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Topography and climate are more important drivers of long-term, post-fire vegetation assembly than time-since-fire in the Sonoran Desert, US

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Keywords
Arid land; Chronosequence; Fire; Sonoran Desert; Succession; Time-since-fire; Vegetation assembly; Vegetation structure

Abbreviation
TSF = time-since-fire.

Nomenclature
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Abstract

Questions: Do abiotic environmental filters or time-since-fire (TSF) explain more variability in post-fire vegetation assembly? Do these influences vary between vegetation structure and composition, and across spatial scales?

Location: Sonoran Desert of southwestern Arizona, US.

Methods: We measured perennial vegetation in a chronosequence of 13 fires (8–33 yr TSF) spanning a broad regional gradient. The relative influence of environmental filters (topography and climate) and TSF were compared as predictors of long-term, post-fire vegetation assembly. Analyses considered different measures of vegetation structure (cover, height and density) and scales of community organization (species composition, structure and landscape).

Results: Species and growth form composition did not exhibit directional responses with increasing TSF, but sorted along abiotic gradients. Differences in vegetation cover and height between burned and unburned control areas were attributed primarily to gradients of topography and climate. In contrast, vegetation density initially increased in burned areas but declined to pre-burn levels with increasing TSF. The strongest predictors of landscape-scale recovery of vegetation cover, height and density were elevation, post-fire precipitation and average annual precipitation, respectively. Recovery of vegetation height was positively correlated with precipitation in the first year following fire, suggesting that abiotic conditions of the immediate post-fire environment may drive long-term variability in vegetation structure.

Conclusions: We find substantial evidence that environmental filters, rather than TSF, drive the majority of variability in long-term, post-fire vegetation assembly within the Sonoran Desert. Careful consideration of spatial variability in abiotic conditions may benefit post-fire vegetation modelling, as well as fire management and restoration strategies.

Introduction

Fire is a key evolutionary force in fire-prone ecosystems, with effects spanning species and functional group composition through landscape-scale vegetation structure, productivity and diversity (Pausas et al. 2004; Bond & Keeley 2005; Pausas & Verdu 2008). Ecosystems subjected to novel fire regimes may undergo profound changes that are difficult to predict, including persistent losses of vegetation cover and diversity (Brooks 2012), increased erosion (Soulard et al. 2013), changes in demographic processes (DeFalco et al. 2010), transitions to alternative community states (Rodrigo et al. 2004; Davies et al. 2012) or increased dominance of invasive species (Brooks et al. 2004). In desert ecosystems of the southwestern United States, fire size and frequency have reached unprecedented levels over the last several decades due to an invasive annual grass/fire feedback cycle (Schmid & Rogers 1988; D'Antonio & Vitousek 1992; Brooks & Matchett 2006), in which invasive annuals establish fuel loads capable of sustaining large-scale wildfires following years of high rainfall (Gray et al. 2014). Perennial vegetation is not adapted to fire in these environments, and dominant species such as creosote bush (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*) and saguaro cactus (*Carnegia gigantea*) may be reduced or eliminated (Brown & Minnich 1986; Esque et al. 2004; DeFalco

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et al. 2010), potentially impacting populations of threatened wildlife, including the Mojave and Sonoran desert tortoises (*Gopherus agasizii* and *G. morafkai*, respectively; Brooks & Esque 2002; Esque et al. 2003).

Despite an increasing number of studies, many aspects of post-fire vegetation assembly in deserts remain poorly understood (Abella 2009; Engel & Abella 2011). In particular, the degree to which topographic and climatic gradients shape vegetation recovery is largely speculative, although growing evidence indicates that such factors drive variability in both fire severity and ecosystem response (Grace & Keeley 2006; Diouf et al. 2012; Levick et al. 2012; Clarke et al. 2014). The *environmental-filter* hypothesis stipulates that post-fire vegetation assembly is primarily influenced by abiotic conditions, such as climatic, topographic or edaphic gradients (Keeley et al. 2005). Consequently, species and vegetation responses to fire are sorted along spatially variable abiotic gradients that together account for the majority of variability in post-fire vegetation assembly. In contrast, the *fire-interval* hypothesis predicts that variation in the fire-return interval (i.e. time-since-fire, TSF) is the primary determinant of post-fire vegetation (Bond & van Wilgen 1996; Keeley et al. 2005). Thus, species composition exhibits a directional trajectory with increasing TSF, becoming either more or less similar to pre-burned conditions. Fire may also lead to alternative stable vegetation states when variability in plant colonization of burned areas is subsequently maintained by species interactions; as a result, vegetation becomes less similar to pre-burned conditions through time (e.g. Rodrigo et al. 2004; Davies et al. 2012). The two hypotheses need not be viewed as mutually exclusive, however, and the importance of TSF vs environmental filters may vary across different attributes of vegetation structure (e.g. vegetation cover vs density) or different spatial scales (e.g. species composition vs vegetation structure).

Existing evidence from arid environments supports both hypotheses. Vegetation cover of burned areas in the Mojave Desert is strongly correlated with TSF (Abella 2009; Vamstad & Rotenberry 2010), and species composition has demonstrated partial return to pre-fire composition following several decades (Engel & Abella 2011). However, precipitation influences the level of post-fire resprouting within arid environments (Clarke et al. 2005; Pausas & Bradstock 2007; Nano & Clarke 2011), with long-term consequences for community structure (Arnan et al. 2007). Understanding the relative influences of TSF and environmental filters is important for managing desert landscapes subjected to novel fire regimes, particularly in terms of prioritizing restoration activities or evaluating impacts to habitat of threatened species. However, increasing such knowledge requires regional analyses incorporating both environmental heterogeneity and a range in TSF, whereas existing studies from the southwestern US deserts are largely focused on short-term responses of desert vegetation to fire (McLaughlin & Bowers 1982; Cave & Patten 1984; Brown & Minnich 1986; Brooks & Matchett 2003; Esque et al. 2013) or limited geographic extents (Minnich 1995; Alford 2001; Vamstad & Rotenberry 2010; Steers & Allen 2011; but see Engel & Abella 2011).

In this study, we adopt a space-for-time approach to evaluate the relative influences of environmental filters and TSF on post-fire vegetation assembly in the Sonoran Desert, focusing on the drivers shaping medium- to long-term vegetation response. To do so, we sampled perennial vegetation from a chronosequence of 13 fires ranging in TSF from 8–33 yrs and spanning a broad regional extent. Our analysis considers different scales of community organization and different attributes of vegetation structure (cover, height and density). We hypothesized that: (i) species and growth form composition would primarily reflect environmental filters, while vegetation structure would be strongly influenced by TSF; and (ii) differences between burned and unburned vegetation would persist at all levels of analysis.

