Native and exotic plant species respond differently to wildfire and prescribed fire as revealed by meta-analysis

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Abstract

Questions: Wildfire is a natural disturbance that shapes vegetation characteristics worldwide, while prescribed fire is increasingly used to modify vegetation composition and structure. Due to invasion of many ecosystems by exotic species, a concern of land managers is whether wildfire and prescribed fire alter plant communities in favour of exotics. We assessed the global literature describing community-level responses of native and exotic species groups to wildfire and prescribed fire and characterized the geographic and temporal scope of the data to inform research needs.

Location: Predominantly the United States of America and Australia.

Methods: We used meta-analysis to (1) test whether native and exotic species composition (richness or diversity) and performance (cover, density and biomass) differ in response to wildfire and prescribed fire, and (2) assess how the composition and performance of these species groups vary with time elapsed since fire and habitat types.

Results: Most community-level research on how native and exotic species respond to fire has been conducted in the US and Australia, typically over short time scales, and with a focus on temperate forest and grassland ecosystems. Prescribed fire benefited native composition over short time scales (<1 yr) but, on average, had no effect on native performance, nor on exotic composition or performance. In contrast, wildfire consistently enhanced exotic composition and performance over all time scales, while having no effect on native species composition and significantly reducing native performance. Additionally, responses varied by habitat: native species groups responded positively to prescribed fire in heathlands and to a lesser extent in temperate grasslands, while responding negatively to wildfire in arid shrublands and heathlands, and to a more modest degree in tropical savannas. Exotic species groups responded positively to wildfire in arid shrublands, temperate forests and heathlands.

Conclusions: This quantitative assessment of the literature revealed strong evidence for a positive response of exotics to wildfire, coupled with a striking near-absence of negative responses. The assessment additionally suggests that while prescribed fire does benefit native composition, *on average*, it does not appear to greatly facilitate native performance; however site-specific variation in how communities responded to fire was pronounced, underscoring the importance of local assessments in determining mechanistic drivers and management policy.

Introduction

Fire is an important agent of change in plant communities due to its effect on resource availability and plant competitive interactions (Boerner 1982; Melgoza et al. 1990; Whelan 1995; Romme et al. 2011). Although fire is necessary to maintain vegetation structure and function in some ecosystems (Bond & Keeley 2005), human- and

climate-based alterations to fire frequency may alter its historical influence (Flannigan et al. 2005; Westerling et al. 2006; Lavorel et al. 2007). Fire frequency and ignitions have increased dramatically in many areas worldwide (Cochrane 2003; Westerling et al. 2006), with ongoing human-driven movement of plant species around the globe complicating this issue. Fire can promote invasion by exotic species (D'Antonio 2000) because many exotics are responsive to disturbance and benefit from the competition-free, nutrient-rich environments that often result from fire. Flammable invaders can initiate a feedback loop in which fire-promoted exotics further alter the fire regime to the detriment of native species (D'Antonio & Vitousek 1992; Brooks et al. 2004). Despite concern over the interaction between fire and exotic plant invasion, whether fire generally promotes invasion across ecosystems has not been rigorously tested, nor have potential sources of variation in native and exotic responses to fire been assessed. Given the widespread use of prescribed fire as a vegetation management tool (Pyke et al. 2010), it is crucial to understand the contexts in which fire successfully promotes natives or unintentionally promotes exotic species.

Part of the uncertainty associated with the relationship between fire and plant invasions stems from the spatial and temporal variability associated with both phenomena. For example, the frequency, intensity and extent of fires depend upon fuel quality and availability, weather conditions and topographic gradients (Whelan 1995). Whether a given fire or series of fires will promote exotic populations hinges in part on these many factors and on the phenology of the exotics at the time of the fire (Whelan 1995; Crawford et al. 2001; Keeley et al. 2008). In addition, community characteristics such as native vs exotic propagule supply, or the relative ability of native and exotic species to withstand or regenerate after fire, can determine competitive outcomes in the post-fire environment (Whelan 1995; Buhk et al. 2006; Pyke et al. 2010). Given the numerous factors shaping the interaction between fire and plant invasions, it remains uncertain whether fire generally promotes exotic species invasions across a broad range of conditions. Determining whether post-fire invasions are a widespread phenomenon or are habitat-specific can help prioritize restoration activities associated with wildfires. Further, while prescribed fires can successfully promote native species that have evolved under certain fire regimes or achieve other management goals such as reducing fuel loads (Fernandes & Botelho 2003), their effect on plant communities must be closely evaluated in invaded systems (Brooks & Pyke 2000).

In this study we perform the first quantitative synthesis of the global literature describing the effect of wildfire and prescribed fire on native and exotic species and use meta-analysis to evaluate the effect of fire on plant community responses. First, we characterize the geographic and temporal scope of the data to highlight areas that require further study and to guide our interpretation of the meta-analyses. Second, we test for general responses of native vs exotic species to wildfires and prescribed fires. Finally, we assess ecological contingencies in native and exotic species response to fire in relationship to time since fire and habitat type. While community responses to fire may be best interpreted in light of both the historic fire regime and characteristics of the fires in individual studies, a lack of information in the primary papers prohibited evaluating their roles. Instead we evaluate the differential responses of native compared to exotic species groups to individual fires without assessing features of the fire events or of historic regimes that might have influenced post-fire succession.

