

## LETTER

## Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change

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**Abstract**

Fire regimes in savannas and forests are changing over much of the world. Anticipating the impact of these changes requires understanding how plants are adapted to fire. In this study, we test whether fire imposes a broad selective force on a key fire-tolerance trait, bark thickness, across 572 tree species distributed worldwide. We show that investment in thick bark is a pervasive adaptation in frequently burned areas across savannas and forests in both temperate and tropical regions where surface fires occur. Geographic variability in bark thickness is largely explained by annual burned area and precipitation seasonality. Combining environmental and species distribution data allowed us to assess vulnerability to future climate and fire conditions: tropical rainforests are especially vulnerable, whereas seasonal forests and savannas are more robust. The strong link between fire and bark thickness provides an avenue for assessing the vulnerability of tree communities to fire and demands inclusion in global models.

**Keywords**

Bark thickness, fire ecology, forest, functional traits, global change, savanna.

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**INTRODUCTION**

How plant communities respond to perturbations imposed by novel fire regimes is an important uncertainty in predicting the reaction of ecosystems to future global change (Cochrane *et al.* 1999; Westerling *et al.* 2006). Increased burning in ecosystems that rarely experienced fire historically, such as moist tropical forests (Nepstad *et al.* 1999), can result in rapid ecosystem degradation due to the lack of woody plant species with fire-tolerance traits (Uhl & Kauffman 1990; Cochrane *et al.* 1999). The loss of woody plant biomass during fires produces substantial carbon emissions (van der Werf *et al.* 2010) and may act to accelerate climate change, which is critical given projections of increasing fire occurrence in future climates (Moritz *et al.* 2012). Consequently, predicting the future of the terrestrial carbon sink depends on the ability of ecosystem models to accurately capture the fire tolerance of woody plants to future fire regimes (Huntingford *et al.* 2008).

Fire can be a strong selective force, and many tree species have evolved traits to better tolerate frequent burning and intense fires (Simon *et al.* 2009; Rosell *et al.* 2014). Variability in plant traits related to fire tolerance can determine the response of ecosystems to fire (Rogers *et al.* 2015), thus requiring a need to understand both the current distribution of traits and the mechanisms that generate their variability. The evolution of fire-tolerance traits within numerous and widely distributed plant species and clades may allow communities

containing those taxa to be more robust to increasing fire frequency (Pellegrini *et al.* 2016). Alternatively, if the global distribution of taxa that have evolved fire-tolerance traits is limited to specific biomes or plant lineages, then some communities may be especially vulnerable. Consequently, understanding the mechanisms leading to the evolution of fire-tolerance traits will give insight into potential constraints on the capacity of ecosystems to respond to changes in fire regimes.

The distribution of fire-tolerance traits in a community is important for determining vulnerability of an ecosystem to increased burning. On short timescales (i.e. years to decades), the potential for loss of woody plant biomass and carbon storage is determined largely by the vulnerability of individuals present in a community (Uhl & Kauffman 1990). Variability in the distribution of fire-tolerance traits within a plant community is important, however, as the distribution determines the potential for fire-tolerant species to replace fire-sensitive ones (i.e. ecological filtering; Cavender-Bares & Reich 2012). Moreover, trait–environment relationships can reveal how environmental conditions may filter species according to their traits, providing insight into the vulnerability of communities to change (Diaz *et al.* 1998). Consequently, we can estimate the ability of plant communities to tolerate increased burning by combining knowledge on the present-day distribution of fire-tolerance traits with projections of future fire regimes presents a means to estimate the ability of plant communities to tolerate increased burning.

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Here, we examine global patterns of a key woody plant trait, bark thickness, which confers fire tolerance for trees in ecosystems with surface fire regimes, such as xeric pine and oak forests (Harmon 1984), rainforests (Brando *et al.* 2012) and savannas (Hoffmann *et al.* 2009; Lawes *et al.* 2011). Bark is important because it helps protect the stem from overheating during a surface fire, conferring resistance to losses of aboveground biomass through either plant death or topkill. Although other traits can also influence whether fire actually kills a tree, such as resprouting capacity (Clarke *et al.* 2010; Pausas *et al.* 2016), bark thickness has been shown in numerous studies across multiple ecosystems to be a critical trait for the vulnerability of plant bole biomass – the largest carbon storage pool in trees – to fire (explaining the majority of the variability in biomass losses with  $r^2 \geq 0.80$ ; Harmon 1984; Van Nieuwstadt & Sheil 2005; Hoffmann *et al.* 2009; Brando *et al.* 2012; Pellegrini *et al.* 2016). Crown fire regimes are also important for a number of ecosystems, where plants contain a suite of adaptations either to resist crown char (by growing tall and dropping branches) or recruit quickly after a stand-replacing fire (through adaptations like serotinous cones; Rogers *et al.* 2015). However, here we focus on bark thickness and ecosystems with surface fire regimes. Although absolute bark thickness generally increases with stem size, plant species differ in their relative investment in bark. Consequently, we quantify bark investment as the thickness of bark at a standardised stem diameter (i.e. relative bark thickness).

We examine patterns of bark thickness to better understand ecosystem vulnerability to fire by addressing three questions: (i) how does bark thickness differ across species in different biomes and regions, (ii) to what degree do differences in fire frequency and fire–climate interactions filter species' relative bark thickness and (iii) based on current bark thickness distributions and projected changes in climate and fire, how does the vulnerability to future fire regimes differ across savannas and forests worldwide?

