BRITISH ECOLOGICAL SOCIETY

JSTOR

SPECIAL FEATURE: LONG-TERM DYNAMICS AND IMPACTS OF PLANT INVASIONS

Alternative pathways to landscape transformation: invasive grasses, burn severity and fire frequency in arid ecosystems

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Summary

1. Arid ecosystems are often vulnerable to transformation to invasive-dominated states following fire, but data on persistence of these states are sparse. The grass/fire cycle is a feedback process between invasive annual grasses and fire frequency that often leads to the formation of alternative vegetation states dominated by the invasive grasses. However, other components of fire regimes, such as burn severity, also have the potential to produce long-term vegetation transformations. Our goal was to evaluate the influence of both fire frequency and burn severity on the transformation of woody-dominated communities to communities dominated by invasive grasses in major elevation zones of the Mojave Desert of western North America.

2. We used a chronosequence design to collect data on herbaceous and woody cover at 229 unburned reference plots and 578 plots that burned between 1972 and 2010. We stratified the plots by elevation zone (low, mid, high), fire frequency (1–3 times) and years post-fire (YPF; 1–5, 6–10, 11–20 and 21–40 YPF). Burn severity for each plot was estimated by the difference normalized burn ratio.

3. We identified two broad post-fire successional pathways. One was an outcome of fire frequency, resulting in a strong potential transformation via the grass/fire cycle. The second pathway was driven by burn severity, the critical aspect being that long-term transformation of a community could occur from just one fire in areas that burned at high or sometimes moderate severity. Dominance by invasive grasses was most likely to occur in low-and high-elevation communities; cover of native herbaceous species was often greater than that of invasive grasses in the mid-elevation zone.

4. *Synthesis.* Invasive grasses can dominate a site that burned only one time in many decades at high severity, or a site that burned at low severity but multiple times in the same time period. However, high burn severity may predispose areas to more frequent fire because they have relatively high cover of invasive annual grass, suggesting burn severity and fire frequency have both independent and synergistic effects. Resilience in vegetation structure following fire in many arid communities may be limited to a narrow window of low burn severity in areas that have not burned in many decades.

Key-words: biological invasions, chronosequence, community structure, deserts, disturbance, fire regimes, invasive species, resilience, resistance, secondary succession

Introduction

Disturbances are particularly important in creating conditions and opportunities favourable for invasion by non-native plants (Rejmanek 1989; Hobbs & Huenneke 1992; Mack *et al.* 2000). If impacts from invasive plants are of sufficient magnitude, they sometimes alter the disturbance regime that had

facilitated their colonization, establishment and spread (Theoharides & Dukes 2007). This can result in positive feedbacks between the invader and altered disturbance regime, whereby they interact and promote the persistence of one another (Hobbs *et al.* 2006).

As with other types of disturbance, the occurrence of fire over large spatial extents and long periods of time is termed a regime and described statistically by the frequency, severity, seasonality, size, extent and spatial complexity of fire events

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(Sugihara 2006). Fire regimes are influenced by topography, climate and fuels (vegetation). If these constraints change, then the fire regime is also likely to change, but the rates of change among the constraints are vastly different. Topography is essentially fixed, at least over ecological time scales, and climate shifts tend to occur over decades or more (Mitchell & Karoly 2001). In contrast, vegetation can change rapidly and is the factor most likely to cause initial changes to fire regimes (Brooks 2008).

Fire has been historically infrequent in arid and semi-arid deserts compared to other ecoregions due to sparse and discontinuous vegetation. With infrequent exposure to fire over evolutionary time, native desert vegetation tends to have few adaptations and generally low resilience to fire (Brooks, Minnich & Matchett in press). As a result, the abundance and diversity of native desert vegetation can decline when plant invasions change fuel characteristics and fire behaviour in ways that alter the historical fire regime (Brooks 2008).

Invasion of desert shrublands by non-native grasses is one of the most widely cited examples of plant invasions altering fire regimes via a process called the grass/fire cycle (D'Antonio & Vitousek 1992; D'Antonio 2000; Brooks et al. 2004). Increased cover of invasive annual grass (invasive grass from hereon) increases both the chance of a fire igniting and facilitating fire spread (Brooks 1999; Fuentes-Ramirez et al. 2015). This often decreases the time interval between the previous and subsequent fire as well as the extent of burning. More frequent and extensive burns decrease abundance of woody plants because native desert shrubs and trees have low resilience to fire, whereas annual grasses and forbs (especially non-natives) typically increase because they tend to be disturbance adapted and have high resilience to fire (Keeley 2001; Brooks 2008). In all likelihood, high burn severity results in similar reductions in woody plant abundance, as evidenced by positive associations between the amount of shrub biomass consumed by fire and their post-fire survival rates (Brooks, Minnich & Matchett in press). Thus, more frequent or high severity fire could potentially result in landscape transformation of desert shrublands to alternative vegetation states dominated by invasive annual grasses.

In this study, we examined both the individual and interactive roles of burn severity and fire frequency in altering fire regimes and long-term dominance of invasive annual grasses in the Mojave Desert, USA. Although a limited proportion (5%) of the Mojave Desert has burned in the last 50 years (McKinley, Brooks & Klinger in press), there has been concern the grass/fire cycle is becoming more prevalent in areas that have burned (Brooks & Esque 2002; Brooks 2012). The prevailing fire regime is characterized by a mid-to-late summer fire season, long return intervals (typically >100 years), relatively limited spatial extent and very heterogeneous burn severity patterns (Brooks, Minnich & Matchett in press; McKinley, Brooks & Klinger in press). In some years, the number of fires and overall area burned are several orders of magnitude greater than usual, but such years appear to be separated by many decades or even centuries (Brooks & Matchett 2006; R. Klinger, R. A. McKinley & M. Brooks,

unpublished data). Fire in the Mojave Desert is most prevalent in the eastern part and mid to high-elevation communities where precipitation is greatest (Tagestad et al. 2016). The elevational gradient in precipitation results in a similar gradient in woody cover; hence, fire in mid-and high-elevation communities is limited more by ignition (lightning) than fuel, while fire in lower elevations is limited more by fuel than ignition (Brooks & Matchett 2006). If the grass/fire cycle became more common, then there would be considerable potential for an increase in the overall extent of burning throughout the Mojave Desert. This is because dry, highly flammable invasive grass cover would likely increase the chance of ignition in mid and high-elevation communities and increase fuel loads in lower elevation communities. In effect, conversion of communities to long-term dominance by invasive grasses could weaken or, possibly, break down the current constraint that precipitation puts on fire occurrence across a large portion of the Mojave Desert. Moreover, years with very large fire events that are now rare could become more common.

Invasive grass, especially Bromus rubens L. (red brome), Bromus tectorum L. (cheatgrass) and Schismus spp. (Schismus arabicus Nees, Schismus barbatus (Loefl. ex L.) Thell.), are known to create higher and more persistent cover into the summer fire season in the Mojave Desert than the native annual grasses Vulpia spp. (Vulpia octoflora (Walter) Rydb. Vulpia microstachys (Nutt.) Munro), non-native forbs or native forbs (Brooks 1999). Many studies in the Mojave Desert have shown abundance of both native and non-native vegetation changes after fire and also vary with time since fire, sometimes resulting in communities once dominated by native woody shrubs being converted to ones where herbaceous species, and especially invasive grass, either dominate or are a much greater part of the community than prior to burning (Callison, Brotherson & Bowns 1985; Minnich 1995; Lei 1999; Brooks & Matchett 2003, 2006; Webb et al. 2003; Abella 2009; Abella et al. 2011). It has generally been thought resistance to invasion and resilience from fire (Brooks & Chambers 2011) were lowest in mid-elevation areas in the Mojave Desert because biophysical conditions were the most favourable for invasive grasses (Brooks & Matchett 2006, Brooks, Minnich & Matchett in press). Most studies in the Mojave Desert though have been of relatively short duration (<5 years since burning) and restricted to a particular vegetation type (e.g. creosote or blackbrush scrub). Thus, a general understanding of the degree to which elevation, fire frequency and burn severity interact and lead to the formation of long-term alternative vegetation states has been lacking.