Methods

Literature search

We searched the ISI Web of Knowledge (WOK) database on 24 October 2012 using the following search string: TS = ((*fire OR burn*) AND (native plant* OR indigenous plant* OR endemic plant* OR plant invad* OR invasive plant* OR naturali* plant* OR establish* plant* OR alien plant* OR exotic plant* OR introduced plant* OR exotic plant* OR non-indigenous OR casual OR weed*) NOT ant* NOT "power plant") AND (SU = Agriculture OR SU = Biodiversity & Conservation OR SU = Environmental Sciences & Ecology OR SU = Evolutionary Biology OR SU = Forestry OR SU = Plant Sciences). This search returned 3377 studies. We then searched the database with the same search string, but included AND between the native and introduced descriptors, which returned 95 additional studies. We scanned the abstracts of all 3472 studies and excluded studies that did not address the effects of fire on invasion. This resulted in 698 studies that we further assessed. Studies were included in the meta-analysis if they met the following criteria:

1 The study reported the effects of either prescribed fire or wildfire on one or more plant communities or functional group parameters (including species richness, species diversity, plant cover, biomass, density or seed bank characteristics) using paired burned and unburned plots or data gathered before and after a fire event in natural or semi-natural (e.g. managed for restoration) habitats.

2 Community response to fire was presented separately for native and/or exotic species groups and included information necessary to calculate an effect size (i.e. mean, SD or SE and sample size) that could be extracted directly from text or tables, or using Datathief III software (B. Tummers 2006, http://datathief.org).

Forty-three studies from the WOK search met these criteria. We searched the cited references of all 43 studies and identified 184 additional studies, of which 11 met the above criteria. Of these 54 studies, we excluded three on seed banks due to low replication and one technical report that contained data subsequently published in other papers in our list, bringing the total to 50 studies containing 268 separate comparisons of community response to fire (see Appendix S1 for the full list of studies). Although there is a large literature on the effect of fire on vegetation, many studies could not be included because they did not separate community response metrics by native and exotic status, or they did not report a suitable estimate of variability (i.e. SD or SE).

Treatment of the data

The nature of fire events, which are unpredictable and large scale in the case of wildfires, and logistically constrained in the case of prescribed fires, can make it difficult to achieve treatment replication. To maximize the available information we chose to include all studies that met our inclusion criteria, whether replicated at the scale of treatment (52% of studies) or at the scale of plots within single burned and unburned areas (i.e. pseudo-replicated *sensu* Hurlbert 1984; 48% of studies). This is justified given that pseudo-replication is less problematic when large treatment effects are expected or when the studied phenomena occur over large spatial scales (Hurlbert 1984). Further, the cumulative effect size (i.e. the average response) generated for fully replicated studies was of the same magnitude and direction as that generated for pseudo-replicated studies (Appendix S2), indicating a lack of bias due to study design and thus justifying use of the full data set.

Most studies contained more than one comparison because they reported: (1) the responses of both native and exotic species groups, occasionally further delineated by functional group; (2) a measure of either species richness or diversity, plus a measure of percentage cover, density or biomass of the species groups; (3) fire effects in distinct communities or more than one independent fire event; or (4) responses to fire at more than one point in time, during different seasons or in relationship to fires of different severity. During the process of data extraction, we included all available response metrics for native and exotic species. These include richness and diversity, which we term *composition*, and cover, density and biomass, which we term *performance*. For studies reporting community responses from more than one location we made an informed decision, based on the authors' assessment of the biological similarity of the community types as well as the direction and magnitude of the responses to fire, about whether to average over location or treat locations

separately. Independent wildfire events reported by the same authors were considered separate data points. When data from the same location were presented as a time series, we extracted values for the first and last time points to capture the shorter- and longer-term responses of the community, respectively. For six studies that reported the effect of burning in different seasons we included all responses because the authors often hypothesized different outcomes depending on the timing of the burn. For a small subset of studies with several burn categories, we adopted the most severe category. We did this in an effort to reduce further pseudo-replication within the data set.

One of the largest sources of multiple comparisons within studies was the inclusion of both native and exotic community responses to fire; given that this is the comparison of interest, these data cannot be combined. A second main source of multiple comparisons was the inclusion of more than one time point at which vegetation was sampled following fire. To explore potential issues of pseudo-replication associated with extracting two time points from the same study (e.g. caused by a correlation in responses across time points at the same study location), we conducted a full analysis that included both the first and second time points (268 comparisons), and then a reduced analysis that included only the first time point (206 comparisons). Because the full and reduced analyses yielded qualitatively comparable results (Appendix S3), we chose to maximize the available data by using both the first and last time points when reported.

Meta-analysis

Assessment of biases in the available data

To inform our interpretation of the meta-analytic models, we formally assessed potential biases in the available data by testing for significant correlations among the categorical variables of fire type, time since fire and habitat type using chi-square tests of independence and residual analysis. Additionally, when conducting meta-analysis it is important to explore whether the extracted studies are in some way biased, as can happen when studies with significant results are preferentially published relative to those without (i.e. the file-drawer problem; Rosenthal 1979; Palmer 1999). We explored this potential publication bias by generating (1) a funnel plot of effect size vs study replication; (2) the fail-safe number, which estimates the additional number of studies required to nullify observed significant effect sizes at alpha = 0.05; (3) a normal quantile plot, in which the distribution of effect sizes is compared against the standard normal distribution; and (4) a rank correlation test of effect size vs sample size using Kendall's tau. Because of the nature of the data, in which native and exotic comparisons were the unit of analysis, sample sizes

were based on the number of comparisons in each vegetation category, rather than individual studies *per se*.