## METHODS

### Dataset compilation

We compiled a dataset of bark thickness investment across 572 abundant woody plant species distributed across biomes worldwide from published and unpublished sources (Table S1). To account for the influence of stem size and allometric equations reported (which varied from linear to saturating), we calculated bark thickness at three stem diameters – 10, 20 and 30 cm – which spanned the critical range of stem size over which trees are most vulnerable to topkill and comprise a large proportion of tree biomass in savannas and forests (Uhl & Kauffman 1990). We also verified that our results were robust to alternative calculations of bark thickness (*Supplementary Information, SI*).

### Comparison among biomes and continents

We classified species as being associated with savanna vs. forest biomes because these biomes have different fire regimes and woody plant species tend to specialise in either savanna

or forest biomes, but not both (Hoffmann *et al.* 2012). Savannas are defined as ecosystems with intermediate tree cover (20–80%) and a continuous grassy layer, while forests have complete woody cover and grasses are minimal to absent (Staver *et al.* 2011). Species were grouped as specialising on savanna or forest biomes based on how they were categorised by the authors of each paper. In all cases where we compare bark thickness between savanna and forest biomes, we are referring to the comparison of species classified as specialising on either biome.

It is more difficult to classify species and make generalisations of fire regime differences between biomes in temperate forests and savannas (here we focused on North America in particular) given that (i) species can occur in multiple habitats (e.g. savannas, woodlands, forests) and (ii) forests can also experience a range of fire frequencies. Consequently, we complement our analysis with a detailed dataset specific to North America (*SI*) that classifies species into multiple habitat types based on a synthesis of existing distribution data. This allowed us to further test (i) whether species associated with more open vegetation (savannas and woodlands) experience fires more frequently than those with closed vegetation (mixed woodlands and forests) and (ii) how species' bark investment varied across these habitats.

To evaluate the potential for crown fire regimes to influence our results, we took advantage of the tendency for many North American forests, especially those dominated by gymnosperms, to experience crown fires. Consequently, we investigate the potential role of exposure to crown fire in modifying the relationship between bark and fire by testing how angiosperms vs. gymnosperms differ in their bark investment and bark–fire relationships (*SI*).

Comparisons between species grouped into different biomes (and other habitat classifications in North America) were performed using ANOVAS, with the potential covariate interactions among biome, continent and region (i.e. tropical vs. temperate locations) evaluated using ANCOVAS.

### Establishing environmental conditions for each species

We determined the spatial distribution of species using field georeferenced locations from the global biodiversity information facility (GBIF) to obtain global occurrence data (Fig. S1). These distribution data were combined with burned area and climate data to obtain the average environmental conditions over the distribution of each species. In all cases, the mapped area distributions cover the complete ranges of all the included species. For fire, we analysed two burned area datasets spanning 10 and 19 years, which are currently the longest temporal records of global fire patterns available. This assumes that relatively recent spatial patterns of fire frequency have structured patterns in bark thickness. The first fire dataset is the annual burned area product from the global fire emissions database 3 with small fires (spanning 2001–2010, hereafter referred to as GFED3s), which aims to account for detection of fires in closed-canopy forests (Randerson *et al.* 2012; Giglio *et al.* 2013). The second is the annual burned area product from GFED4, which spans 1997–2015, but does not yet have the correction for small fires. We focus our

analyses on the shorter time-series GFED3s because the systematically lower measured frequency of fires in forests in GFED4 (*SI*) likely misses the key role of small fires in forest areas. Nonetheless, our results are qualitatively consistent when using the longer GFED4 record (*SI*).

Here, we were concerned with the climate factors that have the potential to influence fire behaviour. Consequently, we focused on precipitation during the driest and wettest quarters of the year in the WorldClim database (Hijmans *et al.* 2005). Higher precipitation in the driest quarter can increase fuel moisture and thus reduce burned area and intensity. On the other hand, higher precipitation in the wettest quarter can increase fire intensity in biomes with grasses (which grow but then dry out, becoming highly flammable in the dry season; Govender *et al.* 2006).

To determine the relative impact of fire, climate and the interaction between climate and biome on relative bark thickness, we performed model selection on generalised additive models using the lowest Akaike information criterion (AIC), with a threshold of 2. Model selection was used to assess variable importance as well as the potential for nonlinear relationships. We focus on the results for 10-cm stems, but results from other stem diameters are presented in the *SI*, all of which yielded qualitatively similar results. Bark thickness and annual burned area were log-transformed prior to analysis to reduce heteroscedasticity.

#### Comparison across taxonomic groups

We used linear mixed-effects models to compare the bark thickness of savanna and forest species nested within their corresponding genera and families, using either family or genus as random effects. Consequently, this analysis is only performed on the species where both savanna and forest species are present in the same genus or family. We also performed a regression between the mean bark thickness of savanna species and forest species grouped within each genus and family. This was used to determine whether the bark thickness of savanna species was correlated with the bark thickness in forest species.

#### Vulnerability to future changes

To estimate the vulnerability of plant communities to future changes in climate and fire, we aggregated individuals into  $1^\circ \times 1^\circ$  grid cells across the globe using the GBIF distribution data to calculate mean bark thickness values for each grid cell (incorporating the abundance of individuals within a species and the bark thickness for that species). We performed this aggregation process separately for savanna and forest species because of the potential Biome  $\times$  Climate interaction. We refer to these spatially aggregated values as 'community' bark thickness. Climate and burned area data were also calculated for each grid cell. We fit a generalised additive model between bark thickness and environmental data across all grid cells for both savanna and forest communities (statistical fits and a verification that our results are robust to spatial autocorrelation are in the *SI*).