We addressed three questions: (i) To what degree are short and long-term dominance of post-fire communities by invasive grasses influenced by burn severity? (ii) Does the likelihood of invasive grass dominance of post-fire communities vary with elevation? (iii) How persistent are invasive grass-dominated communities in sites that burned once in the last 40 years compared to those that burned two or more times? To answer these questions, we compared the degree to which cover of woody, herbaceous (forb + grass) and invasive grass

species varied along gradients of burn severity among different combinations of elevation zone, fire frequency and years after burning. Based on previous studies as well as a general conceptual model of the grass/fire cycle (Brooks 2008), we expected high fire frequency to lead to low resilience of native desert vegetation and low resistance to invasion by invasive annual grasses (Brooks *et al.* 2016). There is very little understanding of the effect burn severity has on invasive plants, but two studies indicated the potential for cover of invasive annual grasses being greater in sites that burned at high severity (Hunter *et al.* 2006; Hebel, Smith & Cromack 2009). Therefore, we predicted that greater fire frequency and burn severity would result in: (i) a lower ratio of woody: herbaceous vegetation cover; (ii) lower cover of woody vegetation; (iii) higher cover of herbaceous vegetation; and (iv) dominance of herbaceous vegetation by invasive annual grasses. We also predicted that these responses would be most likely in mid-elevation communities. From a fire perspective, an increase in cover of invasive grasses constitutes a change in fuelbed structure. Therefore, we interpreted conditions most conducive to a grass/fire cycle to be those associated with extreme and/or persistent changes in fuelbed characteristics.

Materials and methods

STUDY REGION

The Mojave Desert ($\approx$152 000 km^2; Fig. 1) is transitional between the colder Great Basin Desert to the north and warmer Sonoran Desert to the south (Rundel & Gibson 1996). The topography is extremely varied and characterized by numerous small mountain ranges and valleys. Elevation ranges from -85 to 3635 m, although
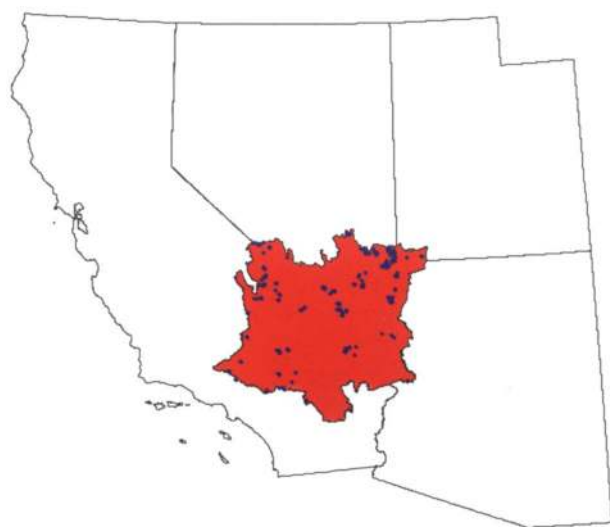

Fig. 1. The distribution of 807 plots (blue points) where vegetation was sampled in burned ($N = 578$) and unburned conditions ($N = 229$) within the Mojave Desert (red) in the southwestern United States. Each plot was sampled once in either 2009, 2011, 2012 or 2013. Fire had occurred in the burned plots 1–3 times since 1972.

most of the ecoregion is between 600 and 1600 m. Most precipitation occurs during the winter and early spring ($\approx$70%), with the annual total varying with elevation (5–13 cm in lower elevations, 25–75 cm at higher elevations) (Hereford, Webb & Longpre 2006; Tagestad *et al.* 2016). The temperature extremes in the Mojave Desert are very wide, ranging from lows of -20 °C (high elevation) to -5 °C (low elevation) during the winter and highs of 30 °C (high elevation) to 50 °C (low elevation) in the summer.

The variation in topography and climate results in considerable heterogeneity in vegetation, but there is zonation in structure and composition of community types along elevation gradients (Brooks & Matchett 2006; Brooks, Minnich & Matchett in press). The low-elevation zone ($\approx$<1200 m) is comprised primarily of low-statured shrubs with bare ground or a very sparse herbaceous layer between the shrubs (interspaces). The zone is usually considered to have relatively low to moderate resistance to invasive grasses and low resilience to fire (Brooks *et al.* 2016). The middle-elevation zone ($\approx$>1200 and <$\approx$1800 m) is dominated by shrubs, but their density is greater and they are taller than in the low-elevation zone. Interspaces in the middle-elevation zone are smaller in area, and they have greater herbaceous cover than in the low-elevation zone. Vegetation communities in the middle-elevation zone are considered to have low resistance to invasive grasses and low resilience to fire (Brooks & Matchett 2006). The high-elevation zone ($\approx$>1800 m) is comprised of a mix of tall shrubs and short-statured trees. Interspace area and herbaceous cover are relatively limited because of the density of shrubs and trees. Vegetation communities in the high-elevation zone are generally thought to be relatively resistant to invasive grasses and resilient to fire (Brooks *et al.* 2016).

Non-native plant species in upland areas of the Mojave Desert are usually herbaceous (Brooks 2009), and in areas of disturbance can often be a significant component of or dominate ground cover (Brooks & Pyke 2001; Brooks & Berry 2006). Invasive grasses that can dominate burned areas and increase chances of a grass/fire cycle include *Schismus* spp. in the low-elevation zone, *B. rubens* in the mid-elevation zone and lower parts of the high elevation zone, and *B. tectorum* in the high-elevation zone (Brooks, Minnich & Matchett in press; E. Underwood, R. Klinger & M. Brooks unpublished data). Besides the three annual grass taxa, the invasive annual forb *Erodium cicutarium* (L.) L'Hér. ex Aiton (red-stemmed stork's bill) can dominate burned areas in the mid-elevation zone and lower parts of the high-elevation zone (Brooks, Minnich & Matchett in press).

ESTIMATION OF BURN SEVERITY AND FIRE FREQUENCY

Burn severity was estimated by the differenced normalized burn ratio (dNBR; Eidenshink *et al.* 2007). dNBR is derived from Landsat satellite near-infrared and short-wave infrared bands to compare reflectance from areas pre- and post-fire. Differenced normalized burn ratio images are compiled, processed and archived by the Monitoring Trends in Burn Severity program (MTBS; http://www.mtbs.gov/) and routinely used to map fires throughout North America (Eidenshink *et al.* 2007). Images are acquired every 16 days throughout the year at a spatial resolution of 30 m. A detailed description is given in McKinley, Brooks & Klinger (in press) on the procedures we used to develop dNBR maps for all fires >405 ha throughout the Mojave Desert from 1972 through 2010. In brief, we acquired images of fire perimeters and dNBR from the MTBS archive for the period 1984 through 2010. The MTBS program does not compile images prior to 1984; therefore, we developed our own fire perimeter and dNBR

maps for the period from 1972 through 1983. Landsat images were acquired from the USGS Earth Resources Observation and Science Center (EROS). Perimeters were located by manually comparing images at the peak of the growing season (March through June depending on elevation) and at the end of the fire season (October to November). Differenced normalized burn ratio was derived from the closest cloud-free image after a fire occurred (post-fire image) and a cloud-free image near peak growing season prior to the fire (pre-fire image). Fire frequency was determined using a Geographic Information System (GIS; ESRI http://www.esri.com/) to overlay the individual fire perimeters and map their overlap over time. The GIS was used to extract dNBR and fire frequency values for all plots located within burned areas.