Models of the response of native and exotics species groups to wildfire and prescribed fire, the effects of time since fire and habitat type

All analyses were conducted in MetaWin v 2.0 (Sinauer Associates, Sunderland, MA, US) using resampling techniques that are robust to non-normal data and a weighting factor that accounts for among-study variation in sampling effort (Adams et al. 1997; Gurevitch & Hedges 1999; Rosenberg et al. 1999). Cumulative effect sizes (i.e. the average response across all studies after accounting for study size) of zero indicate no difference between burned and unburned sites, positive effect sizes indicate a positive response to burns, and negative effect sizes a negative response. We first assessed total heterogeneity (Qt) in the direction and magnitude of the responses of all 268 study comparisons to test whether there was structure in the data that should be explored further (see Rosenberg et al. 1999). For all subsequent analyses we grouped responses according to origin (native or exotic) in order to perform separate meta-analyses on these subsets of data. We explored the effect of wildfire vs prescribed fire separately for native and exotic composition (richness and diversity) and performance (cover, density and biomass). We then included both the composition and performance responses (to increase replication) in models to explore the effect of time since fire (<1 yr, 1–3 yrs, 3–10 yrs and >10 yrs) and habitat type associated with the study location (cf. Table 1 for a description of habitat types). It was not possible to look at responses by plant life form (grasses, forbs, woody plants) because most studies reported responses of the entire native/exotic assemblage at the site, reporting, e.g. 'native richness' or 'exotic cover'. These all-inclusive metrics predominantly captured herbaceous species and may have included early recruitment/growth of woody plant seedlings (see Appendix S4 for further explanation). Cumulative effect sizes were considered significant when their bias-corrected 95% bootstrap confidence intervals did not overlap zero based on 999 iterations. Random effects models were used in all cases, as is appropriate for ecological data (Gurevitch & Hedges 1999). We note that while it would have been ideal to build full statistical models containing all moderator variables and their interactions, this was impossible due to correlations among the variables (e.g. Barto & Rillig 2010). Thus, the meta-analytic models are not designed to function as formal hypothesis tests of multiple underlying mechanisms, but rather as quantitative assessments of *patterns* in the data.

Results and Discussion

Literature search

Community-level metrics capture the response of co-occurring species to disturbance, encapsulating the outcome of multiple community assembly processes including dispersal, establishment and competitive interactions. This makes them particularly appropriate for capturing the overall impacts of fire on invasion, yet our search revealed that such data are only beginning to come to light. The studies resulting from the extensive literature search (Appendix S1) were largely conducted in the US (40 studies) and Australia (seven studies), and all findings should be interpreted in this light. Surprisingly, there were no

Table 1. Description of habitat types assigned to study locations.

Habitat Type*	Sub-types	Examples
Desert and desert-like shrubland	Shrub steppe	Mountain big sagebrush (*Artemisia tridentata*)
	Warm desert scrub	Honey mesquite (*Prosopis glandulosa*) and blackbrush (*Coleogyne ramosissima*)
	Salt desert and inland alkali-sink scrub	*Artemisia–Atriplex* shrubland
Heathland	Mediterranean-type scrub	Coastal sage scrub, maritime chaparral, mattoral shrublands and oak savanna
	Wet and dry sclerophyll forest/woodland	*Eucalyptus* forest and *Acacia acuminata–Eucalyptus loxophleba* woodland
Temperate grassland	Prairie	Tallgrass prairie of the Great Plains; California serpentine and annual grasslands
	Desert grassland	Chihuahuan Desert grassland
	Steppe	Semi-arid grasslands (*Bouteloua* sp., *Aristida* sp.)
Temperate forest	Temperate summergreen deciduous and mixed evergreen–deciduous forest	Mixed deciduous forest (e.g. *Fagus*, *Juglans* and *Pinus*)
	Temperate and montane coniferous forest	Ponderosa pine–Douglas-fir; Pinyon–Juniper woodland
Tropical savanna[†]	Savanna grassland	Central coastal lowlands of Hawaii
	Savanna woodland and parkland	Eastern coastal lowlands of Hawaii; seasonal submontane zone of Hawaii; *Brachystegia–Julbernardia* savanna of Zimbabwe

*Adapted from the classification system of the Mildred E. Mathias Botanical Garden, University of California, Los Angeles; Additional habitat types with minimal representation include tropical forest (one study) and understorey vegetation response in a pine (*Pinus ponderosa*) plantation (one study); Study locations fall along a disturbance continuum ranging from mostly intact to degraded, and include areas being actively managed for restoration.
[†]Hawaiian tropical savannas transition from seasonally dry woodlands and shrublands to savannas as a result of burning.

suitable data describing community-level effects of fire on invasion in other fire-prone areas of the world, including much of South America, the fynbos of South Africa and mediterranean regions other than California (Cochrane 2003; Bond & Keeley 2005; Krawchuk et al. 2009). The temporal scope of the studies was skewed, with 65% of vegetation surveys occurring within 3 yrs of fire, 26% occurring from 3 to 10 yrs following fire and only 9% occurring more than 10 yrs after fire. This demonstrates a lack of long-term data needed to gauge the persistence of fire effects on composition and performance. The majority of studies were conducted in temperate grassland (34%) and temperate forest (28%) ecosystems. Other relatively common ecosystems included heathland (broadly defined; 16%), desert shrubland (12%) and to a lesser extent tropical savannas (8%; see Table 1 for a definitions of each habitat type). Of the 33 studies focused on prescribed fire, 55% had the explicit goal of restoring native species, while 15% had the goal to reduce exotic species. The remaining prescribed fire studies explored shrub encroachment into grasslands or did not state an *a priori* goal regarding management of natives or exotics.