We then used the regressions between climate, fire and community bark thickness to project the future expected

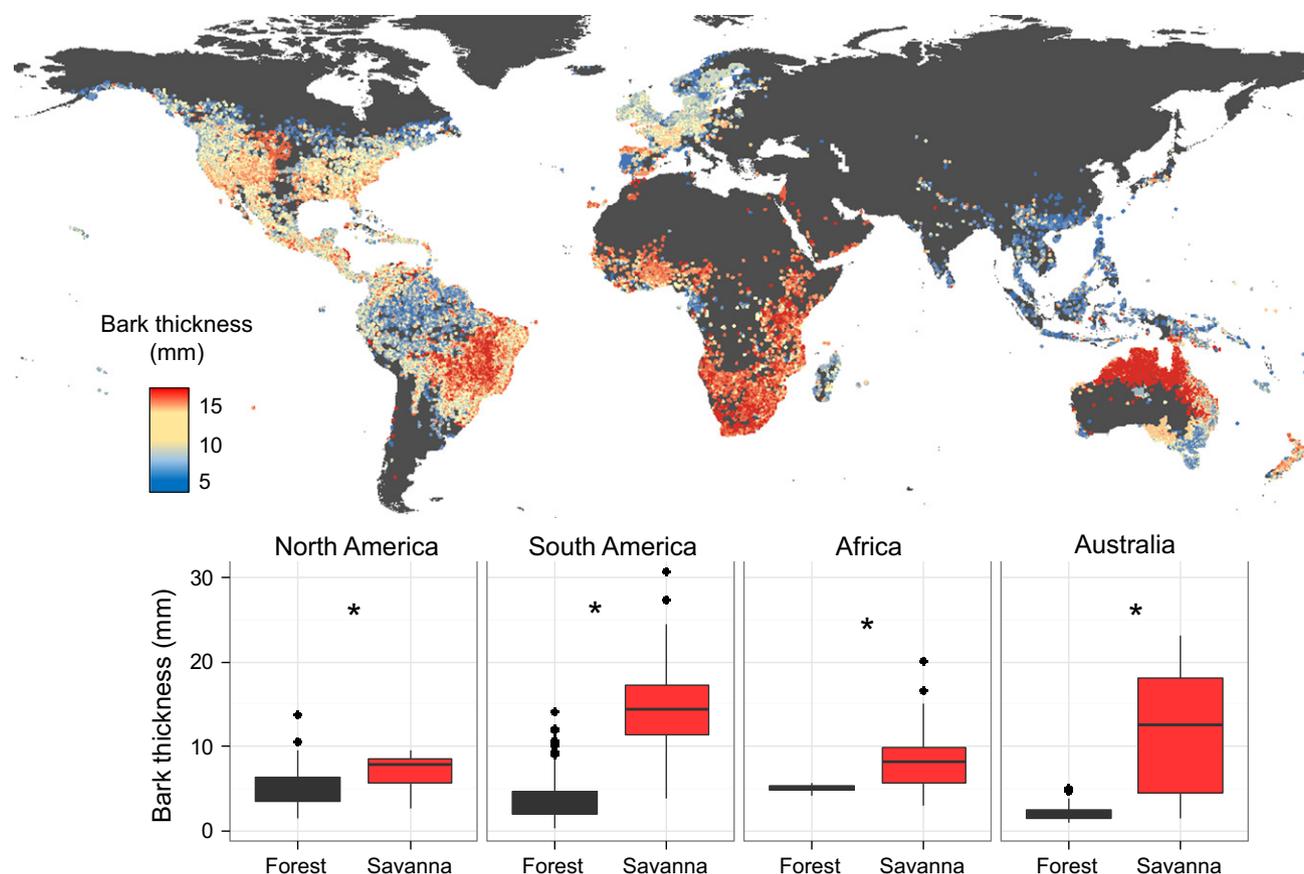
distribution of bark thickness according to future fire and climate conditions. Future climate conditions were determined from five climatic models obtained via CMIP5 outputs for 2070 RCP8.5 scenario (*SI*). Future fire conditions come from a recent output of annual burned area from LPJ-GUESS-SIMFIRE (Knorr *et al.* 2016b), which incorporates future climates, human populations and fuel loads (*SI*), for 2071–2100 RCP8.5 scenario. We chose the high emissions scenario to quantify an upper bound on potential changes in fire regimes. We averaged forecasted values across all models within each grid cell. To evaluate climate uncertainty, we used the standard deviation among climate model precipitation projections to calculate 'wet' and 'dry' (+1 vs. -1 standard deviation in precipitation, respectively) future scenarios. Potential uncertainty in the fire projection is presented in the Discussion section.

The robustness of communities to change was then quantified by comparing the current distribution of bark thickness within grid cells with the expected future distribution. Specifically, we used the log-transformed community means and variances to generate a normal distribution of bark thicknesses for each grid cell. Next, we used the projected community mean bark thicknesses to generate a normal distribution curve of future bark thickness for each grid cell, assuming that present-day variances remained unchanged. The ability of a particular community to achieve the future expected bark thickness was quantified as the area under the two probability densities (Fig. S2), which is known as the overlapping coefficient (OVL; Inman & Bradley 1989). Here, we interpret the OVL to be a measure of robustness because it estimates the fraction of individuals with bark thicknesses compatible with future conditions. Consequently, the OVL estimates the potential for an ecosystem to adjust to more extreme conditions through shifts in the abundance of individuals from its current species pool. Importantly, this metric estimates only the relative robustness of grid cells, and it does not predict the percent of individual trees that will be lost.