Methods

Study area

The Sonoran Desert spans ca. 275 000 km^2 in the southwestern US and Mexico and is the third largest desert in North America (MacMahon 2000). Precipitation is bimodal and nearly evenly split between winter and summer. Although at least five distinct vegetation subdivisions have been recognized within this ecoregion (Turner & Brown 1994; MacMahon 2000), we sampled perennial vegetation from fires occurring in the Arizona Upland and Lower Colorado River Valley subdivisions. Arizona upland vegetation is characterized by sub-trees (*Parkinsonia* spp., *Prosopis* spp., *Olneya tesota*), together with shrubs (*Larrea tridentata*, *Acacia* spp., *Simmondsia chinensis*) and the iconic Saguaro cactus (*Carnegiea gigantea*). Lower Colorado River Valley vegetation is dominated by shrubs (*Larrea tridentata*, *Encelia farinosa*), with sub-trees restricted to drainages. Various species of cacti (*Cylindropuntia* spp., *Opuntia* spp., *Ferocactus* spp.) and grasses (*Pleuraphis* spp., *Aristida* spp., *Muhlenbergia* spp.) occur in both subdivisions, but the dominant physiognomy is shrubland. Diverse spring and summer annual floras are also expressed in wetter years.

Arizona upland sites receive a mean annual precipitation of approximately 290 mm and mean annual maximum temperatures of 29 °C (Turner & Brown 1994). Lower Colorado River Valley sites are generally lower in elevation and receive less annual precipitation (130 mm), along with warmer maximum temperatures (annual mean of 30 °C). Sonoran Desert soils are derived primarily from

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igneous materials, including granite, basalt and rhyolitic tuff. Metamporphic schists and gneiss are also common along slopes, while conglomerate may occur in drainages (MacMahon 2000). Arizona upland sites are mountainous and topographically complex, with steep gradients in elevation, slope and aspect occurring over relatively small areas. Common geomorphic features include slopes, ridges, bajadas and washes.

Fire boundary delineation and vegetation sampling

We selected 13 fires with years of occurrence ranging from 1980 to 2005 (33–8 yrs TSF, respectively; Fig. 1). Spatial coordinates, area burned and ignition dates for each fire are provided in Appendix S1. Prior to field sampling, we obtained geospatial polygons of fire perimeters by calculating the relativized difference in normalized burn ratio (RdNBR) from Landsat 5 Thematic Mapper imagery recorded pre- and post-fire (see Appendix S2 for detailed methods; Miller & Thode 2007). For three fires that occurred in 1980, pre-dating Landsat 5, we delineated fire boundaries by calculating the difference in normalized difference vegetation index (NDVI) for pre-and post-fire Landsat 3 Multispectral Scanner images. We then generated random points within each fire using the 'create random points' tool in ArcGIS v 9.3 (Redlands, CA, US). Unburned sample points, also randomly generated, were located as close as possible to each fire (e.g. <1 km) and were similar in topography and aspect to burned areas. Environmental characteristics of paired burned and unburned study areas are provided in Appendix S1.

At each random sample point, we measured perennial vegetation cover, height and density on a 50-m transect line. Vegetation cover was measured using the line-intercept technique, in which the lengths of all perennial plants intersecting the transect line, identified to the species level, were recorded. The height of each individual perennial plant intersecting the transect line was also measured at its tallest point on or off the line intercept. Plant density was measured on each transect by counting each individual perennial plant rooted inside 25, 2 m × 1 m quadrats centred at equal intervals along the 50-m transect line. Transect-level vegetation density was then calculated as the number of perennial plants per square meter. All measured plants were identified to the species level. We sampled from 12–24 transects at each fire, evenly divided between burned and unburned control areas, and with more transects in the larger fires. Field sampling was conducted between Mar and Nov 2013.

Data analysis

Environmental filters

We derived a set of environmental variables for analysis that were reflective of the steep topographic and climatic gradients of our study region, and that we hypothesized would serve as environmental filters influencing post-fire vegetation assembly (Table 1). Elevation, slope and aspect were based on a 30-m digital elevation model (DEM) obtained from the National Elevation Dataset (http://ned.usgs.gov/). Precipitation variables were based on the PRISM climate model (Daly et al. 2008;

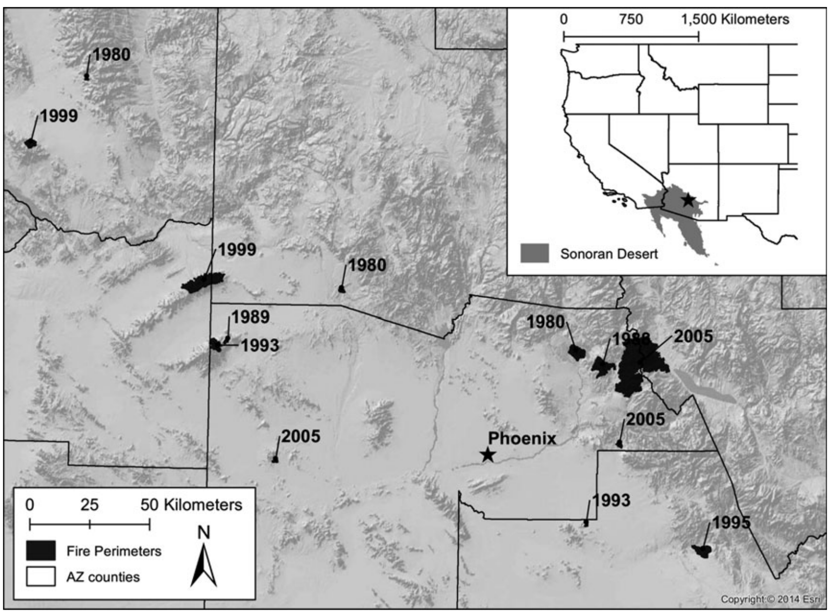

Fig. 1. Perimeters of fires sampled in the Sonoran Desert ecoregion of central Arizona, USA.

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Table 1. Environmental variables extracted at sample points.

Variable and Units	Source
Elevation (m)	30 m DEM
Slope (°)	30 m DEM
Aspect Northness	cos(Aspect × π/180), calculated from 30 m DEM
Annual Precipitation (mm)	PRISM[1] 800 m interpolated climatic normal, 1981–2010
Post-Fire Precipitation (mm)	PRISM[1] 4 km interpolated historic climate grids. Total precipitation received from January–December of first year post-fire
Distance to Edge (m)	Planar distance of sample points to burn edge

[1]Daly et al. (2008), available at http://prism.oregonstate.edu.

http://prism.oregonstate.edu). The distance of burned sample points to the fire boundary – hereafter termed 'distance-to-edge' – was also included as a predictor, as this could influence species' dispersal into burned areas (e.g. Coop et al. 2010). These distances were calculated using the 'near' tool in ArcGIS v 9.3. Correlations between environmental variables were investigated prior to analysis, and it was determined that only annual precipitation and post-fire precipitation were well correlated ($r = 0.71$). Since post-fire precipitation was also not expected to influence vegetation at unburned sample points, we included this variable only in the landscape scale analyses, in which response variables were indices of vegetation recovery rather than transect-level measurements.