Meta-analysis

Assessment of biases in the available data

The correlation analysis demonstrated that the available data were in some cases over- or under-represented for different combinations of fire type, time since fire and habitat type, suggesting several foci for future research. These include: (1) a need for more short-term data describing response to wildfires and more long-term data on response to prescribed fires (Table 2a); (2) more data on the response of grassland communities to wildfire and tropical savanna communities to prescribed fire (Table 2b); (3) additional data describing short-term responses to fire in desert shrubland, temperate forests and tropical savannas; and (4) more long-term data on responses in temperate grasslands and heathlands (Table 2c). The restricted scope of the studies we identified reflects the difficulty associated with studying fires over the large spatial and temporal scales needed to fully understand their impacts (van Mantgem & Schwilk 2009). It also reflects a concentration of research in regions where fires have had highly visible economic and social impacts, where fire science has a long history, and where increasing fire activity has coincided with encroachment of housing into wildland vegetation (e.g. western and southwestern US where 62% of the studies were conducted; Schoennagel et al. 2009).

We did not find any evidence for publication bias based on the four methods of data exploration detailed in the Methods section (results presented in Appendix S5).

Table 2. a, b, c. Results of correlation analysis conducted to determine relationships between the three moderator variables (fire type, time since fire and habitat type) used in the meta-analytic models. Significant correlations were tested using a chi-square test of independence. The degree to which the observed number of comparisons in each cell departs from the expected number based on the available data is represented by the adjusted residuals (in parentheses; numbers are SD). Positive residuals reflect a surplus of observations, and negative residuals a deficit. Residuals >2 or ≤2 (shaded background) are significant at alpha = 0.05.

a*	Number of Comparisons		
Time Since Fire	Prescribed Fire	Wildfire	Total[†]
<1 yr	71 (3.1)	22 (−3.1)	93
1–3 yrs	50 (−0.29)	30 (0.29)	80
3–10 yrs	31 (−3.8)	38 (3.8)	69
>10 yrs	19 (1.0)	7 (−1.0)	26
Total[†]	171	97	268

b**	Number of Comparisons		
Habitat Type	Prescribed Fire	Wildfire	Total[†]
Desert Shrubland	13 (−1.5)	11 (1.5)	24
Heathland	22 (−1.8)	18 (1.8)	40
Temperate Forest	54 (0.97)	21 (−0.97)	75
Temperate Grassland	85 (5.7)	10 (−5.7)	95
Savanna	3 (−6.8)	25 (6.8)	28
Total[†]	177	85	262

c***	Number of Comparisons				
Habitat Type	<1 yr	1–3 yrs	3–10 yrs	>10 yrs	Total[†]
Desert Shrubland	3 (−2.2)	3 (−1.7)	6 (0.41)	9 (5.8)	21
Heathland	24 (3.2)	9 (−1.3)	8 (−0.85)	0 (−2.2)	33
Temperate Forest	14 (−3.9)	33 (2.8)	25 (1.9)	5 (−0.88)	77
Temperate Grassland	53 (5.1)	30 (0.28)	8 (−4.6)	4 (−1.9)	95
Savanna	0 (−4.1)	5 (−1.5)	18 (5.1)	5 (1.8)	28
Total[†]	94	80	65	23	262

*X^2 = 19.3; P = 0.0001.
**X^2 = 148; P < 0.0001.
***X^2 = 92.5; P < 0.0001.
[†]Comparison totals that do not sum to 268 are due to habitat types with minimal representation (tropical forest and plantation; Table 1) that were not included in the correlation analysis.

Overall response of native and exotic species groups to prescribed fire and wildfire

Averaging across all study comparisons there was significant total heterogeneity in effect sizes (Qt = 622.7, df = 267, P < 0.0001), indicating structure in the data that warranted further exploration. The categorical comparison of prescribed fire and wildfire revealed significant differences in how these fires affect native and exotic species

(Table 3, Comparison A). A positive response of native species was mostly seen in management situations, yet while the composition of natives can be enhanced by prescribed fire (Fig. 1a), this does not necessarily translate into increased performance (Fig. 1b). Given that 70% of the prescribed fire studies had the goal of promoting native species (either by favouring natives or by controlling exotics), these results indicate, on average, only moderate success, at least during the time scales available for study. There are several reasons why this pattern in performance may emerge. First, the short-term nature of many sampling efforts following prescribed fire, with 42% of surveys happening within 1 yr (Table 2a), simply may not be sufficient elapsed time to capture increases in performance. Second, many of the studies were experimental in nature, with the goal of identifying best practices or of exploring fire effects under different scenarios. Third, in some cases the native species propagule pool, including the seed bank, may be too depleted to support successful colonization even when post-fire conditions are favourable (e.g. Bock & Bock 1992). Last, it may reflect the difficulty of conducting prescribed fires at times that mimic the natural seasonality of fire (Knapp et al. 2006). We found that while most prescribed fires (71% of comparisons) were conducted in either autumn or spring, a majority of wildfires (64% of comparisons) burned in the summer. Different ecosystems have historical burning seasons that occur when vegetation is either dormant, growing or on the cusp between these phenological stages (Knapp et al. 2009; Howe 2011). Departures in the timing of prescribed fire from the historic norm could alter fire characteristics such that native plants cannot optimally respond. Despite potential challenges of enhancing native species performance with prescribed fires, such fires do not appear to consistently promote exotic species (Fig. 1c).