VEGETATION SAMPLING

Plant cover was recorded to species in 807 plots within (burned plots; $N = 578$) or adjacent to (unburned plots; $N = 229$) the perimeters of 53 fires that occurred entirely within or overlapped the Mojave Desert ecoregional boundary (Fig. 1). We used a chronosequence design (space-for-time substitution) to stratify the plots by intervals of years post-fire (YPF; 1–5, 6–10, 11–20 and 21–40 YPF), as well as elevation zone (low, mid, high; 57–2305 m) and fire frequency (burned 1–3 times since 1972). To account for variability related to topography, soils, and historical and current land use, we randomly selected a 1-km^2 site entirely within or outside the fire perimeters, then randomly selected 3–7 plots within each site. Each plot was sampled once during the study. Sampling was conducted in the spring (March through May) of 2009, 2011, 2012 and 2013 and timed to match peak vegetation production in each elevation zone.

A Geographic Positioning System was used to match the plots as closely as possible with the corner of a dNBR pixel. Each plot was 0·1 ha (32 m × 32 m) and contained three randomly positioned 25-m transects. Point intercept sampling was conducted at 0·5-m intervals along each transect ($N = 50$ points per transect, 150 points per plot). All plants intercepted by a wooden rod (1 mm diameter) were recorded to species at each point. Species cover in each plot was estimated as the sum of point intercepts for each species divided by 150. Plant authority was based on the USDA Plants Database (https://plants.usda.gov/java/).

DATA ANALYSIS

In general, cover of herbaceous plants is likely to increase while woody cover is likely to decrease following burning. Thus, we reasoned that resilience in vegetation structure and the potential for the development of a grass/fire cycle could be measured in three ways: (i) the log-ratio of woody-to-herbaceous cover, (ii) total woody and herbaceous cover and (iii) total and relative cover of invasive annual grass in the herbaceous layer of a community. The log-ratio would allow us to evaluate the relative amounts of woody and herbaceous cover over time, while total cover would allow us to identify whether changes in the ratio were a result of changes in woody or herbaceous cover. The absolute and relative cover of invasive annual grass would allow us to evaluate the period of time and degree to which they either dominated or were a significant component of post-fire communities. We could not measure persistence at individual sites but instead evaluated it using the YPF factor across sites.

All trees, shrubs and sub-shrubs, all of which were native, were grouped into a woody species category. Trees comprised 23·6% and

shrubs comprised 76·4% of woody cover in unburned reference plots. Invasive grasses, forbs and perennial grasses were grouped into an herbaceous species category. Invasive grasses comprised 30%, forbs (annual, biennial and perennial) 38% and perennial grasses 32% of the herbaceous cover in unburned plots. Invasive grasses were dominated by the non-native species *B. rubens* (24·3%), *B. tectorum* (19·7%) and *Schismus* spp. (52·5%), with the native *Vulpia* spp. (3·5%) comprising a much lesser proportion. We chose to include *Vulpia* spp. in the invasive grass category because we felt that its grass/fire cycle effects as an annual grass fuel were similar to the vastly more abundant non-native annual grass species. The log-ratio of woody and herbaceous plant cover was calculated as $\log_e$ (total woody cover/total herbaceous cover). Relative cover of annual grasses was calculated as the proportion of herbaceous cover (annual grass cover/total herbaceous cover).

We used generalized linear mixed models (GLMM's) to analyse our three measures of resilience of vegetation structure, but the pattern of burning across the ecoregion constrained our analysis of how fire frequency could be specified in the models. A large proportion of area in the 2005 and 2006 fires occurred in mid and high-elevation sites that had burned in the late 1970s and 1980s. Thus, while we had adequate sample sizes across YPF intervals and elevation zones for the plots that had burned just once since 1972, most plots that burned multiple times since 1972 were in the low-elevation zone and between 1–5 YPF or 25–35 YPF. Therefore, we partitioned the analyses into three groups, unburned (reference) plots in the three elevation zones, plots that burned once since 1972 (single burn plots) in the three elevation zones and plots that burned 1–3 times since 1972 (multiple burn plots) in the low-elevation zone.

For the unburned plots, we specified elevation zone as the fixed effect. The fixed effects in the group of single burn plots were YPF interval, elevation zone and burn severity (dNBR). The fixed effects in the group of multiple burn plots included the combination of fire frequency and YPF interval (1 burn/1–5 YPF, 1 burn/25–35 YPF, 2–3 burns/1–5 YPF, 2–3 burns/25–35 YPF) and burn severity. Site was specified as a random effect in all models. The year of sampling was not included as a random effect because there were too few levels ($N = 4$) (Bolker *et al.* 2009), and a preliminary analysis indicated Site accounted for 4×–8× more of the model deviance than year of sampling.

For burned plots (single and multiple), we conducted an initial analysis to determine the most appropriate random effect structure to use in the models (Zuur *et al.* 2009). We used the bias-corrected version of Akaike's information criterion (AIC$_c$) and AIC$_c$ weights (*w*AIC$_c$; Burnham & Anderson 2002) to compare random slope (dNBR) + intercept and random intercept models. Fixed effects in the comparisons were interactions among YPF interval, elevation zone and burn severity (the most complex combination; Zuur *et al.* 2009). If the random slope + intercept and random intercept models had similar levels of support, then we selected the random intercept model based on the principle of parsimony.

After determining the most appropriate random effect structure, we specified five models to evaluate the importance of additive and multiplicative combinations of the fixed effects for the single burn group (Appendix S1, Supporting Information, Table SA1), and four models to evaluate fixed effects for the multiple burn group (Table SA2). A Gaussian error structure and identity link were specified for models of the log-ratio of woody/herbaceous cover. Because absolute cover values for each of the vegetation classes could be >100%, we rounded them to the nearest whole number and specified a Poisson error structure and log link for those models. Relative cover values are

constrained to an interval of 0–1 after dividing them by 100. We logit transformed the 0–1 values and then specified a Gaussian error structure and identity link for those models.

If wAIC$_c$ for the model with the lowest AIC$_c$ value was $\geq$0·8, then that model was selected as the best supported one. If wAIC$_c$ for the model with the lowest AIC$_c$ value was <0·8, then we: (i) determined if the 95% CIs of the parameters in the competing models overlapped zero; and (ii) conducted log-ratio tests among the competing models to evaluate whether there were parameters that could be removed from a given model. If there was not sufficient justification for selecting one model over another after inspecting the CIs and conducting log-ratio tests, we derived the final parameter estimates by model averaging (Burnham & Anderson 2002).

We used the LME4 package (Bates *et al.* 2015) in R (R Core Team 2016) to conduct the GLMMs, and the AICCMODAVG package (Mazerolle 2017) to derive model averaged parameter estimates. For reporting results in the text, we use the upper bound of the YPF interval for succinctness but emphasize that it represents an interval of time (e.g. "…at 10 YPF…" is 6–10 YPF).

Results

Model selection statistics for all analyses are presented in Appendix S1.