Fire severity in the Sonoran Desert likely ranges from surface to crown fire, depending on the degree of annual fuel buildup (Brooks & Minnich 2006), and this variability could influence vegetation recovery. However, ground-based measurements of fire severity were not available for the chronosequence of fires we selected. Instead, we conducted a multi-temporal remote sensing analysis to determine whether RdNBR – a spectral index used to measure fire severity (Miller & Thode 2007) – could predict vegetation recovery (Appendix S2). This analysis was conducted for the ten fires that occurred between 1988 and 2005, for which Landsat 5 Thematic Mapper imagery was available. Results indicated that fire severity was comparable among fires and that vegetation was not influenced by variability in RdNBR. Further discussion of these results is available in Appendix S2.

Species and growth form response to fire

Perennial plant species are often categorized according to their post-fire regeneration mechanism as resprouters, seeders or facultative species (Pausas et al. 2004). However, many Sonoran Desert species cannot be so categorized due to the lack of existing systematic studies. Moreover, because large fires are a novel, invasive species-driven disturbance in this environment, regeneration mechanisms are not well evolved in perennial plants (Brooks & Minnich 2006). For these reasons, we instead adopted a growth form categorization (trees, shrubs, sub-shrubs, cacti, forbs and grasses), which has shown predictive capacity following fires in other deserts (Shryock et al. 2014). Growth form relates to fundamental aspects of species' life histories that shape disturbance–response mechanisms (Lavorel et al. 1997) and therefore provides a useful distinction when regeneration mechanisms are unknown.

We partitioned variability in composition of perennial species and growth forms into additive components explained by burn treatment (burned or unburned), environmental variables (Table 1) and TSF using distance-based permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). TSF was represented as a burn treatment × decade interaction, where burned and unburned transects from each fire were grouped according to the decade in which the fire occurred (2000s, 1990s and 1980s). Models included two-way interactions between burn treatment, distance-to-edge and environmental variables, but not interactions between environmental variables alone. Additionally, to determine whether there were persistent but non-directional changes in species or growth form composition, we computed separate PERMANOVA models for fires grouped by decade (2000s, 1990s and 1980s) with burn treatment as the sole predictor. Model significance was assessed via pseudo-F ratios and permuted P-values (10 000 permutations). All tests were performed using the Bray-Curtis distance measure and the 'vegan' package in R v 3.0.3 (R Foundation for Statistical Computing, Vienna, AT). Species that occurred on less than five transects were excluded prior to analyses.

To further evaluate whether species composition in burned areas exhibited a directional response with increasing TSF, as expected under the fire-interval hypothesis, we conducted principal response curve (PRC) analyses for species and growth forms. This technique is similar to redundancy analysis (RDA) but uses a single axis to express the rate of compositional turnover through time with respect to a reference condition (van den Brink & ter Braak 1999). In PRC diagrams, this reference condition (here represented by unburned control transects) is fixed at zero and indicated by a horizontal line, while separate lines show departure from the reference condition for each treatment (burned transects) as a function of time. Species scores along this axis reflect the change in abundance of each species in the treatments relative to the control. To represent time, we coded TSF as a factor with five levels: 10, 15, 20, 25 and 30 yr post-fire. The significance of both treatment (burn) and time (TSF) terms in PRC models were evaluated by permutation tests. PRC models were fit using the 'vegan' package in R v 3.0.3.

Because growth forms often show disparate responses to fire (e.g. Keeley et al. 2006; Shryock et al. 2014), we modelled transect-level cover of growth forms against environmental variables and TSF using linear mixed-effects models (LME). Fire location was treated as a random effect, while burn treatment (burned or unburned) and environmental variables (excluding post-fire precipitation; Table 1) were treated as fixed effects. As in previous models, we expressed TSF as a burn treatment × decade interaction and included two-way interactions between burn treatment, distance-to-edge and environmental variables. Models were calculated using all combinations of selected explanatory variables and ranked according to bias-corrected Akaike information criterion (AICc). Prior to identifying a candidate set of best-supported models, we removed overly complex models when a nested form (i.e. containing a subset of the parameters) had a lower AICc (Grueber et al. 2011). We then retained models with ΔAICc < 4 and calculated Akaike weights (w_i; Anderson 2008) for this candidate model set. Goodness-of-fit measures were calculated following Nakagawa & Schielzeth (2013), including: R^2_m, or the variability explained by fixed effect terms, and R^2_c, the variability explained by both fixed and random effects. Additionally, for each term in the candidate model sets, we calculated a measure of relative importance by summing Akaike weights for all candidate models in which the term occurred. To visualize the separate influences of fixed effect terms in candidate models, we calculated parameter effect plots (Fox 2003) with 95% confidence intervals (CI) surrounding model-averaged predictions for each term. In these displays, the explanatory variable of interest is varied across its range of observed values while other terms are held at their medians. We chose not to display effect plots for interaction terms when the respective main effects were better supported (i.e. higher Akaike weight) among candidate models. Standardized model-averaged parameter estimates are provided in Appendix S3. Calculations were performed using R v 3.0.3 with the 'lme4', 'AICcmodavg' and 'effects' packages (Fox 2003).

Response of vegetation structure to fire

To investigate influences operating at the level of vegetation structure, we modelled changes in transect-level vegetation cover, height and density using LME models, with fire identity treated as a random effect and environmental variables (excluding post-fire precipitation; Table 1), along with TSF (burn treatment × decade interaction), treated as fixed effects. As outlined above, candidate models with ΔAICc < 4 were selected (after removing overly complex models through the nesting criterion) and goodness-of-fit values (R^2_m and R^2_c; Nakagawa & Schielzeth 2013) were calculated for each, together with relative importance values and model-averaged effect plots (Fox 2003) for terms. Vegetation height and density were square root-transformed prior to analysis to meet model assumptions. Standardized model-averaged parameter estimates are available in Appendix S3.