While wildfires did not significantly affect native composition (Fig. 1a), they had a clear negative effect on native performance (Fig. 1b). In contrast, wildfires favoured exotics in terms of both composition and performance (Fig. 1 c, d). Because wildfires are typically larger, more variable and potentially more intense than prescribed fires (Graham et al. 2004), they may more readily promote invasion. For example, the size of a burned area determines its degree of contact with propagules dispersing from outside of the burn perimeter. When exotics are sparsely distributed on the landscape (i.e. propagule pressure is low), the large burned areas that often result from wildfires have more chance of coming into contact with sources of exotic propagules (Keeley 2006). In addition to the many extrinsic environmental factors that shape community response to fire, intrinsic trait-mediated differences in how species respond to disturbance are likely to be important. For example, exotic species often invest highly in reproduction and growth, which can help them rapidly colonize open, resource-rich spaces (Harrod & Reichard 2000; van Kleunen et al. 2010). Further, exotic species can exhibit higher phenotypic plasticity in response to environmental fluctuations than natives, with herbaceous exotics responding particularly strongly to increased light availability (Davidson et al. 2011), as often occurs following

Table 3. Summary of statistics estimating the between-group (Q_b) vs within-group (Q_w) heterogeneity of several random effects categorical models (designated as 'Comparison A' through 'Comparison C' in the Results) testing the effect of fire on native and exotic species. Significant Q_b indicates significant differences between groups, and significant Q_w indicates residual heterogeneity within groups after accounting for between-group heterogeneity. Degrees of freedom (in parentheses following test statistics) for Q_w represent the number of effect size comparisons minus 1.

	Native Response				Exotic Response			
	Q_b	P	Q_w	P	Q_b	P	Q_w	P
Comparison A								
Prescribed Fire vs Wildfire								
Composition	3.9 (1)	0.05	91.0 (43)	<0.0001	12.0 (1)	0.0005	74.1 (42)	0.002
Performance	15.8 (1)	<0.0001	178.6 (88)	<0.0001	13.0 (1)	0.0003	185.8 (87)	<0.0001
Comparison B*								
Time Points[†]								
Prescribed	2.0 (3)	0.58	163.2 (91)	<0.0001	3.9 (3)	0.28	148.0 (80)	<0.0001
Wildfire[#]	—	—	—	—	1.52 (3)	0.68	98.2 (45)	<0.0001
Comparison C*								
Habitat Type[$]								
Prescribed	12.4 (3)	0.006	158.7 (89)	<0.0001	5.7 (3)	0.12	143.7 (77)	<0.0001
Wildfire	16.4 (4)	0.002	60.2 (33)	0.003	43.8 (4)	<0.0001	82.6 (42)	0.0002

*Comparisons B and C include both composition and performance as the response metrics.
[†]Time points are <1 yr, 1–3 yrs, 3–10 yrs and >10 yrs following fire.
[#]Replication within time points was too low to assess temporal variation in native response to wildfire.
[$]Habitat types include desert shrubland, heathland, temperate grassland, temperate forest and tropical savanna; see Table 1.
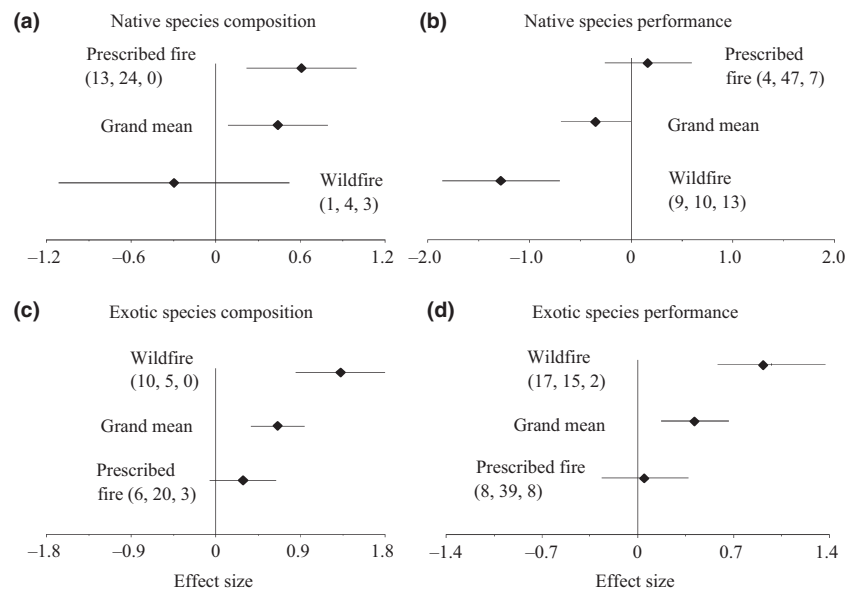
Fig. 1. Cumulative effect sizes showing the response of native and exotic species composition and performance to prescribed fire and wildfire. Composition includes measures of species richness and diversity. Performance includes measures of species cover, density and biomass. Grand mean is the effect size averaging over prescribed fire and wildfire. Cumulative effect sizes are significant when their bias-corrected 95% bootstrap confidence intervals do not overlap zero based on 999 iterations. Parentheses contain the number of individual effect sizes that were significantly greater than zero, no different from zero, or significantly less than zero, respectively.

fire. Regardless of the various mechanisms that underlie the positive response of exotics to wildfire, it is striking that they showed a negative response in only 4% of the cases (Fig. 1c, d).