EFFECT OF BURN SEVERITY ACROSS ELEVATION ZONES IN SINGLE BURN PLOTS

Woody:herbaceous cover ratio

In general, the woody:herbaceous cover ratio indicated that shrub cover had a long-term negative response and herbaceous cover a long-term positive to response to burn severity. The ratio increased systematically with elevation in unburned plots (Table 1, Appendix S1). It had a strong negative relationship

Table 1. Means, standard errors (SE) and 95% confidence intervals (CI) of five vegetation structure variables from 229 unburned plots in the Mojave Desert, 2009–2013. Woody–herbaceous ratio is the log$_e$ ratio between total woody and herbaceous cover. Cover of invasive annual grass was comprised almost entirely of invasive annual species (>96%). Zone is one of three elevation zones (low <1200 m, mid 1200 m < x < 1800 m, high >1800 m)

Variable	Zone	Mean	SE	95% CI
Woody:Herbaceous	Low	0·842	0·394	0·448–1·236
Cover Ratio	Mid	1·416	0·403	1·013–1·819
	High	2·057	0·378	1·679–2·436
Woody Absolute Cover	Low	15·3	1·8	11·8–18·9
	Mid	18·0	2·3	13·5–22·4
	High	22·3	2·4	17·6–27·0
Herbaceous Absolute Cover	Low	3·3	1·2	1·1–5·6
	Mid	2·7	1·0	0·7–4·7
	High	2·8	0·9	1·0–4·5
Invasive Grass Absolute	Low	1·4	0·6	0·8–2·0
Cover	Mid	1·5	0·7	0·8–2·2
	High	0·7	0·3	0·4–1·0
Invasive Grass Relative	Low	19·6	8·8	11·4–31·5
Cover	Mid	44·3	14·7	28·5–61·3
	High	3·4	0·6	2·0–5·8

Table 2. Summary statistics of the difference normalized burn ratio (dNBR) collected within the perimeters of 252 fires that occurred in the Mojave Desert between 1984 and 2007. The statistics were calculated from 37,918 random points. Zone is one of three elevation zones (low <1200 m, mid 1200 m < x < 1800 m, high >1800 m)

Zone	Mean	SE	Median	Maximum
Low	201·4	0·7	178	930
Mid	237·7	1·3	226	681
High	421·7	2·5	443	816

with dNBR at 5 YPF, especially in the high-elevation zone where the highest levels of burn severity were observed (over 2× that of low or middle elevations; Table 2). Although the relationship weakened during subsequent years (Fig. 2), the likelihood of the ratio returning to levels similar to unburned sites after 40 YPF still depended on burn severity. At high levels of dNBR, the ratio was lower than unburned levels in all zones after 40 YPF. The ratio was similar to that in unburned plots by 40 YPF at low to moderate levels of dNBR in the middle and high-elevation zones, but in the low-elevation zone it approached that of unburned plots at 40 YPF only when dNBR was low.

Woody absolute cover

Woody cover increased systematically with elevation in unburned plots (Table 1, Appendix S1) and was negatively associated with dNBR (Fig. 3). Across elevation zones, woody cover was 1·5×–3× greater in unburned plots than plots at 40 YPF for high levels of dNBR and generally was lower at intermediate levels of dNBR than in unburned plots after the same period of time. At lower levels of dNBR, recovery of woody cover varied among elevation zones; it approached that in unburned plots at 20 YPF and had reached them by 40 YPF in the low-elevation zone, while in the middle and high-elevation zones it had reached levels similar to unburned plots after 40 YPF.

Herbaceous absolute cover

Herbaceous cover in unburned plots was low, generally ranging from 1% to 5%, and did not vary substantially among elevation zones (Table 1, Appendix S1). It had a strong positive relationship with dNBR in the low-and high-elevation zones but was much weaker in the mid-elevation zone. Although the relationship diminished over time in all elevation zones, herbaceous cover was greater in burned than unburned plots for 20–40 YPF (Fig. 4) except at the lowest levels of dNBR.

Invasive grass cover

Absolute cover of invasive grass in unburned plots was low (<3%) and did not vary among elevation zones (Table 1, Appendix S1). The relationship absolute cover had with dNBR was weak and variable in the low-and middle-elevation zones but strong and positive in the high zone (Fig. 5). In
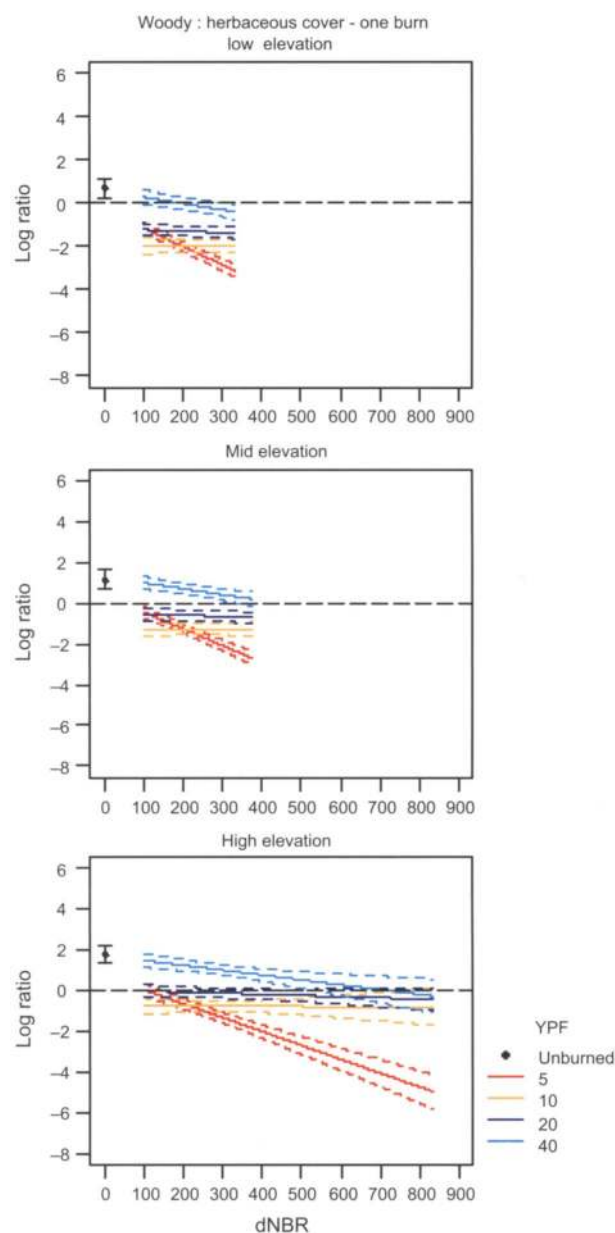
Fig. 2. The log$_e$ ratio ($\pm$95% CIs; dashed lines) of woody:herbaceous cover across a gradient of burn severity (dNBR) in three elevation zones (low <1200 m, mid 1200 < x < 1800 m, high >1800 m) and five intervals of years post-fire (YPF; 5 = 1–5 YPF, 10 = 6–10 YPF, 20 = 11–20 YPF, 40 = 21–40 YPF) in plots that had burned one time since 1972 in the Mojave Desert. The estimates were based on a chronosequence (space-for-time substitution) design where plots burned one time since 1972 were sampled in 2009, 2011, 2012 and 2013. Dashed coloured lines are 95% confidence intervals. The dashed black line is where cover values of woody and herbaceous cover are equal.