Landscape-scale vegetation recovery

We calculated burned/unburned ratios for average vegetation cover, height and density as a means of expressing the level of vegetation recovery – or, conversely, departure from undisturbed conditions – for each fire (n = 13). These ratios were derived by averaging values for each vegetation response across burned and unburned control transects separately, and then dividing the burned estimate by the unburned estimate. The importance of TSF on landscape-scale recovery patterns was first evaluated by fitting linear regression models with fire year as predictor of each burned/unburned ratio. We then evaluated a set of candidate models including all combinations (n = 32) of TSF and four other environmental variables that were averaged across transects for each fire: elevation, annual precipitation, post-fire precipitation and distance-to-edge (Table 1). Interaction terms were not included in these models to preserve degrees of freedom (*df*). Models were ranked according to AICc.

Results

Species and growth form response to fire

We identified 127 perennial species in measurements of vegetation cover and density (Appendix S4). Species composition differed significantly between burned and unburned areas in PERMANOVA, but no significant burn × decade interaction was detected (Table 2). In tests of individual decade groups, species composition differed significantly between burned and unburned areas for fires that occurred in the 2000s and 1990s, but not for 1980s fires. Annual precipitation explained the largest amount of variability in species composition, while elevation and aspect northness explained the second and third most variability, respectively (Table 2). Of the interaction terms, only burn × elevation explained a significant amount of variability, suggesting that elevation mediates the effect of fire on species composition.

Burn treatment explained a larger proportion of the variability in growth form composition than in overall species composition (Table 2). However, elevation and annual precipitation explained the most variability in growth form composition, while aspect northness and slope also had significant influences. Of the interaction terms, only burn × annual precipitation had a significant influence,

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Table 2. Influence of burn treatment, topography, climate and TSF on post-fire composition of species and growth forms in the Sonoran Desert, US, based on PERMANOVA models.

	Species Composition			Growth Forms	
	Terms	pseudo-*F*		Terms	pseudo-*F*
All Years	Burn	4.75***	All Years	Burn	11.20***
	Annual precip.	20.11***		Annual precip.	17.73***
	Aspect northness	7.87***		Aspect northness	4.43**
	Elevation	13.45***		Elevation	23.68***
	Slope	2.71**		Slope	3.22*
	Burn × Ann. precip.	1.48		Burn × Ann. precip.	2.51*
	Burn × Aspect north.	1.24		Burn × Aspect north.	1.35
	Burn × Decade	1.38		Burn × Decade	0.83
	Burn × Distance	1.53		Burn × Distance	1.98
	Burn × Elevation	2.12*		Burn × Elevation	2.10
	Burn × Slope	1.12		Burn × Slope	0.34
2000s	Burn	2.41*	2000s	Burn	2.08
1990s	Burn	2.50*	1990s	Burn	4.81**
1980s	Burn	1.28	1980s	Burn	3.04*

$*P < 0.05$ $**P < 0.01$ $***P < 0.001$.

suggesting that annual precipitation mediates the response of growth forms to fire. Although no significant burn × decade interaction was present, we found significant differences in growth form composition between burned and unburned transects from 1990s and 1980s fires (Table 2).

Principal response curves (PRC) indicated that fire changed the composition of species and growth forms, but that burned areas did not become either more or less similar to unburned controls with increasing TSF (Fig. 2a,b). The PRC model for species composition included a significant effect of burn treatment ($F = 4.48$, $P < 0.001$) but not TSF ($F = 1.04$, $P = 0.388$). The PRC model for growth forms followed the same pattern: burn treatment had a significant influence (pseudo-$F = 13.08$, $P < 0.001$), but not TSF (pseudo-$F = 0.55$, $P = 0.876$). Based on the species scores (Fig. 2a; Appendix S4), *Parkinsonia microphylla*, *Ambrosia deltoidea* and *Eriogonum fasciculatum* were most reduced in burned areas relative to unburned controls. In contrast, *Encelia farinosa* and *Pleuraphis rigida* exhibited the largest increases in cover in burned areas. Among growth forms, shrubs were most reduced in burned areas relative to unburned controls, followed by trees and cacti. Forbs, subshrubs and grasses all showed increased abundance in burned areas (Fig. 2b).

Burn treatment and environmental filters (elevation, annual precipitation and aspect northness) showed high relative importance in LME candidate model sets for transect-level cover of all growth forms, whereas TSF (burn × decade interaction) influenced only forbs and cacti (Fig. 3). The best-fitted candidate models ($R^2_m > 0.40$; Appendix S5) were obtained for grass and shrub cover, while models for tree cover explained relatively little variability ($R^2_m < 0.10$; Appendix S5). Tree cover was reduced in burned relative to unburned controls and on northerly aspects (Fig. 4a). Shrub cover increased with both higher elevation and annual precipitation irrespective of burn treatment, but burned shrub cover was lowest relative to

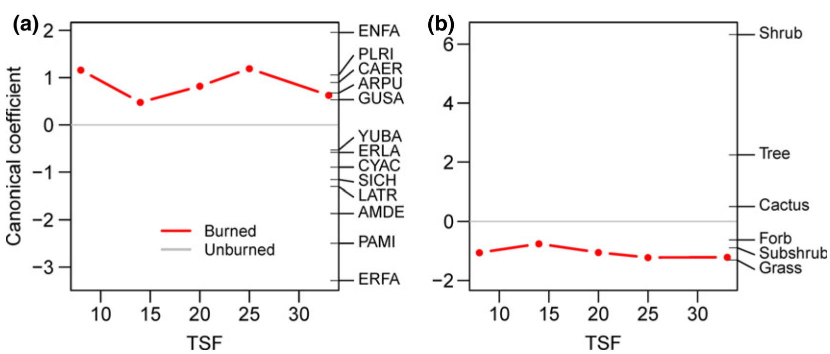

Fig. 2. Principle response curves expressing the rate of change in burned (**a**) species composition and (**b**) growth form composition relative to unburned areas as a function of time-since-fire (TSF) in the Sonoran Desert, USA. Individual species and growth form scores are displayed on the right axis (higher scores indicate a stronger response). Translation of species codes is provided in Appendix S4.

