring on the side of failing to identify an alternative stable state when one is forming is more serious than falsely identifying one when a system may instead be latently resilient. A way forward to address these uncertainties could be further integrating resilience and ecological stability research with experimental research of contingency effects, community assembly/disassembly, species or ecosystem component additions or removals, strengths of ecological networks within ecosystems, and importance of ecosystem structural and compositional components to ecosystem multi-functionality (Oliver et al. 2015, Craven et al. 2018, Manning et al. 2018). Developing short-term, early indicators of trajectories toward resilience or alternative stable states seems vital for applying resilience theory in ecosystems with long-lived individuals, such as in our study, to enable management interventions before opportune windows may have closed.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1432/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kwh70rz1x>