Fig. 3. The relationship of woody cover with burn severity (dNBR) among four classes of years post-fire (YPF; 5 = 1–5 YPF, 10 = 6–10 YPF, 20 = 11–20 YPF, 40 = 21–40 YPF) in three elevation zones (low <1200 m, mid 1200 < x < 1800 m, high >1800 m) in plots that had burned one time since 1972 in the Mojave Desert. Dashed lines are 95% confidence intervals.

burned plots, cover values peaked between 10 and 20 YPF then decreased after that across all elevation zones, but they differed greatly among the zones at 40 YPF. Absolute cover values were 2×–3× greater in burned than unburned plots in the low-and mid-elevation zone but generally less than 5% (Fig. 5). In contrast, they ranged from 5% to almost 20% at 40 YPF in the high-elevation zone.
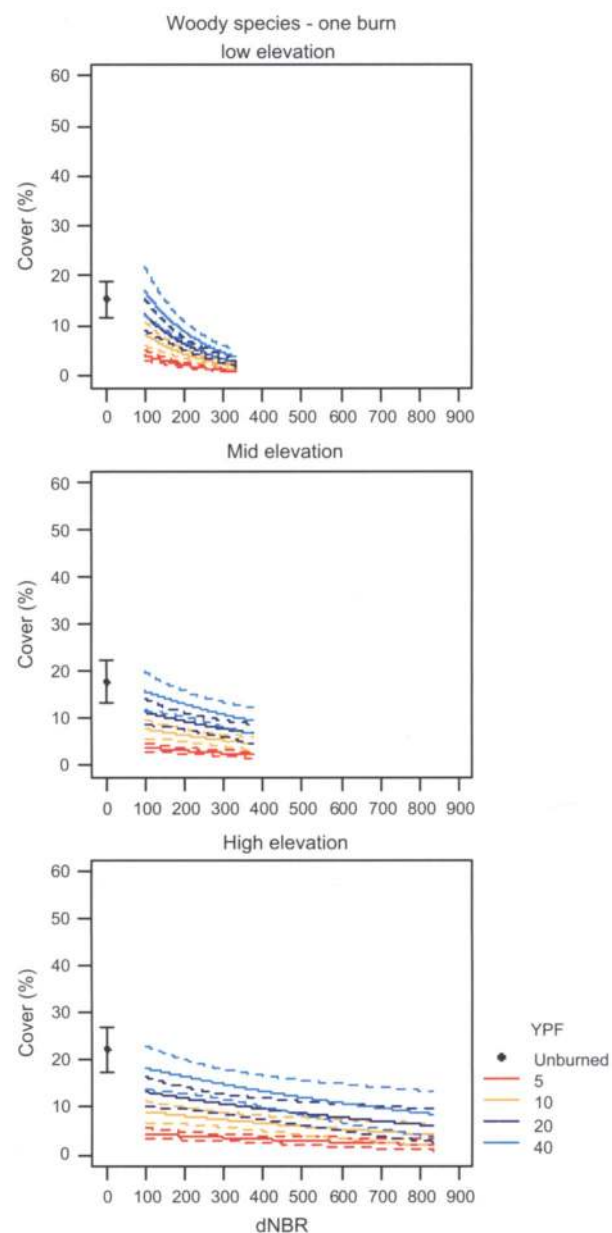
Relative cover of invasive grass comprised almost 50% of total herbaceous cover in unburned plots in the mid-elevation zone, which was more than 2× greater than the low zone and 9× greater than the high zone (Table 1). In burned plots, invasive relative cover had clear interactions with time since fire, elevation zone and burn severity (Fig. 6). There was a strong negative relationship with dNBR in the low-elevation zone, but it was absent in the middle zone and weakly positive in the high zone (Fig. 6). Although relative cover increased over time in all three elevation zones, especially between 5 YPF and 10 YPF, it decreased in the first 5 YPF
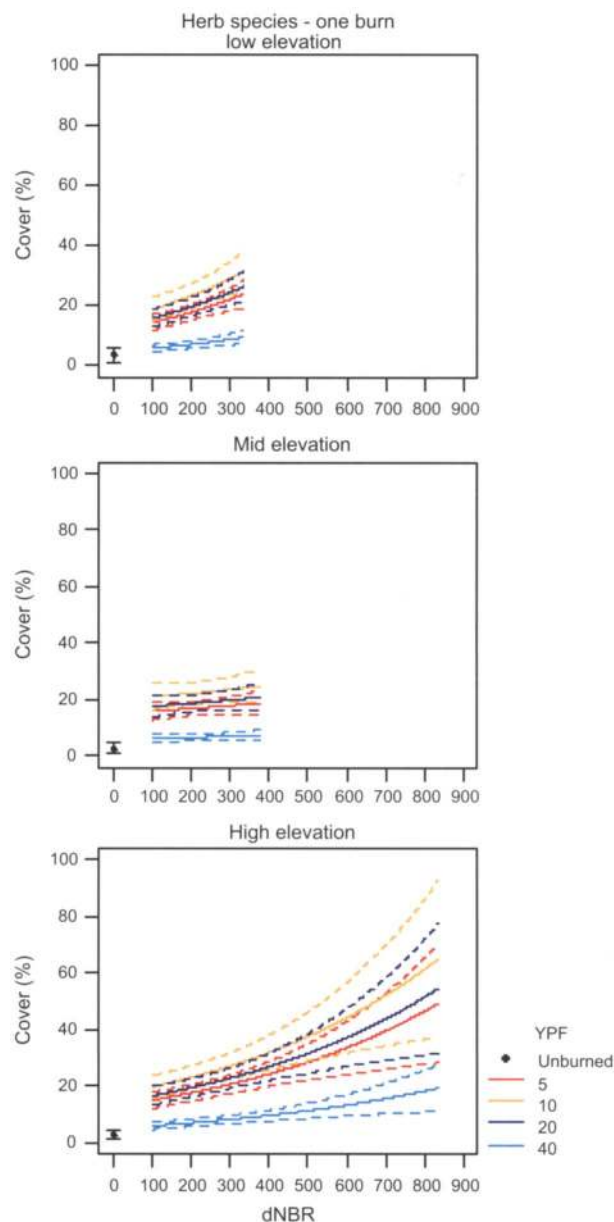
Fig. 4. The relationship of herbaceous cover with burn severity (dNBR) among four classes of years post-fire (YPF; 5 = 1–5 YPF, 10 = 6–10 YPF, 20 = 11–20 YPF, 40 = 21–40 YPF) in three elevation zones (low <1200 m, mid 1200 < x < 1800 m, high >1800 m) in plots that had burned one time since 1972 in the Mojave Desert. Dashed lines are 95% confidence intervals.
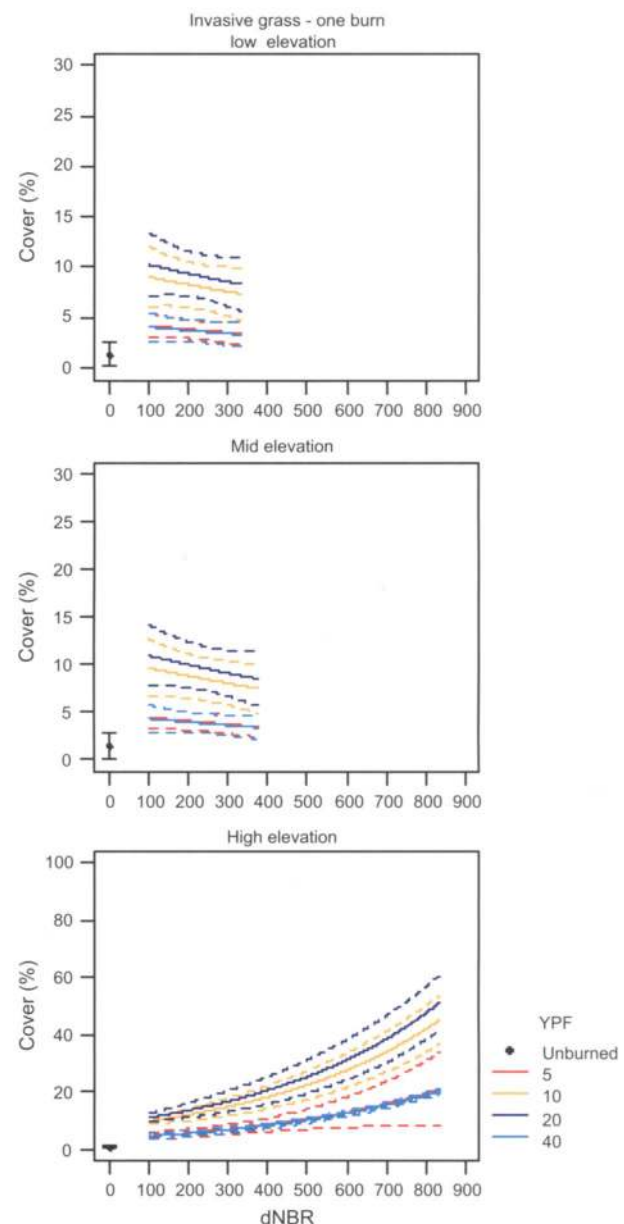
Fig. 5. The relationship of annual grass absolute cover with burn severity (dNBR) among four classes of years post-fire (YPF; 5 = 1–5 YPF, 10 = 6–10 YPF, 20 = 11–20 YPF, 40 = 21–40 YPF) in three elevation zones (low <1200 m, mid 1200 < x < 1800 m, high >1800 m) in plots that had burned one time since 1972 in the Mojave Desert. Dashed lines are 95% confidence intervals.