#### RESULTS

At the biome scale, bark was three-fold thicker in tree species specialised in fire-frequent savannas vs. fire-infrequent forests (Fig. 1, Tables 1 and S2). This pattern was observed across Africa, Australia and the Americas, each of which contain extensive savanna-forest boundaries (Fig. 1, Tables 1 and S3), and was robust to variation in stem size and alternative calculations of relative bark thickness (Fig. S3, Table S3). We confirmed that savanna species differed broadly from forest species in their characteristic fire regimes using remotely sensed estimates of annual burned area from both the longer time series ( $F_{1,569} = 154.8$ ,  $P < 0.0001$ ) and the shorter time series that corrects for small fires ( $F_{1,570} = 187$ ,  $P < 0.0001$ ).

Within the broad global pattern, differences in bark thickness between savanna vs. forest species differed in magnitude across regions and continents (Figs 2, S4 and S5, Tables S2–S4). In the tropics, savanna species had 3.3-fold thicker bark than forest species, while in temperate regions, this difference was only 1.4-fold (Table S2), consistent with the greater



**Figure 1** Broad evidence for high bark investment in savanna environments. Comparison of bark thickness, normalised to a 10-cm stem size, in plant species across the globe. Map was generated using an inverse distance weighted approach to create spatial averages of trait values from global biodiversity information facility occurrence data within distances of  $0.5^\circ$  around each observation point. Dark grey areas indicate locations that do not contain species distribution/bark thickness data. Colour ramp is pivoted on the median of bark thickness to illustrate relative variability across the globe. The box-plot comparisons between savanna and forest species are across four continents that contain extensive savanna-forest ecotones. Statistics and sample sizes are in Table S2; \* indicates  $P < 0.05$ .

Variables included	Dev (%)	AIC
<b>Mean_fire + Precip_Wetq × Biome + Precip_Dryq × Biome</b>	<b>50.20</b>	930
<b>Mean_fire + Precip_Wetq × Biome + Precip_Dryq</b>	<b>49.90</b>	930
Mean_fire + Precip_Wetq + Precip_Dryq × Biome	47.40	961
Mean_fire + Precip_Wetq + Precip_Dryq + Biome	46.50	965
Precip_Wetq + Precip_Dryq + Biome	46.30	966
Mean_fire + Precip_Dryq + Biome	44.80	984
Mean_fire + Precip_Wetq + Biome	40.80	992
Mean_fire + Biome	35.60	1,049
Biome	35.50	1,066
Mean_fire + Precip_Wetq + Precip_Dryq	30.20	1,065
Mean_fire	21.60	1,180

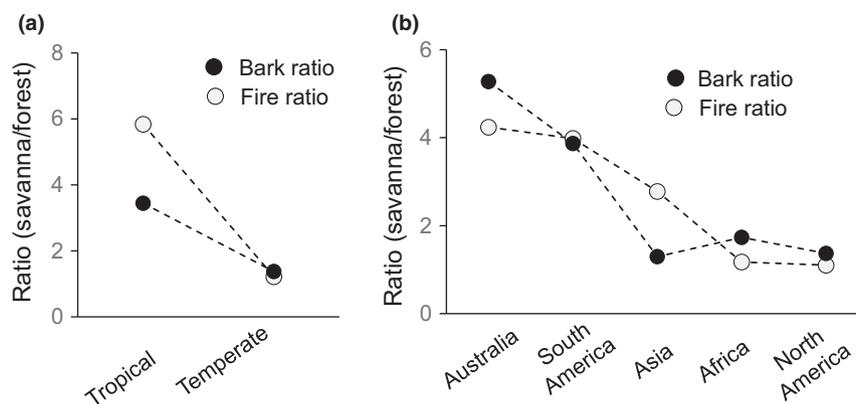
Dev refers to deviance explained. Mean\_fire = annual burned area, Precip\_Wetq = precipitation in the wettest quarter, Precip\_Dryq = precipitation in the driest quarter, Biome = biome a species specialised in (either savanna or forest). The best fit models are highlighted in bold; we utilised the more parsimonious of the two.

between-biome differences in the fire frequency characterising species distributions in the tropics (Fig. 2).

Among continents, there was substantial variability in the bark thickness of species both in the savanna and forest

**Table 1** Statistical results from generalised additive models between log bark thickness (for stems 10 cm in size), fire, climate and biome using model selection

biomes (Continent × Biome interaction:  $F_{4,562} = 15.6$ ,  $P < 0.0001$ , Figs 1 and S5, Tables S2 and S4). As a result, Australia and South America had the starkest contrast between biomes, with savanna species having 5.3- and 3.8-fold



**Figure 2** Difference between savanna and forest species across regions and continents. Comparison of the ratio of the mean bark investment and fire frequency of savanna vs. forest species between regions (a) and among continents (b). In all cases, the ratio is calculated by dividing the savanna value (averaged within either the region or continent) by the forest value. Significance of the interactions was determined by ANOVAs. (a) Region  $\times$  Biome interaction for fire ( $F_{1,568} = 26.4$ ,  $P < 0.0001$ ) and bark thickness ( $F_{1,568} = 26.0$ ,  $P < 0.0001$ ). (b) Continent  $\times$  Biome interaction for fire ( $F_{4,562} = 4.54$ ,  $P = 0.0013$ ) and bark thickness ( $F_{4,562} = 15.6$ ,  $P < 0.0001$ ). For specific comparison among continents, see Table S4.

thicker bark than forest species, respectively (Figs 1, 2 and S5, Tables S2 and S4). On the other hand, North American and African savanna species were only 1.4- and 1.8-fold thicker than forest species (Figs 1, 2 and S5, Table S4). Only in Asia did we not find a significant difference between biomes (Table S3), although there were data on only a few savanna species ( $n = 5$ ). Consistent with the Continent  $\times$  Biome interaction for bark thickness, we also found a significant interaction for fire frequency ( $F_{4,562} = 4.54$ ,  $P = 0.0013$ ). Subsequently, the contrast in bark thickness between savanna and forest species was largely consistent with the contrast in fire frequencies that characterised their distributions (Fig. 2).