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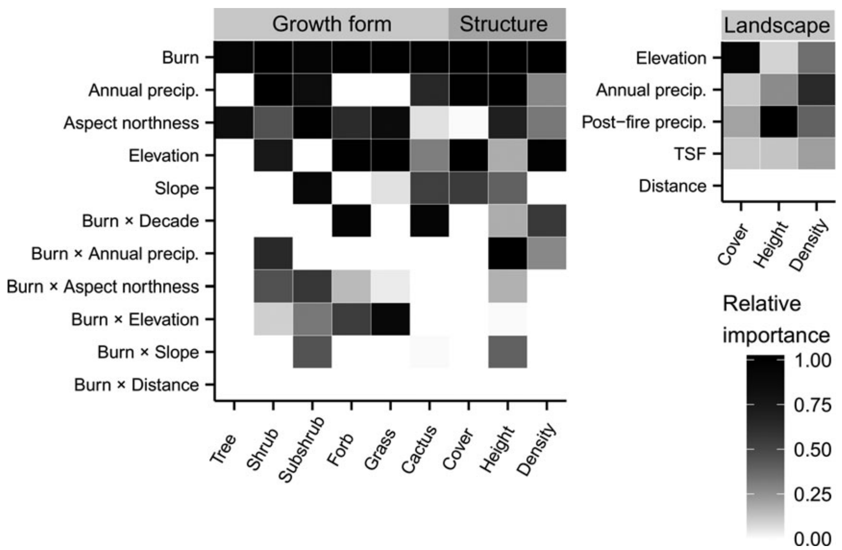

Fig. 3. Relative importance of terms in candidate model sets predicting cover of perennial growth forms (left), vegetation structure (middle), and landscape-scale vegetation recovery (right) with respect to burn treatment, topography, climate, TSF, and distance-to-edge of fire in the Sonoran Desert, USA. Relative importance is defined as the sum of Akaike weights (w_i) for all candidate models (ΔAICc < 4) in which a term appears.

unburned controls where annual precipitation was high (Fig. 4b). Sub-shrub cover in burned areas exceeded that of unburned controls on steep slopes and northerly aspects (Fig. 4c). Sub-shrub cover also increased with both higher elevation and annual precipitation irrespective of burn treatment. Cactus cover was reduced in burned areas relative to unburned controls for fires that occurred in the 2000s, but no such difference was found in older fires (Fig. 4d). At higher elevations, grass and forb cover in burned areas exceeded that of unburned controls (Fig. 4e, f, respectively). Grass cover also increased on northerly aspects (Fig. 4e). Forb cover was highest in burned areas of the 2000s fires, but did not differ between burned and unburned controls in older fires (Fig. 4f).

Response of vegetation structure to fire

Overall percentage vegetation cover was reduced in burned areas (27.21 ± 1.47%) relative to unburned controls (33.05 ± 1.48%). Burn treatment, elevation and annual precipitation had the greatest relative importance among terms in candidate models (Fig. 3). The model with lowest AICc included burn treatment, elevation, slope and annual precipitation as predictors (R^2_m = 0.52, R^2_c = 0.63; Appendix S5) and was well supported (w_i = 0.55). Cover increased with increasing elevation, slope and annual precipitation (Fig. 5a). The burn treatment × decade interaction, reflecting TSF, was absent among candidate models, and first appeared in a model with ΔAICc = 4.72.

Vegetation density (plants·m^{-2}) was higher in burned (3.00 ± 0.22) relative to unburned controls (2.35 ± 0.18). Burn treatment, elevation and TSF had the greatest relative importance among terms in candidate models (Fig. 3). The burn treatment × decade interaction occurred in both the first- and third-ranked models (Appendix S5). Burned areas in the first decade following fire showed higher vegetation densities relative to unburned areas (Burned: 4.19 ± 0.16; Unburned: 2.78 ± 0.16) than burned areas two decades (Burned: 2.18 ± 0.11; Unburned: 1.59 ± 0.11) and three decades (Burned: 2.47 ± 0.13; Unburned: 2.35 ± 0.13) following fire (Fig. 5b). Vegetation density increased with increasing elevation and along more northerly aspects in the model with lowest AICc (R^2_m = 0.40, R^2_c = 0.54, w_i = 0.34; Appendix S5). Vegetation density also increased to a greater extent in burned areas relative to unburned controls where annual precipitation was lowest (Fig. 5b).

Average vegetation height was reduced in burned areas (53.90 ± 0.28 cm) relative to unburned controls (75.35 ± 0.28 cm). Burn treatment, burn treatment × annual precipitation and aspect northness had the greatest relative importance among terms in candidate models (Fig. 3). The model with lowest AICc included burn treatment × annual precipitation and burn treatment × slope interactions, together with aspect northness (R^2_m = 0.26, R^2_c = 0.52; w_i = 0.22; Appendix S5). Reductions in vegetation height in burned areas relative to unburned controls were most pronounced on relatively flat surfaces and where annual precipitation was lowest (Fig. 5c). The burn treatment × decade interaction, reflecting TSF, was present in the third-ranked model (ΔAICc = 0.369, w_i = 0.18; Appendix S5). Reductions of