in the middle zone while increasing in the high zone during this same period. In the low-elevation zone, its response in the first 5 YPF depended on burn severity (Fig. 6).

EFFECTS OF FIRE FREQUENCY IN THE LOW-ELEVATION ZONE

Woody:herbaceous cover ratio

The woody:herbaceous cover ratio became negative after burning and remained so for several decades (Table 3). The ratio was 1·5×–2× lower in multiple burn than single burn

plots, and there was a negative relationship between the ratio and dNBR (parameter estimate = −0·6795 ± 0·1086 SE).

Woody absolute cover

There was a strong negative relationship between woody cover and dNBR across fire frequency/YPF classes (parameter estimate = −0·939 ± 0·118 SE). Woody cover in burned plots was approximately one-fifth of that in the unburned
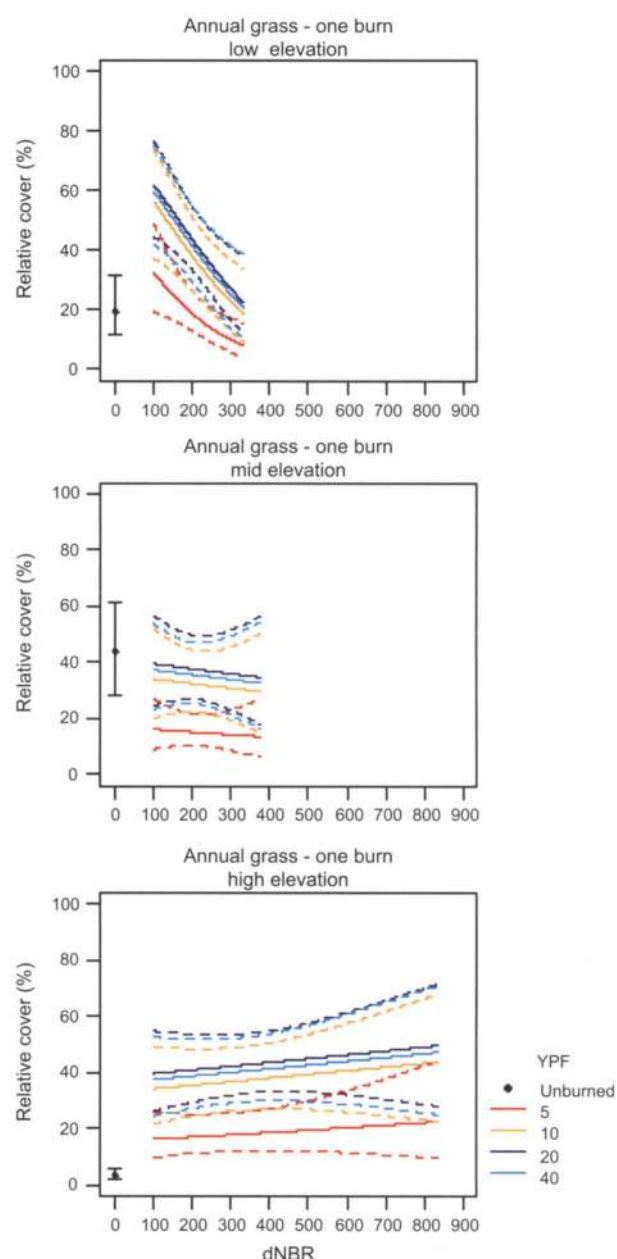
Fig. 6. The relationship between relative cover of annual grass and burn severity (dNBR) among four classes of years post-fire (YPF; 5 = 1–5 YPF, 10 = 6–10 YPF, 20 = 11–20 YPF, 40 = 21–40 YPF) in three elevation zones (low <1200 m, mid 1200 < x < 1800 m, high >1800 m) in plots that had burned one time since 1972 in the Mojave Desert. Dashed lines are 95% confidence intervals.

plots (Table 3), but there were no meaningful differences in cover among the YPF intervals within each fire frequency class.

Herbaceous absolute cover

Herbaceous cover was generally 3× greater in single burn plots than unburned plots, but it was 6×–7× greater in multiple burn plots than in unburned plots (Table 3). There was a

strong positive relationship between herbaceous cover and dNBR (parameter estimate = 0·272 ± 0·084 SE).

Invasive grass absolute cover

Mean invasive grass cover was more than 3× greater in single burn plots 25–35 YPF as well as multiple burn plots in both YPF intervals than in the unburned plots (Table 3). Cover was similar among those frequency/YPF combinations, but in general it remained <15% (Table 3).

Invasive grass relative cover

Relative cover of invasive grasses was greatest in multiple burn plots at 5 YPF (Table 3). It was more than 2·5× greater in this fire frequency/YPF combination than in unburned plots and generally comprised the dominant cover type. Relative cover values of invasive grass decreased over time in multiple burn plots and were similar to those in unburned plots after 40 YPF (Table 3).

Discussion

Feedbacks between biological invasions and fire regimes can lead to conversion of woody communities to invasive annual grass-dominated communities through the process of increased fire frequency (D'Antonio & Vitousek 1992; Brooks *et al.* 2004; Brooks 2008). In contrast, there has been very little attention given to other components of fire regimes that could potentially promote such transformations, especially burn severity (D'Antonio 2000; Hunter *et al.* 2006; Hebel, Smith & Cromack 2009). Across four decades and an ecoregion-scale, we found that burn severity was at least as important as fire frequency in promoting long-term conversion of woody-dominated communities to herbaceous-dominated communities in the Mojave Desert. Moreover, there appeared to be at least two broad pathways by which such conversions could occur; one from high burn severity and the other from high fire frequency.