Response of native and exotic species as a function of time since fire

Exploring the effect of time since fire (Table 3, Comparison B) revealed that, on average, native composition and performance (included in a single model) exhibit a positive short-term response (<1 yr) to prescribed fire, but that this response does not remain significant over time (Fig. 2a). The comparisons driving this significant short-term response came from several habitats where fire-induced removal of litter and clearing of the canopy allowed herbaceous plants to either recruit from seed (Morgan 2001; Grant 2003; Tix & Charvat 2005) or exhibit a flush of renewed vegetative growth (Ayala-A et al. 2012) shortly after fire. Such a rapid response suggests that propagule recruitment was from within the burned area rather than from outside dispersal, underscoring the importance of maintaining intact native seed banks. While exotic species composition and performance did not exhibit patterns associated with time since prescribed fire, they had a significantly positive response to wildfire over all time intervals spanning from <1 yr to >10 yrs (Fig. 2b). This suggests that exotic species successfully colonize the post-fire environment and subsequently persist despite successional

changes in the community that alter competitive dynamics. For example, several authors reported that species with ruderal characteristics (e.g. *Bromus tectorum, Erodium cicutarium, Taraxacum officinale* and several thistles) contributed to longer-term increases in exotics following fire (Tunison et al. 1994; Brooks & Matchett 2003; Huisinga et al. 2005; Floyd et al. 2006; Haubensak et al. 2009). Successful rapid reproduction in the initial post-fire years may allow a build-up of exotic seed in the soil, thereby increasing propagule pressure and local recruitment, potentially leading to persistent populations even in the absence of future major disturbance (Gioria et al. 2012).

Response of native and exotic species by habitat: Prescribed fire

Separation of studies by habitat (Table 3, Comparison C) revealed that prescribed fire significantly benefits native species in heathlands (Fig. 3a). In contrast, prescribed fire did not have an effect in temperate forests or desert shrubland habitats (Fig. 3a). Indeed, natives exhibited mostly neutral responses in both temperate grasslands (despite the trend toward a positive response) and forests, the two habitat types with the largest number of effect sizes (Fig. 3a). The positive effect size in heathlands reflects the response of herbaceous understorey species in a reclaimed Australian *Eucalypt* woodland (Grant 2003) and native perennial forbs and grasses in a highly invaded oak savanna ecosystem in Canada (see Table 1; MacDougall &
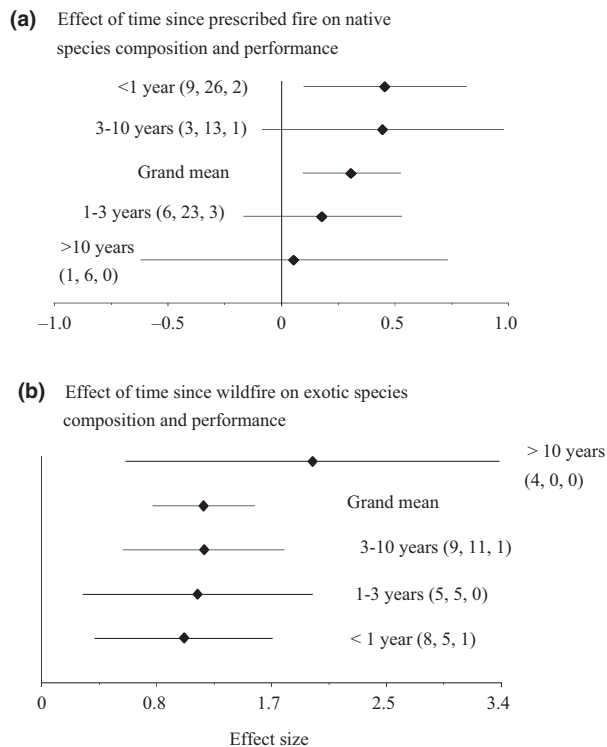
(a) Effect of time since prescribed fire on native
species composition and performance

(b) Effect of time since wildfire on exotic species
composition and performance

Fig. 2. Cumulative effect sizes describing the effect of time since fire (<1 yr, 1–3 yrs, 3–10 yrs, >10 yrs) on (**a**) native species composition (i.e. richness and diversity) and native performance (i.e. cover, density and biomass) in response to prescribed fire, and (**b**) exotic species composition and performance in response to wildfire. Composition and performance responses were both included in the model to increase replication within time points. However, there was not enough replication within time points to explore native response to wildfire over time. Because there were no significant patterns associated with exotic response to time since prescribed fire, we do not include it here. Grand mean is the effect size averaging over all time intervals. See Fig. 1 for details.