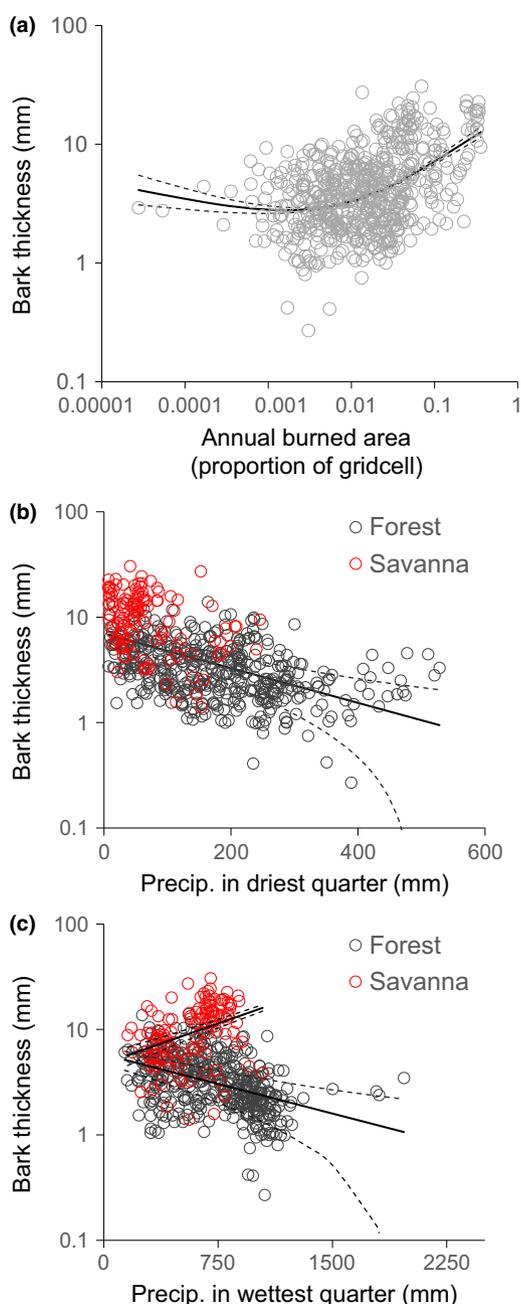
A more detailed evaluation of the habitat preferences of species in North America revealed qualitatively similar results: species that predominantly occurred in savanna habitats experienced a higher frequency of burning than those found only in forests (GFED3s:  $F_{2,74} = 9.15$ ,  $P = 0.0002$ , GFED4:  $F_{2,74} = 10.75$ ,  $P < 0.0001$ ); correspondingly, species that predominantly occurred in savannas tended to have 1.4-fold thicker bark than those found only in forests ( $F_{2,74} = 4.1$ ,  $P = 0.020$ ), in spite of North American forest species experiencing relatively frequent burning (SI, Fig. S6).

Globally, variation in bark thickness across species was significantly related to the fire regime and the interaction between climate and fire that characterised a species' distribution. First, annual burned area alone explained 20% of the global variation in bark thickness, with bark thickness increasing as a nonlinear function of the annual burned area that characterised a species' distribution (Fig. 3a, Table 1). Second, species found in areas with lower dry season rainfall had thicker bark in both savannas and forests (Fig. 3b, Table 1), likely a result of the negative relationships between dry season moisture and annual burned area ( $t = -3.726$ ,  $P < 0.001$ ) and fire intensity (Govender *et al.* 2006). Third, there was a significant interaction between the biome a species specialised on and precipitation in the wet season: bark thickness of savanna species increased with wet-season precipitation whereas bark thickness of forest species decreased

(Fig. 3c, Table 1). This climate–biome interaction likely reflects adaption to the higher fuel loads and more intense fires in the more productive wetter savannas, which our remote sensing fire metric cannot capture but has been well established across savannas (Williams *et al.* 1999; Govender *et al.* 2006). All conclusions were robust to variation in stem diameter (Table S5) and the different burned area products (Fig. S7, Tables S6 and S7). AIC-based model selection illustrated that the most parsimonious model included annual burned area and biome–precipitation interactions and explained 50% of the deviance in bark thickness across all 572 woody plant species (Table 1).

The potential for crown fire regimes to influence our results was explored by evaluating bark–fire relationships across plant communities in North America, under the assumption that gymnosperm forest species have a higher probability of experiencing crown fires and may invest less in bark. Across all species, fire frequency appears to be a less powerful, but still significant, predictor of bark thickness (explaining 7.6% of deviance across species, Table S8). Gymnosperm and angiosperm species did not significantly differ in bark thickness when we considered either all species or only forest species (SI). However, when gymnosperms were analysed alone, we found that the significant relationship between bark and fire frequency depended on the habitat (savanna vs. forest) of a species ( $F_{1,24} = 5.16$ ,  $P = 0.032$ ), with no relationship between fire and bark in species that occurred only in forests. Consequently, the relationship between fire frequency and bark becomes less significant in habitats prone to crown fires.