We expected that higher burn severity and fire frequency would result in a long-term low ratio of woody:herbaceous cover, primarily because woody cover would be drastically reduced (O'Leary & Minnich 1981; Brown & Minnich 1986) and remain so while herbaceous cover increased (Steers & Allen 2012). This was generally so, although there was evidence of resilience in the lower ranges of severity in single burn sites. In mid and upper ranges of severity, woody cover in single burn plots tended to remain below and herbaceous cover above that in unburned plots. Burn severity was an important effect in multiple burn plots, but shorter fire return intervals (i.e. high frequency of burning) appeared to compound or even outweigh severity effects and there was no indication of resilience in vegetation structure in these sites. Resilience in woody cover several decades following fire has been reported in the Mojave Desert and adjacent Colorado Desert (Abella 2009; Steers & Allen 2011), and resprouting following fire is known to occur in some woody species (Brooks, Minnich & Matchett in press; Abella *et al.* 2009).

Table 3. Means, standard errors (SE) and 95% confidence intervals (CI) for five vegetation structure variables in five fire frequency (Frequency)/ years post-fire interval (YPF) combinations in the low-elevation zone (<1200 m) in the Mojave Desert. The fire frequency levels were Unburned, 1 burn or 2–3 burns since 1972. The YPF intervals were 1–5 years or 25–35 years. Woody–herbaceous ratio is the log_e ratio between total woody and herbaceous cover. Cover of annual grass was comprised almost entirely of invasive annual species (>99%)

Variable	Frequency	YPF	Mean	SE	95% CI
Woody:Herbaceous	Unburned		0·553	0·213	0·136–0·97
Ratio	1	1–5	−1·651	0·308	−2·254 to −1·048
	1	25–35	−1·613	0·209	−2·022 to −1·205
	2–3	1–5	−3·259	0·392	−4·027 to −2·491
	2–3	25–35	−2·691	0·360	−3·396 to −1·986
Woody Absolute Cover (%)	Unburned		15·3	2·0	11·4–19·3
	1	1–5	3·2	0·4	2·5–3·9
	1	25–35	3·2	0·4	2·5–3·9
	2–3	1–5	0·3	0·1	0·1–0·5
	2–3	25–35	0·3	0·1	0·1–0·5
Herbaceous Absolute Cover (%)	Unburned		5·7	1·4	2·8–8·5
	1	1–5	15·8	3·8	8·4–23·1
	1	25–35	18·0	3·1	11·9–24·0
	2–3	1–5	38·5	10·2	18·5–58·5
	2–3	25–35	34·2	7·8	19·0–49·5
Annual Grass Absolute Cover (%)	Unburned		2·3	0·8	0·8–3·8
	1	1–5	2·5	0·7	1·0–3·9
	1	25–35	8·3	1·5	5·4–11·3
	2–3	1–5	8·8	2·3	4·3–13·2
	2–3	25–35	8·9	2·2	4·5–13·2
Annual Grass Relative Cover (%)	Unburned		15·4	5·2	9·3–24·5
	1	1–5	7·9	1·2	5·5–11·1
	1	25–35	28·1	7·5	23·3–33·4
	2–3	1–5	54·2	14·2	44·8–63·2
	2–3	25–35	20·0	9·1	11·8–31·9

But it is also known that resprouting rates for many woody species are low (Abella 2009) and some species are almost always killed by fire (e.g. *Coleogyne ramosissima* Torr.; Callison, Brotherson & Bowns 1985; Brooks & Matchett 2003). Moreover, woody diversity in post-fire communities in the Mojave Desert is lower than that in unburned communities, indirectly indicating limited resilience for most species (Steers & Allen 2011). Given the range in burn severity within and among elevation zones we observed, and most woody species not having an extensive evolutionary history with fire (Brooks, Minnich & Matchett in press), it is likely resilience in woody cover in the Mojave Desert will most often be restricted to areas that burn at low severity in the low-and mid-elevation zones.

It appears many post-fire vegetation communities in the Mojave Desert will have greater herbaceous cover than in unburned communities and these will be persistent states (Brooks 2009; Steers & Allen 2012). This does not necessarily mean though that invasive grasses will dominate the communities. While they may often comprise a significant proportion of relative cover after burning, persistent invasive grass-dominated communities (i.e. relative cover >50%) appear to be most likely to occur at lower and higher elevations, even in areas with frequent fire. Invasive grasses may be an important component of herbaceous cover several decades after fire in the mid-elevation zone, but our data indicate their relative cover among herbaceous species will often be

similar to that in unburned sites. Burn severity influenced patterns of invasive grass cover, but the magnitude and direction of its importance varied considerably among elevation zones and time since fire. This context dependency (D'Antonio, Tunison & Loh 2000; Ostoja, Schupp & Klinger 2013) was likely not just a result of variation in burn severity among the elevation zones but also due to several other factors, including differences among the zones in biophysical conditions, burn severity effects on the soil seed bank and biotic interactions.

Biophysical conditions are harsher in the low-elevation zone than the mid-and high-elevation zones (Brooks, Minnich & Matchett in press), and higher burn severity could intensify these conditions and make low-elevation sites less favourable (i.e. increased resistance) for invasive grasses. This could be due to nutrient loss or changes in soil texture that reduce infiltration of already limited water resources (Johansen 2003; Fuentes-Ramirez *et al.* 2015). However, if nutrient loss, altered soil properties or reduced water availability were consistently important effects, then we would expect to have seen a negative relationship between dNBR and absolute cover in the early years after a fire, but this was not the case.

Recovery of invasive grass cover following fires depends on germination from the soil seed bank and colonization from unburned sites. Several studies in the Mojave Desert have shown that fire reduces seed banks of invasive grasses in burned areas, especially under shrubs (Abella *et al.* 2009; Esque, Young & Tracy 2010; Jurand & Abella 2013).

However, they continue to dominate the seed bank in burned areas and recovery to pre-burn levels is rapid (Jurand & Abella 2013). We found that, across elevation zones, cover of invasive grasses was low in the first 5 years after a fire and then increased for the next 15–20 years. This is what one would expect as conditions improved for greater colonization from unburned propagule sources and seedling establishment from the seed bank. We also found that 1–2 decades after burning cover of invasive grass in the low-and mid-elevation zones was greater when burn severity was lower, which is consistent with the hypothesis that depletion of their seed banks increases as a result of greater heating (Abella *et al.* 2009; Esque, Young & Tracy 2010). The relationship of cover with burn severity in the high-elevation zone was opposite that in the low-and mid-elevation zones, but soil and organic litter tend to be deeper at higher elevations so we suspect higher severity burns open up these patches and improves conditions for germination (Meyer, Allen & Beckstead 1997).

Seed and seedling predation by rodents can have significant effects on post-fire vegetation communities in the deserts of North America, including reducing establishment of invasive grasses (St. Clair *et al.* 2016). Rodents are an especially diverse and abundant group in the Mojave Desert (Stevens, Tello & Steele 2012) and are known to consume *Bromus* seeds (Beatley 1969). Although fire tends to reduce diversity of rodents in the initial years after burning, habitat use and abundance of some seed predator species (e.g. *Dipodomys*) (Vamstad & Rotenberry 2010; Horn, McMillan & St. Clair 2012) are greater in burned than unburned areas in the initial years after burning. These species could have strong effects on establishment of invasive grass seedlings and indirectly dampen or mask physical effects of burn severity. However, there can be strong spatial and temporal variation in composition and abundance of desert rodent assemblages (Beatley 1976; Price, Waser & McDonald 2000; Mena & Vázquez-Domínguez 2005; Stapp 2010). Thus, it is likely the intensity of seed predation is also spatially and temporally variable, with diminishing effects as time since fire increases.