Turkington 2006). However, in both heathland systems the positive response by natives was associated with a concurrent positive response by exotic annuals (Fig. 3b) of the Asteraceae and Poaceae families that possess wind-dispersed seeds or had persistent soil seed banks.

While the response of natives to prescribed fire in grasslands was not statistically significant (Fig. 3a), there were several positive responses associated with tallgrass prairie sites dominated by native, fire-responsive C_4 grasses (Tix & Charvat 2005; Franson & Scholes 2011; Howe 2011; Hall et al. 2012). This suggests consistent success using prescribed fire in this historically fire-maintained plant community (Howe 2011), although both neutral and positive outcomes were often observed at the same study locations. Differences in the positive vs neutral responses were attributable to the timing of the post-fire survey (i.e. shortly post-fire or after some time had elapsed; Franson &

Scholes 2011), the functional group captured by the measurement (native graminoids vs native forbs or woody species; Hall et al. 2012) or the season of prescribed fire (summer or spring; Howe 2011).

Finally, despite an average neutral effect of prescribed fire on exotic species in grasslands (Fig. 3b), there were several positive and negative individual effects. Exotics responded positively in remnant perennial grassland of western Victoria, Australia (Morgan 2001); in two California grasslands (Pollak & Kan 1998; Gillespie & Allen 2004); and in a native *Festuca* prairie of Washington State (Rook et al. 2011). Strongly responding exotics included annual grasses/rushes in the Australian grassland, short-lived forbs in the two California grasslands and perennial forbs in the Washington prairie. The negative response of exotics in grasslands was largely due to short-lived Eurasian grasses, including species of *Avena, Bromus, Lolium* and *Vulpia,* in three separate California grasslands (Pollak & Kan 1998; Klinger & Messer 2001; Gillespie & Allen 2004). This negative response contrasts with the positive response of short-lived exotic forbs in these same grasslands and highlights the challenge of optimizing burn prescriptions when co-occurring species have disparate life-history characteristics (Pyke et al. 2010).

Response of native and exotic species by habitat: Wildfire

The most pronounced response to wildfire occurred in desert shrubland habitats, where natives had a strong negative response and exotics a strong positive response (Fig. 3c, d). These studies occurred in arid shrublands of the western US that have been invaded by *Bromus tectorum* and other Eurasian weeds (Brooks & Matchett 2003; Haubensak et al. 2009). Because native shrubs are slow to regenerate following fire, they are likely to be displaced by faster-growing herbaceous species. This can progress into a positive feedback loop if species like *B. tectorum*, which have different fuel characteristics than native shrubs, become dominant and eventually shorten fire return intervals such that the native shrubs cannot recover between successive fires (Mack 1989; Whisenant 1990; Brooks et al. 2004; Balch et al. 2013).

Natives also responded negatively to wildfire in heathlands, including the Argentine matoral (Nuñez & Raffaele 2007) and serpentine and sandstone chaparral in California (Safford & Harrison 2004), again in contrast to the positive response of exotics (Fig. 3c, d). As with desert shrubland habitats, the negative response of natives in heathlands reflects the slow canopy regeneration of woody species vs the rapid regeneration and/or recruitment of herbaceous exotics following disturbance. Under non-invaded conditions, such reductions in shrub cover allow for native species turnover and regeneration. Indeed, there were
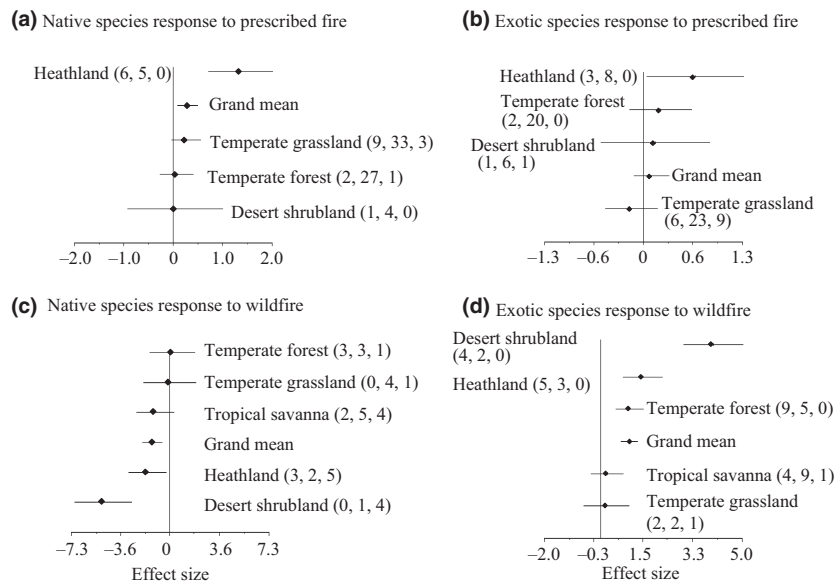
(a) Native species response to prescribed fire

(b) Exotic species response to prescribed fire

(c) Native species response to wildfire

(d) Exotic species response to wildfire

Fig. 3. Cumulative effect sizes describing the effect of habitat type on the response of native and exotic species composition and performance to prescribed fire (panels **a**, **b**) and wildfire (panels **c**, **d**). Composition and performance responses were both included in the model to increase replication within habitat types. Grand mean is the effect size averaging over all habitat types. See Fig. 1 for details.

significant increases in native shrub seedling density following fire in the California chaparral (Safford & Harrison 2004). However, when exotic propagules are present, they can rapidly take advantage of this regeneration niche, which was historically exploited by natives alone.