Comparisons among congeneric and confamilial species illustrated that bark thickness varies environment across diverse plant lineages. Species associated with the savanna biome had 2.07-fold thicker bark than their congeneric forest counterparts ( $n = 32$  genera, 156 species,  $t = 8.46$ ,  $P < 0.0001$ ; Fig. 4a). At the family level, savanna species had 2.59-fold thicker bark than their forest-associated counterparts ( $n = 36$  families, 377 species,  $t = 20.52$ ,  $P < 0.0001$ ; Fig. S8). Moreover, there was no significant relationship between the bark



**Figure 3** Key role of environment in determining the relative bark thickness of plant species. (a) Bark thickness of a species vs. the mean annual burned area of a species' distribution across all species on log-transformed annual burned area and bark thickness normalised to a 10-cm stem size. Solid line represents model fit. Appropriate nonlinear fit determined using model selection (nonlinear fit AIC = 1,180, linear fit AIC = 1,209). Bark thickness of savanna and forest species vs. mean climate of a species' distribution for precipitation in the driest quarter (b) and wettest quarter (c), solid line indicates fitted model relationship with the dashed lines indicating 95% confidence intervals. Separate lines were fitted in (c) because of the significant climate–biome interaction. The complete model of annual burned area, precipitation and biome explained 50% of the variation in bark thickness.

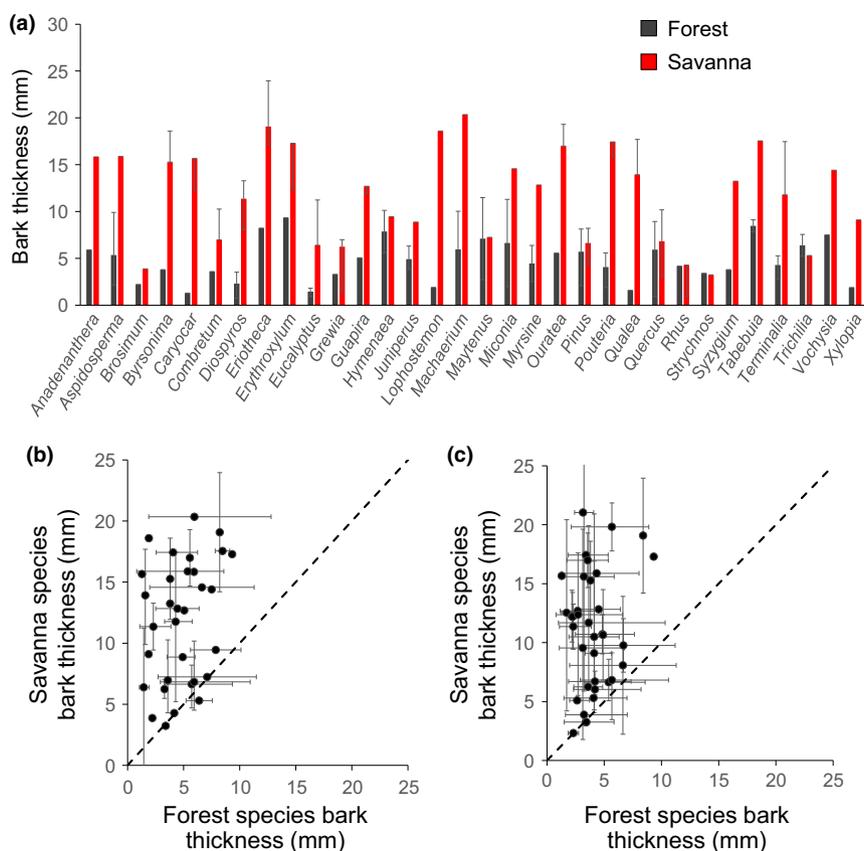
thicknesses of forest and savanna species from the same genus or family ( $r^2 < 0.01$ ,  $P = 0.29$  and  $r^2 < 0.01$ ,  $P > 0.5$ , respectively; Fig. 4b,c). This illustrates that investment in bark by savanna species is independent from investment in bark by closely related forest species.

Fire frequency is expected to increase in many areas that currently contain savanna and forest species. Specifically, 61 and 63% of savanna- and forest-containing grid cells are expected to experience increases in the proportion of area burned each year, respectively, in a high emissions climate scenario (Fig. 5a). However, the robustness of plant communities is forecasted to vary widely among biomes. Communities of savanna species have higher robustness than communities of forest species, on average, despite having higher fire frequencies and experiencing equivalent relative gains in annual burned area (Figs 5 and S9). Accordingly, the distribution of robustness across grid cells reveals that 93% of savanna grid cells had > 50% of individuals with traits consistent with future fire conditions, whereas only 62% of forest grid cells exceeded the threshold of 50% (Fig. S9c). The qualitative trends were consistent regardless of different precipitation scenarios, although on average forest communities tended to be less robust under the 'dry' scenario (only 55% of cells exceeded the threshold of 50%) and more robust under the 'wet' scenario (63% of cells exceeded the threshold of 50%), while savanna community showed little change (both scenarios had ~ 93% of cells above the threshold). Savanna tree communities tend to be robust because of the abundance of thick-barked species that can persist even with increased annual burned area.

Variability in the potential robustness across regions identified sensitive areas, such as moist tropical forests and temperate forests in western North America, which have the lowest forecasted robustness (Fig. 5a). However, some areas of forest in western North America and transitional tropical forest at savanna-forest ecotones in South America have relatively high robustness (Fig. 5c,d), perhaps due to the historical presence of fire in these contrasting forests having selected for thicker barked species (Harmon 1984; Paine *et al.* 2010). Importantly, this analysis of vulnerability is to surface fire regimes, and further analysis of the western North American forests that can experience crown fires in addition to surface fires is warranted.

## DISCUSSION

Thick bark is a fire-tolerance trait and the distribution of community bark thickness reflects consistent filtering of species with thin bark from areas prone to surface fires. The physics that govern how fire kills a tree are consistent across biomes: the insulation provided by bark protects the tissue inside the stem from overheating. As a result, thick bark is remarkably consistent in reducing the loss of aboveground stem biomass to fire across ecosystems (Uhl & Kauffman 1990; Lawes *et al.* 2011), even in ecosystems that can also experience crown fires such as western North America forests



**Figure 4** Savanna species have consistently thicker bark than their congeners. (a) Comparison of bark thickness in species specialising in savannas vs. forests in the same genus across 32 genera containing 156 species. Scatter plots compare the bark thicknesses of savanna vs. forest species within each genus (b) and family (c). Error bars are  $\pm$  95% confidence intervals. The dashed line illustrates a 1-to-1 line. Bark was normalised to a 10-cm stem size.