Competition among invasive and native plants, especially for limited water, is a well-recognized and extensive interaction in North American deserts (Brooks 2000; DeFalco, Fernandez & Nowak 2007; Gremer *et al.* 2013). Although most competition studies have focused on negative effects of invasive grasses on native herbaceous species in the Mojave Desert (Brooks 2000; DeFalco *et al.* 2003; DeFalco, Fernandez & Nowak 2007), our data suggested that competitive effects from forbs on invasive grass intensified 20–40 years after burning. Forbs, especially the non-native *E. cicutarium*, generally have a positive response to burning in the Mojave Desert (Brooks & Matchett 2003, 2006). Total herbaceous cover had a positive relationship with dNBR in the low-elevation zone, especially in the first 20 years after fire. Given the relatively constant relationship invasive grass cover had with burn severity in lower elevations, the implication is that forbs comprised a higher proportion of the cover than did invasive grass. Therefore, we suspect diffuse competition from forbs

was the most likely reason for why we observed relatively low cover of invasive grass at higher levels of burn severity in the low-elevation zone. Biophysical conditions in the middle-elevations are favourable for invasive grasses (Brooks & Chambers 2011), but they probably are as well for forbs, especially *E. cicutarium* (Brooks & Matchett 2003). Cover of both forbs and invasive grasses peaked 10–20 years after burning in the mid-elevations, but cover of invasive grasses tended to decrease with burn severity while forb cover generally increased with severity. As in the low-elevation zone, diffuse competition from forbs is a reasonable explanation of why invasive grass was an important but not dominant component of herbaceous cover in the mid-elevation zone. In contrast with the low-and mid-elevation zones, cover of forbs and invasive grass had similar patterns over time in the high-elevation zone. This suggests competition from forbs was relatively weak in this zone, and it is worth noting that *E. cicutarium* is uncommon at higher elevations. It appears that there is an elevation gradient in competition intensity in the Mojave Desert (Maestre *et al.* 2009), with the greatest effects in lower elevations.

Burn severity and fire frequency had important effects on woody and total herbaceous cover in the multiple burn plots, but cover of invasive grass was influenced by burn frequency and independent of burn severity. We must be cautious extrapolating these patterns to the mid-and high-elevation zones, but suspect they are similar. This is because: (i) there is no evidence to suggest woody cover in the mid-and high-elevation zones would not be lost to the same degree as in the low elevation zone after frequent fire; (ii) *B. rubens* and *B. tectorum* are known to dominate cover in areas that burn at high frequency (Brooks 1999; Brooks *et al.* 2016); and (iii) feedbacks between invasive grass and frequent fire have been well-described for many years (Brooks *et al.* 2004; Brooks 2008). Nevertheless, there might be important differences between the zones, such as the rate at which communities are transformed or relative abundance of grasses and forbs (Engel & Abella 2011). In addition, we are unable to state with a reasonable level of assurance what happens to invasive grass cover between 5 and 25 years after fire in the multiple burn plots, although we suspect similar dynamics as those in the single burn plots. This is because absolute cover of the invasive grasses was very comparable in single and multiple burn plots 35 years after burning, and the decrease in relative cover of invasive grass and increase in relative cover of forbs in the multiple burn plots paralleled that in single burn plots.

The most important outcome from either the burn severity or fire frequency pathway may be that invasive grasses remain a significant component of herbaceous cover 35–40 years after burning, regardless of whether they are the dominant group or not. From a fire perspective, this constitutes a major alteration to the fuelbed and clearly enhances chances of a grass/fire cycle developing. It is likely much of the region is at risk of this; *Schismus*, *B. rubens* and *B. tectorum* occur across the region, and although the peak of each species abundance occurs at a different elevation, their distributions have considerable geographic and elevation overlap

(Brooks & Berry 2006). In addition, *E. cicutarium* can reach high levels of abundance after fire and its distribution overlaps that of *Schismus* and *B. rubens* (Brooks & Berry 2006). *Erodium cicutarium* is not known to alter fire regimes, but it can dominate herbaceous cover in many burned sites and suppress abundance of native species (Brooks & Matchett 2003). Thus, either individually or in combination, it can be expected that the three invasive grass species and *E. cicutarium* will often comprise a major long-term component of post-fire herbaceous vegetation throughout most of the region.

Ideally, long-term studies of succession patterns in post-disturbance communities would be done with a time series design, with individual plots sampled for many years at regular, evenly spaced intervals (Pickett 1989). Because this is usually impractical, chronosequence designs have long been used as an alternative. Although the chronosequence approach has been criticized (Johnson & Miyanishi 2008), many of the potential problems can be mitigated with adequate replication, appropriate reference conditions and a clear understanding of the limits imposed by the space-for-time framework. We were able to account for variability among plots both in the design of our sampling and the statistical models we used, and we had a large number of unburned plots to evaluate convergence of succession trajectories towards well-defined reference conditions (Walker *et al.* 2010). Nevertheless, the chronosequence design does impose some limits to the inferences we can make. It would be inappropriate to say vegetation structure *returned* (or not) to pre-burn conditions because this would require a pre-fire/post-fire time series design. Rather, the most appropriate interpretation is that the trajectories were *consistent* with that expected from a plot returning (or not) to pre-burn conditions. We also did not derive estimates of the time it might take for some conditions to be similar to reference conditions. Not only would this be extrapolating beyond the time limits of our data and likely give misleading estimates, the cross-sectional rather than longitudinal nature of the data makes it illogical to do so. This is because each plot represents a single point and not a series. We suspect that trajectories in some of the burn plots that appeared to be approaching those of unburned plots would do so within several more decades, but that is only a cautious qualitative assessment.

Conclusions

To the best of our knowledge, no prior studies have examined relationships among burn severity, fire frequency and invasive grasses over such an extensive geographic area and relatively long time period. Even though persistent herbaceous communities resulted from both the burn severity and fire frequency pathways, that did not necessarily mean invasive grasses dominated cover. Rather, dominance by invasive grass depended upon number of years since burning and elevation zone. Furthermore, there may be a temporal window when the grass/fire cycle is most likely to develop. Cover of invasive grass appeared to peak between 10 and 20 years after burning, so we suspect this is when these areas are most susceptible to burning.

In one sense, a case might be made that burn severity takes precedence over fire frequency in the Mojave Desert. This is because our findings indicate a grass/fire cycle is not required for the long-term conversion of woody-dominated communities to herbaceous-dominated ones. But in another sense high burn severity may predispose areas to more frequent fire because they have relatively high cover of invasive grass. Furthermore, invasive grass can dominate cover in areas with frequent fire even if burn severity is low or moderate. Therefore, we believe the most appropriate perspective is that burn severity and fire frequency can have either independent or synergistic effects.

Although our study occurred within the Mojave Desert, it is likely the burn severity pathway leading to long-term dominance of burned areas by invasive grasses occurs in other deserts in North America. Invasive plants have been widely implicated in the increased number and/or size of fires in the Great Basin and Sonoran Desert (Brooks & Pyke 2001; Balch *et al.* 2013; McDonald & McPherson 2013; Gray, Dickson & Zachmann 2014), and the grass/fire cycle has been the main focus as the process responsible for the formation of alternative states. Prior to this study, it might have been thought that burned areas in the North American deserts that had longer fire return intervals were less likely to become dominated by invasive grass, but this may often not be the case.

Authors' contributions

Acknowledgements

Data accessibility

Data deposited at USGS (https://doi.org/10.5066/F79022PZ).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Model selection.