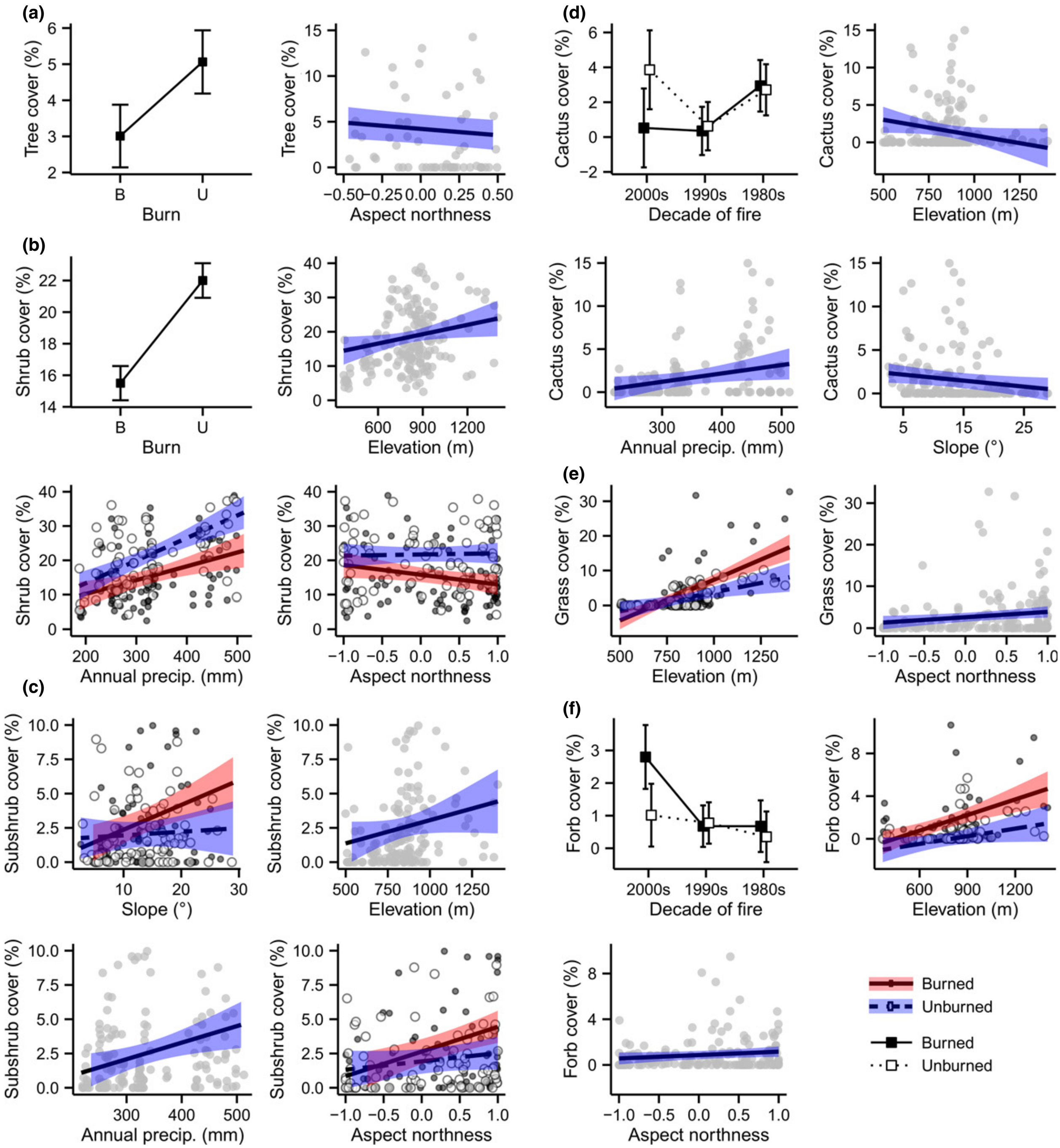

Fig. 4. Modal-averaged parameters predicting cover of perennial growth forms with respect to burn treatment, topography, climate, and time-since-fire. Shaded bands indicate 95% confidence intervals. Panels with separate predictions for burned and unburned areas show interaction terms. Growth forms include: (**a**) tree, (**b**) shrub, (**c**) subshrub, (**d**) cactus, (**e**) grass, and (**f**) forb.

vegetation height in burned areas were larger in the first decade following fire (Burned: 34.95 ± 0.54 cm; Unburned: 66.97 ± 0.52 cm) than in the second (Burned: 59.10 ± 0.34 cm; Unburned: 76.82 ± 0.37 cm) and third (Burned: 61.98 ± 0.43 cm; Unburned: 80.24 ± 0.42 cm) post-fire decades.

Landscape-scale vegetation recovery

Burned/unburned ratios ranged from a low of 0.48 to a high of 1.07 (mean = 0.79) for vegetation cover, from 0.33 to 1.15 (mean = 0.73) for vegetation height and from 0.66 to 2.22 (mean = 1.37) for vegetation density. Regressions

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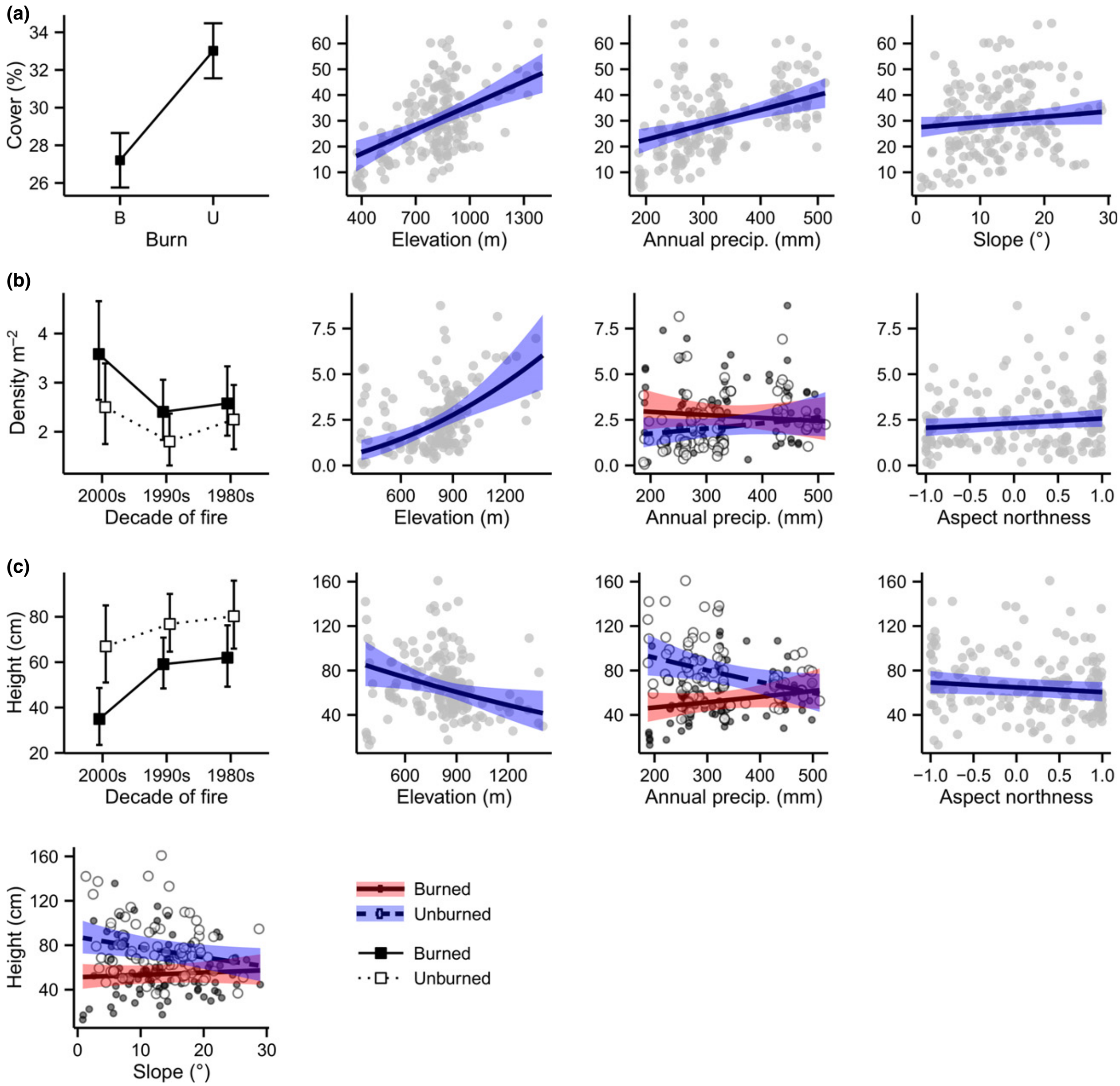

Fig. 5. Model-averaged parameters predicting (**a**) vegetation percentage cover, (**b**) vegetation density, and (**c**) vegetation height with respect to burn treatment, topography, climate, and time-since-fire. Shaded bands indicate 95% confidence intervals. Panels with separate predictions for burned and unburned areas show interaction terms.

including TSF as the sole predictor of vegetation recovery indicated weak relationships (cover: $R^2 = 0.09$; height: $R^2 = 0.08$; density: $R^2 = 0.17$; Fig. 6). In contrast, the models with lowest AICc values included elevation, post-fire precipitation and annual precipitation as predictors for burned/unburned ratios of vegetation cover, height and density, respectively (Appendix S5). The ratio of burned/unburned cover increased with increasing elevation ($R^2 = 0.50$; Fig. 6a), while the ratio of burned/unburned height increased with higher post-fire precipitation ($R^2 = 0.72$; Fig. 6b). In contrast, the ratio of burned/unburned density decreased with higher annual precipitation ($R^2 = 0.41$; Fig. 6c).