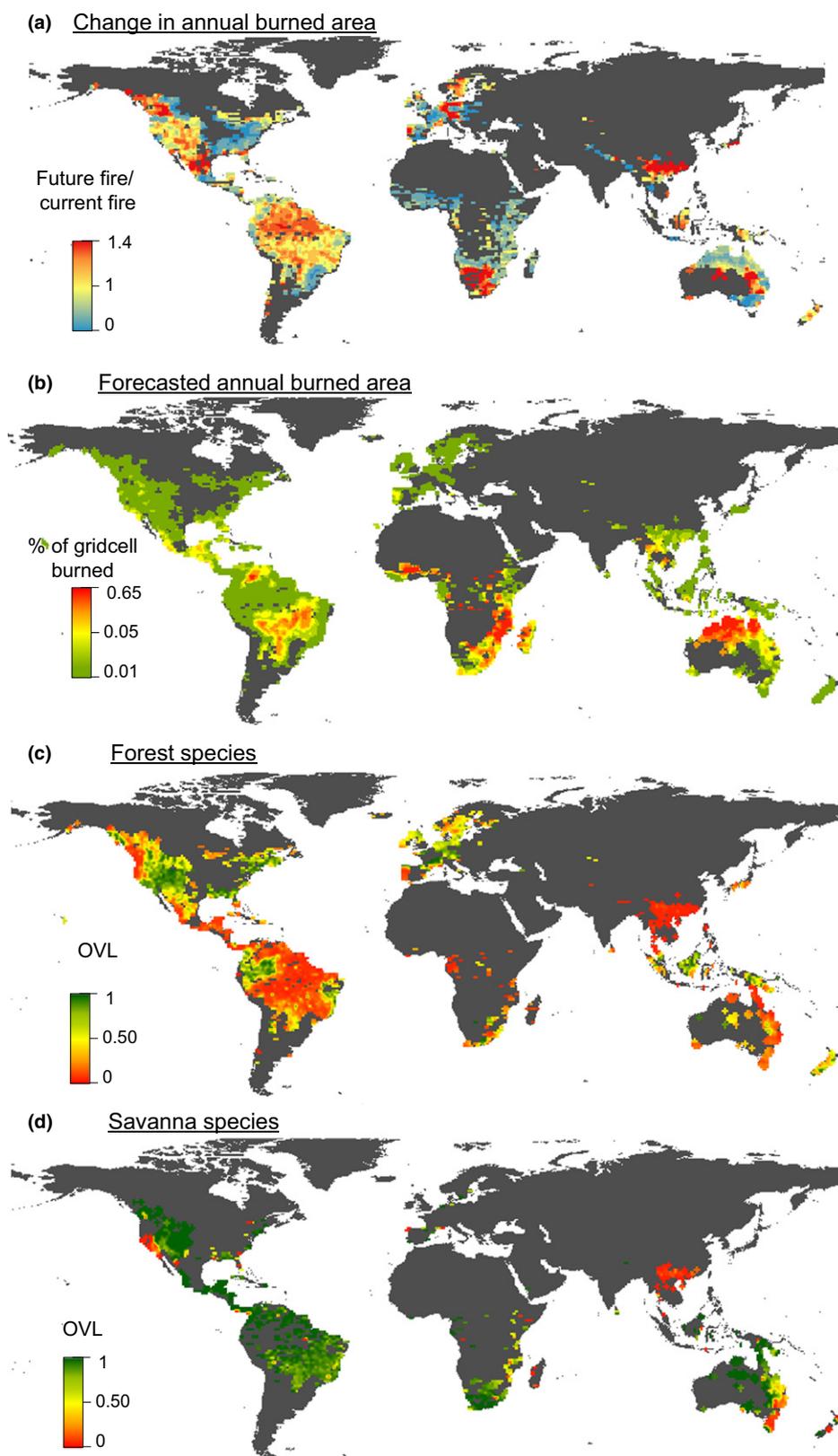
(Harmon 1984). Consequently, a diverse array of seed plant lineages contains a broad range of bark thicknesses, with species from historically fire-prone environments consistently exhibiting higher bark thickness than their closely related counterparts. This pattern is consistent with the convergent evolution of thick bark as a fire-tolerance adaptation, and this matters because the fire history of some plant communities may have resulted in contemporary trait distributions that are poorly matched to their projected conditions.

The general relationship between frequent fire and bark investment identified here is a substantial advance, especially given that a recent review concluded the paucity of data on bark investment across species limits generalisation (Pausas 2015). Indeed, there has been debate on the role of fire and potential climate–fire interactions in determining species' investment in bark (Hoffmann *et al.* 2012; Poorter *et al.* 2014; Rosell 2016). Our results inform this debate by illustrating the substantial role of fire and fire–climate interactions in determining global patterns of bark investment (Figs 1–3). Additional explanations for variability in bark investment such as defence against pathogens and mechanical stability are likely to contribute to the variability in the relationship between bark investment and fire (Paine *et al.* 2010; Rosell *et al.* 2014). These alternative factors may explain the result in Asia, where we did not find a significant difference in bark thickness between savanna and forest species, although data were

limited. Nonetheless, our relatively simple model predicts 50% of the variance in bark thickness, illustrating that across the globe, investment in thick bark is a consistent adaptation to fire-prone environments.