There was also an almost significant negative trend in how natives respond to wildfire in tropical savannas (Fig. 3c). These studies occurred in several ecotones of seasonally dry woodlands and shrublands in Hawaii, where exotic C_4 grasses cause increasingly frequent wildfires and ultimately a transition to savanna habitat (Hughes et al. 1991; Tunison et al. 1994; D'Antonio et al. 2000). Fire effects differed among ecotones as a function of climate and the identity of the co-occurring native and exotic species. Specifically, wildfire had a strong negative effect on native performance in the seasonal submontane zone, where several native shrubs were fire-intolerant and where fire-stimulated native grasses were absent. However, fire had a more variable effect on native performance in the coastal lowlands, where shrubs exhibited more tolerance to fire and where a widespread native C_4 grass increased following fire (D'Antonio et al. 2000).

Finally, one of the most consistent results of the analysis is that exotic species respond positively to wildfire in temperate forests, represented largely by semi-arid coniferous forests of the western US (Evangelista et al. 2004; Huisinga et al. 2005; Floyd et al. 2006; Freeman et al. 2007; Dodge et al. 2008). These studies typically singled out herbaceous, ruderal exotics such as *Bromus tectorum*, *Cirsium arvense, Carduus nutans, Erodium cicutarium, Taraxa-*

cum officinale and *Verbascum thapsus* as contributing to post-fire invasion. In this region, fire suppression, past logging, drought and increasing temperatures (Veblen et al. 2000; Westerling et al. 2006) have led to the replacement of relatively frequent, low-severity surface fires by high-severity, stand-replacing crown fires (Savage & Mast 2005). The resulting open soils act as fertile ground for exotic species to invade (Crawford et al. 2001), and high-severity fires are powerful predictors of such colonization (Crawford et al. 2001; Hunter et al. 2006). Given the widespread use of fire to manage forest fuel loads in these systems (Stephens & Ruth 2005), the benefits of fuel management should be considered within the context of native and exotic community responses to fire.

Unmeasured sources of variation and future aims

This quantitative assessment of the literature has revealed strong evidence for a positive response of exotic species to wildfire, coupled with a striking near-absence of negative responses. The assessment additionally suggests that, *on average*, prescribed fire does not greatly facilitate the performance of native species. However, we caution against over-generalizing in terms of the moderating variables of time since fire and habitat type, given the relatively few individual effect sizes available in some cases. Additionally, there was clearly unmeasured, site-specific variation in effect sizes associated with each meta-analytic model (see Q_W statistics in Table 3 and Appendix S6, S7 and S8 for the individual effect sizes used to generate the average effects

sizes presented in Figs 1, 2 and 3, respectively). The importance of these site-specific factors indicates that local assessments of mechanistic drivers and fire management policy are most appropriate. There are several factors that determine how a given community will respond to fire including: (1) abiotic factors, especially precipitation and temperature regimes, which shape vegetation characteristics before the fire event and mediate recruitment and competitive dynamics after the fire event; (2) the degree to which a site has already been invaded or has the potential to become invaded through connectivity with source pools (e.g. roads, housing developments, etc.); (3) whether the pattern, frequency and intensity of the current fire regime has departed from the conditions under which natives evolved; and (4) whether fire interacts with other disturbances such as grazing and landscape fragmentation to favour invasion by exotics (Hester & Hobbs 1992). Because all of these factors interact and vary in time and space, management plans should include a dedicated monitoring component to evaluate specific indicators of success and to support a dynamic response to changing conditions.

Finally, despite site-specific sources of variation, these findings support that native and exotic species fundamentally differ in their response to wildfire. In order to link this pattern of differential response to the processes underlying it, future research should: (1) adopt community-level metrics that best capture the impact of fire on suites of co-occurring native and exotic species; (2) better incorporate temporal dynamics by measuring community response from immediately post-fire to several years post-fire at the same site; (3) include a wider range of habitat types that target under-represented yet highly fire-prone regions, especially in areas susceptible to exotic plant invasion; and (4) simultaneously measure community response, physiological traits of dominant fire-sensitive species, environmental factors attending fire events and characteristics of the fire itself.

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Supporting Information

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

Appendix S1. List of papers from which data for the meta-analysis were extracted.

Appendix S2. Comparison of effect sizes generated from studies exploring the response of native and exotic species to fire with replication at the scale of treatments or plots (i.e. pseudo-replicated).

Appendix S3. Model outcomes for meta-analyses conducted with all available study comparisons, including multiple survey time points within studies ($n = 268$) and outcomes for a reduced set of models that included only a single time point per study ($n = 206$).

Appendix S4. Composition and performance responses broken down by how they were presented in the original manuscripts (i.e. response to fire by the entire assemblage of natives/exotics at the site, or by forbs, grasses or woody plants).

Appendix S5. Results of four methods of data exploration that indicate a lack of publication bias.

Appendix S6. Individual effect sizes used to calculate the average effect sizes in Fig. 1.

Appendix S7. Individual effect sizes used to calculate the average effect sizes in Fig. 2.

Appendix S8. Individual effect sizes used to calculate the average effect sizes in Fig. 3.