Discussion

Our study is the first to explore the relative influences of environmental filters and TSF on post-fire vegetation assembly and recovery patterns in the Sonoran Desert. Understanding these influences is essential for predicting

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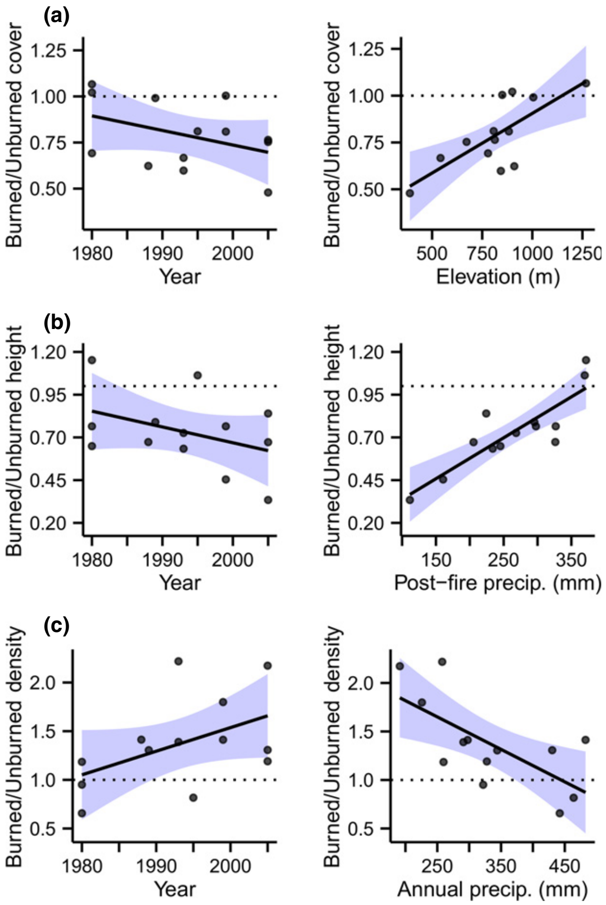

Fig. 6. Linear regressions comparing the influence of TSF (illustrated as year of fire) and environmental filters on the ratios of burned/unburned (**a**) vegetation cover, (**b**) vegetation height, and (**c**) vegetation density. Right panels show the best ranked (ΔAICc = 0) models. Shaded bands indicate 95% confidence intervals surrounding model predictions. Horizontal dashed lines show a burned/unburned ratio of 1 (i.e., no difference).

this ecosystem's response to a novel fire regime and forecasting impacts to habitat of threatened species. Collectively, our results suggest that environmental filters are more influential than TSF in shaping post-fire species composition, vegetation structure and landscape-scale vegetation recovery (a conceptual model for these relationships is presented in Appendix S6). Composition of perennial species and growth forms showed persistent differences between burned and unburned control areas that were best explained by environmental filters (Figs 2 and 3, Table 2). Differences in vegetation cover and height were better explained by environmental filters than TSF, while vegetation density exhibited both temporal and environmentally-driven responses to fire. At a landscape scale, simple topographic or climatic variables were far better predictors of vegetation recovery than TSF (Fig. 6). These results provide compelling evidence that the environmental-filter hypothesis is applicable to post-fire vegetation assembly in the Sonoran Desert, but they do not support our initial hypothesis (i) that species and growth form composition would be more strongly influenced by environmental filters than vegetation structure.

Species and growth form responses to fire

The reasoning behind our initial hypothesis (i) was that environmental filters act predominantly on species traits, favouring species with attributes that increase fitness (Keddy 1992). Hence, vegetation assembly following disturbance reflects habitat-filtering processes of the disturbed environment (Grime 2006; Smart et al. 2006). Our results show considerable variation among growth forms in their responses to fire that may indicate interactions between environmental filters and life-history traits. For example, grasses, forbs and sub-shrubs, which tend to be obligate post-fire seeders (Brooks & Minnich 2006), showed increased abundance in burned areas at higher elevations and along north-facing slopes – favourable microsites for seedling establishment. In contrast, trees, shrubs and cacti were reduced by fire even at these favourable microsites. Long-lived shrubs and trees of the Sonoran Desert are typically weak resprouters (Abella 2009) with large, non-wind dispersed seeds and episodic, climate-driven recruitment (Goldberg & Turner 1986; Cody 2000; Reynolds et al. 2012); collectively, these traits limit post-fire re-establishment (Shryock et al. 2014). Although cacti also have animal-dispersed seeds and episodic recruitment (Godínez-Alvarez et al. 2003), their generation times are shorter than those of dominant shrub or tree species in the Sonoran Desert (Goldberg & Turner 1986), potentially enabling cacti to recover sooner (Fig. 4).

We detected persistent changes in post-fire species composition, but these changes do not appear to constitute alternative stable states. Criteria that define alternative stable states include: (1) change in state results from a single disturbance and is not maintained by repeated perturbations; (2) multiple states can exist within the same environment depending on colonization history; and (3) the alternative state is maintained by autogenic (internal, biotic) rather than allogenic (external, abiotic) processes (Schröder et al. 2005; Mason et al. 2007). Our evaluation of once-burned areas clearly meets the first criterion. Given our space-for-time approach, we are unable to determine the influence of colonization history. However, our results are inconsistent with (3), in that species and growth form composition were predominantly and individually sorted along abiotic gradients. Furthermore, overall vegetation density, forb and cacti cover all showed increasing similarity to unburned vegetation with increasing TSF. Alternative stable state theory also assumes that

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species have had sufficient time to regenerate, which may not be the case in a desert even 33 yrs after fire (Cody 2000). Given these considerations, our results are more in keeping with an environmental filter-based model, in which post-fire vegetation assembly is determined by dispersal limitations and abiotic conditions that restrict which species from among those available in the total species pool are able to establish at a given site (Belyea & Lancaster 1999).