Our characterisation of the climate and fire niches of species using available distribution data allowed us to complement our between-biome analysis with continuous estimates of fire regimes. The consideration of continuous variability in climate and fire illustrated that a substantial amount of the variance among regions within biomes is due to their different fire and rainfall conditions. The variability in fire frequency and rainfall that exist across savanna and forest biomes (Lehmann *et al.* 2014) may help to explain why studies find inconsistent evidence on the degree to which thick bark is an adaptation to frequent fire (Hoffmann *et al.* 2009; Pausas 2015; Rosell 2016). For instance, even within savannas, species' investment in bark increased in areas with more frequent fire and higher wet quarter rainfall (Fig. 3b,c). This climate–fire interaction provides one explanation for the relatively greater investment in bark found in the wet South American savannas relative to the drier African savannas (Dantas & Pausas 2013).

North America presents a number of interesting contrasts to observations from the tropical savanna-forest ecotones. Many forest species in North America experience relatively frequent fires (Fig. S6), likely leading to their higher investment in bark relative to forest species in tropical forests in



**Figure 5** Heterogeneity in robustness. Global distribution of future fire regimes and the overlapping coefficient (OVL) comparing the difference in probability distributions of bark thicknesses between present day and future conditions. (a) Relative change in annual burned area, expressed as the % of a grid cell burned, between the present day (based on 2001–2010 observations) and the future (projections to 2070–2100). (b) Forecasted annual burned area for the 2070–2100 period. (c–d) OVL between present day and future trait distributions for forest (c) and savanna (d) communities. The spatial overlap of coloured points in panels (c) and (d) results from the spatial proximity of savanna and forest biomes in those grid cells. Only grid cells projected to experience gains in fire frequency are mapped in panels (c) and (d).

Australia and South America (Fig. S4). The comparable fire frequencies in savannas and forests in North America is likely to contribute to the small differences in bark thickness between savanna vs. forest congeners in *Pinus* and *Quercus* (Figs 4a and S8). Moreover, although we found that the bark–fire relationships were robust in North America where many species experience mixed fire regimes, gymnosperm trees, which occur in habitats more likely to experience crown fires, had a weaker relationship between bark and fire. Specifically, the bark thickness of gymnosperm forest species was not significantly related to fire frequency, which supports the hypothesis that other traits such as reseeded and resprouting are critical in crown fire ecosystems. Consideration of these other traits will be important for predicting the vulnerability to crown fires and presents a useful expansion to our current study that focused on surface fires.

We predict striking differences in robustness across biomes and regions, identifying especially sensitive areas in carbon-dense forests of the wet tropics where increases in fire activity are forecasted to occur throughout a large area where there are many species of trees that invest relatively little in bark compared to their close relatives around the world (Fig. 5). In contrast, trees in drier tropical forests and the ecotonal areas between savannas and forests invest more in bark (Fig. 3b,c) and are better suited to tolerate the intensifying fire regimes (Fig. 5). Consequently, important heterogeneity exists across forests in different climates not just due to projections in fire activity, but the distribution of species with fire-tolerance traits.

More accurate predictions of vulnerability will be gained as we reduce the uncertainties in the factors driving changes in fire. The future fire projection utilised here identified that assumptions about population growth heavily influence the projections of burned area; however, the direction of the projected fire trends across the areas that we identify as most vulnerable (e.g. moist Neotropical forests) was robust to different population growth and urbanisation scenarios, even though the exact magnitude of change differed (Knorr *et al.* 2016a).

Further insight into mechanisms structuring variability in the vulnerability of ecosystems can be gained by considering other fire-tolerance traits such as resprouting or reseeded from serotinous cones (Ondei *et al.* 2015) that can allow thin barked species to persist in areas frequently burned (Bond & Midgley 2001). Nonetheless, by considering the full trait–environment probability distribution, our models of robustness partially account for the possibility that other traits may modify the relationship between the bark thickness of a species and the fire frequency it experiences. For example, the presence of thin barked species in a frequently burned area, which may be due to their capacity to resprout or rapidly reseed following a fire, will widen the estimated trait distribution and allow for greater variance in bark thickness at a particular fire frequency.

The ability to simulate the effects of fire on ecosystem carbon pools will depend on accurately capturing the distribution of traits within and across communities. Many Dynamic Global Vegetation Models, which are commonly used to forecast change in the global carbon cycle, use fire

modules that represent fire-tolerance traits as static properties of plant functional types, fixed within broad vegetation classifications (Thonicke *et al.* 2010; Li *et al.* 2012). We suggest that using a single bark thickness value per plant functional type fails to capture important heterogeneity in fire tolerance that exists within geographies and ecosystems and may allow for ecological filtering. Consequently, the use of fixed trait means, rather than distributions, may underestimate robustness to fire and lead to large error in estimates of carbon emissions.

We show that the widespread convergence of a fire-tolerance trait, bark thickness, underpins a striking range of robustness exhibited by vegetation communities to future fire regimes. Estimates of ecosystem robustness can be further improved by considering additional traits of the plant community, variation in the rates and mechanisms of trait evolution, and other important disturbances such as drought. Nonetheless, trait-based approaches to assessing robustness to fire have the potential to be powerful predictors of the future response of ecosystems to fire.

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#### DATA ACCESSIBILITY

Unpublished trait data will be made available in Dryad.

#### AUTHORSHIP

AFAP and WRLA conceived of and designed the study. AFAP performed analyses with input from WRLA, TK, CETP and SWP. WAH, SSR, CETP, DS and ACF contributed data. AFAP wrote the first draft of the paper and all authors contributed comments.

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## SUPPORTING INFORMATION

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