Vegetation structure and landscape-scale recovery

Vegetation cover was strongly influenced by elevation and average annual precipitation (Fig. 5a), and elevation was also the strongest predictor of recovery at the landscape scale (Fig. 6a). Elevation and annual precipitation were only weakly correlated across our study sites (r = 0.29), but both reflect gradients in resource availability and exposure. Interactions between precipitation, soil texture and temperature vary along elevation gradients due to alluvial processes and orographic uplift, profoundly influencing the spatio-temporal distribution of desert vegetation (Parker 1991; Medeiros & Drezner 2012; Munson et al. 2012). Our results suggest that abiotic conditions are the primary limiting factor for post-fire re-establishment of vegetation cover in the Sonoran Desert, accounting for the lack of a strong temporal trend in burned/unburned cover ratios across our study sites (Fig. 6a). Rather, re-establishment of vegetation cover varied spatially along elevation and precipitation gradients. Similar results have been obtained in semi-arid savanna (Levick et al. 2012) and mediterranean shrublands (Keeley et al. 2005).

Average vegetation height was primarily influenced by annual precipitation at the transect level, while post-fire precipitation was the strongest predictor of recovery at a landscape scale (Fig. 6b). Given that resprouting species typically re-establish faster than seedlings, these relationships are likely indicative of the post-fire resprouting rate, which is physiologically limited by low precipitation in arid environments but increases with increased precipitation (Pausas & Bradstock 2007; DeFalco et al. 2010; Nano & Clarke 2011). Low to moderate resprouting has been recorded for certain Sonoran Desert species (McLaughlin & Bowers 1982; Cave & Patten 1984; Abella 2009), but the relationship between resprouting and precipitation has not been quantified. However, our results provide indirect evidence that precipitation received in the first post-fire year has long-term effects on vegetation structure in the Sonoran Desert. This relationship likely reflects increased resprouting when more precipitation is available.

Vegetation density increased in burned relative to unburned areas during the first decade following fire, but this difference was no longer apparent with longer TSFs (Fig. 5c). Similar post-fire increases in density have been noted at other Sonoran Desert sites (Steers & Allen 2011), although density may be reduced in the first post-fire year (McLaughlin & Bowers 1982; Cave & Patten 1984). The return to pre-fire density we observed at older burns (TSF > 20) could reflect either density-dependent competitive interactions or the longevity of seedling cohorts that become established soon after fire, but do not regenerate continuously thereafter. Post-fire increases in density were also mediated through environmental filters, particularly annual precipitation. While resprouting increases with precipitation, obligate post-fire seeding species are more abundant in areas receiving less annual precipitation (Pausas & Bradstock 2007; Nano & Clarke 2011). This relationship may explain the negative correlation we detected between annual precipitation and density, which was the strongest predictor of burned/unburned density ratio at a landscape scale (Fig. 6c).

Future research needs

An important question that remains to be addressed is the time scale at which post-fire environmental filters are most influential. Do environmental filters influence vegetation assembly to a greater extent in early post-fire years, or continuously? In our analyses, only the relationship between vegetation height and post-fire precipitation clearly indicates a short-term influence (with long-term implications), while the time scale at which other relationships are most important – e.g. the correlation between recovery of vegetation cover and elevation – is unclear. Understanding whether these relationships represent immediate or continuous mechanisms could substantially improve predictions of post-fire vegetation change. For example, Harvey & Holzman (2014) found that the immediate influence of topographic position on seedling establishment resulted in divergent long-term successional trajectories.

A related research question concerns the extent to which biotic processes interact with environmental filters to influence post-fire vegetation dynamics. Facilitative interactions involving nurse plants are nearly ubiquitous in desert environments (Butterfield et al. 2010) and increase seedling establishment and survival by modulating the effects of limited precipitation (Tielbörger & Kadmon 2000; Butterfield et al. 2010) and affording protection from herbivores (McAuliffe 1986; Holland & Molina-Freaner 2013). The lack of large shrubs and trees could slow post-fire recovery of desert vegetation by limiting facilitative interactions (Abella 2009), whereas vegetation recovery may be faster where the dominant shrubs and trees are able to resprout (Arnan et al. 2007). The degree to which competitive or facilitative species interac-

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tions, mediated by environmental filters, shape post-fire recovery of desert vegetation warrants further study.

Variation in fire size and/or severity can interact with species' regeneration and dispersal mechanisms to create heterogeneity in burned vegetation (Turner et al. 1997; Coop et al. 2010). We did not find evidence that fire severity (Appendix S2) or size (distance-to-edge) influenced post-fire vegetation assembly at our Sonoran Desert study sites. However, sample points were randomly located rather than systematically spaced at increasing distance from fire edges (e.g. Coop et al. 2010), which could reduce our ability to detect edge effects. Moreover, edge effects on seed dispersal are likely moderated by fine-scale topographic barriers characteristic of upland Sonoran Desert sites, such as cliffs and washes, which were not accounted for.

Conclusions

Fire markedly altered Sonoran Desert vegetation communities at different scales of community organization and across a range in TSF (8–33 yr). We found strong support for the environmental-filter hypothesis, in that long-term, post-fire vegetation assembly was influenced more by environmental filters – particularly precipitation and elevation – than by TSF across spatial scales. In particular, landscape-scale recovery of vegetation structure showed closer correspondence to gradients in elevation, post-fire precipitation and annual precipitation than to recovery time. Of relevance to land managers is our finding that vegetation structure recovered faster as elevation and average annual precipitation increased, but that growth form composition showed less similarity to unburned vegetation under the same environmental conditions. We conclude that spatial variability in topography and climate within vegetation types can be more influential than TSF in shaping long-term, post-fire vegetation assembly. Hence, careful consideration of abiotic conditions will likely benefit models of post-fire vegetation dynamics and fire management strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristics of fires and sample points in the Sonoran Desert, US.

Appendix S2. Can a remotely-sensed fire-severity index derived from multi-temporal Landsat imagery predict long-term vegetation recovery in the Sonoran Desert?

Appendix S3. Model averaged coefficients for terms in candidate model sets.

Appendix S4. Species cover and density values.

Appendix S5. Candidate model sets (ΔAICc < 4) predicting perennial vegetation structure (Table 1), cover of perennial growth forms (Table 2), and landscape scale vegetation recovery (Table 3) with respect to burn treatment, topography, climate, and time-since-fire.

Appendix S6. Conceptual model illustrating the relative importance of environental filters and time-since-fire in shaping long-term, post-fire vegetation assembly in the Sonoran Desert of Arizona, US.

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